
Resilience of Southwestern Amazon Forests to Anthropogenic Edge Effects

OLIVER L. PHILLIPS,*†† SAM ROSE,*‡ ABEL MONTEAGUDO MENDOZA,†§
AND PERCY NÚÑEZ VARGAS†

*Earth and Biosphere Institute, School of Geography, University of Leeds, United Kingdom

†Herbario Vargas, Universidad Nacional San Antonio Abad del Cusco, Cusco, Peru

Abstract: *Anthropogenic edge effects can compromise the conservation value of mature tropical forests. To date most edge-effect research in Amazonia has concentrated on forests in relatively seasonal locations or with poor soils in the east of the basin. We present the first evaluation from the relatively richer soils of far western Amazonia on the extent to which mature forest biomass, diversity, and composition are affected by edges. In a southwestern Amazonian landscape we surveyed woody plant diversity, species composition, and biomass in 88 × 0.1 ha samples of unflooded forest that spanned a wide range in soil properties and included samples as close as 50 m and as distant as > 10 km from anthropogenic edges. We applied Mantel tests, multiple regression on distance matrices, and other multivariate techniques to identify anthropogenic effects before and after accounting for soil factors and spatial autocorrelation. The distance to the nearest edge, access point, and the geographical center of the nearest community ("anthropogenic-distance effects") all had no detectable effect on tree biomass or species diversity. Anthropogenic-distance effects on tree species composition were also below the limits of detection and were negligible in comparison with natural environmental and spatial factors. Analysis of the data set's capacity to detect anthropogenic effects confirmed that the forests were not severely affected by edges, although because our study had few plots within 100 m of forest edges, our confidence in patterns in the immediate vicinity of edges is limited. It therefore appears that the conservation value of most "edge" forests in this region has not yet been compromised substantially. We caution that because this is one case study it should not be overinterpreted, but one explanation for our findings may be that western Amazonian tree species are naturally faster growing and more disturbance adapted than those farther east.*

Keywords: conservation value, diversity, forest biomass, mortality, Peru

Resiliencia de Bosques del Suroeste de la Amazonía a Efectos de Borde Antropogénicos

Resumen: *Los cambios antropogénicos pueden comprometer el valor de conservación de bosques tropicales maduros. A la fecha, la mayor parte de la investigación del efecto de borde en la Amazonía se ha concentrado en bosques en localidades relativamente temporales o con suelos pobres en el este de la cuenca. Presentamos la primera evaluación del grado en que la biomasa, diversidad y composición de bosques maduros son afectadas por los bordes en los suelos relativamente más ricos en el lejano oeste de la Amazonía. Muestreamos la diversidad, composición de especies y biomasa de plantas leñosas en 88 parcelas de 0.1 ha en bosques no inundables en un paisaje del suroeste de la Amazonía con una amplia gama de características edáficas y que incluían muestras tan cercanas como 50 m y tan distantes como > 10 km de los bordes antropogénicos. Aplicamos pruebas de Mantel, regresión múltiple en matrices de distancia y otras técnicas multivariadas para identificar los efectos antropogénicos antes y después de considerar los factores edáficos y la autocorrelación espacial. La distancia al borde, punto de acceso y centro geográfico de la comunidad más cercana (efectos antropogénicos-distancia) no tuvieron efecto detectable sobre la biomasa o diversidad de especies de árboles.*

††email o.phillips@leeds.ac.uk

‡Current address: Jurassic Coast World Heritage Site, Dorset County Council, Dorchester, United Kingdom

§Current address: Jardín Botánico de Missouri, Oxapampa, Peru

Paper submitted May 16, 2005; revised manuscript accepted February 13, 2006.

Los efectos antropogénicos-distancia sobre la composición de especies de árboles también estuvieron debajo de los límites de detección y fueron insignificantes en comparación con los factores ambientales y espaciales. El análisis de la capacidad del conjunto de datos para detectar efectos antropogénicos confirmó que los bosques no fueron afectados por los bordes severamente, aunque nuestra confianza en los patrones de la vecindad inmediata del borde es limitada, porque nuestro estudio tenía pocas parcelas a menos de 100 m del borde. Por lo tanto, parece que el valor de conservación de la mayoría de los bosques "borde" en esta región aun no ha sido comprometido sustancialmente. Prevenimos que este es un estudio no debe ser interpretado porque solo es un caso, pero una explicación para nuestros resultados puede ser que las especies de árboles de la Amazonía occidental están naturalmente más adaptadas a perturbaciones y tienen crecimiento más rápido que las del oriente.

Palabras Clave: biomasa forestal, diversidad, mortalidad, Perú, valor de conservación

Introduction

Humans are affecting the tropical landscape in profound ways and no location has been unaffected by our species (Malhi & Phillips 2004). Although outright deforestation constitutes the most severe change and has affected around half the tropical forest biome (e.g., Achard et al. 2002), the sphere of human influence includes less visible processes that also alter old-growth forests (Phillips 1997; Laurance 2004). Large areas of standing forests have been affected by extraction of wildlife and other nontimber forest products. Even where direct human impacts are minimal, the global industrial economy has driven change in ecosystem processes and biodiversity by altering the physical and chemical environment in which forests grow (e.g., Phillips & Gentry 1994; Lewis et al. 2004).

Much recent research has been directed to understanding edge effects and other impacts of fragmentation on remaining forest. Where forest adjoins major clearings, alterations in atmospheric circulation might infiltrate 20 km or more (Silva Dias et al. 2002). Edges represent population sinks for species hunted by humans, which can cause a cascade of faunal and floral imbalances to penetrate farther in (e.g., Woodruffe & Ginsberg 1998; Laurance 2000). In addition, tropical land-use changes have important effects elsewhere. In Costa Rica, for example, deforestation of the Caribbean lowlands is associated with downwind reductions of humidity, clouds, and rainfall (Lawton et al. 2001). Simulations suggest that Amazonian deforestation alters precipitation in distant areas, even at higher latitudes (e.g., Gedney & Valdes 2000; Werth & Avissar 2002), and atmospheric carbon fluxes from fragmented and edge-affected forests supplement those from deforestation, thus increasing the greenhouse warming effects of deforestation (Laurance et al. 1997).

We sought to evaluate the impact of smaller-scale edge effects on mature forests in western Amazonia. Long-term experimental and observational studies in eastern Amazonia show that physical changes occur within the first 300 m of edges and that other phenomena, such as fire, can penetrate up to several kilometers (Nepstad et al. 1999;

Laurance 2004). Here, alterations to the physical environment sharply increase tree mortality and damage (Ferreira & Laurance 1997), and large trees are especially vulnerable (Laurance et al. 2000). These results come from a large, long-term experimental landscape, but elsewhere such physical processes are often supplemented by other anthropic processes, such as extraction of timber, fruit, fiber, and animals concentrated close to the forest edge (e.g., Sirén et al. 2004). Even relatively short-distance effects can aggregate to a large regional impact. For example, Skole and Tucker (1993) show that if a 1-km edge effect is considered typical, then the total area in Amazonian Brazil affected by edges up to 1988 (approximately 341,000 km²) is greater than the area that has been cleared (approximately 230,000 km²).

Work to date on edge processes has focused on areas characterized either by relatively slow growing taxa on poor soils (near Manaus) or by drought-affected, fire-prone forest (locations in eastern Brazilian Amazonia). However, a region as vast as Amazonia (6 million km²) requires more extensive sampling to be adequately characterized, and recent basin-wide research reveals extreme natural heterogeneity, including pronounced gradients in drought sensitivity, fire risk, soil nutrition, tree growth, mortality, productivity, biomass, diversity, and floristic composition (e.g., Terborgh & Andresen 1998; ter Steege et al. 2003; Baker et al. 2004a; Malhi et al. 2004; Nepstad et al. 2004; Phillips et al. 2004). Some of these macroecological patterns have strong coherence. Notably, the northeast to southwest gradient in forest composition is mirrored by differences in soils (richer in southwest), above-ground production and tree mortality (greater in west), and wood density (greater in northeast). Such strong natural gradients can be expected to modify anthropogenic impacts, so conservationists need insight into the biotic impact of edge processes from a wider variety of locations. Uncertainty as to the impacts of anthropogenic edges represents a challenge to conservation biologists, whose input is needed to inform the key policy debate of how we can simultaneously meet both poverty reduction and biodiversity conservation goals (Adams et al. 2004).

For example, to what extent is a hands-off model of protected areas needed to conserve tropical biodiversity and carbon, or to what extent can a mixed-use model serve the same conservation purposes?

Here we provide a new analysis of the impacts of edge processes on tropical forests, taking as our study region a landscape in southwest Amazonia that is ecologically and culturally distinct from the landscapes that have been the main focus of other work to date. We sought to assess the integrated impact of edge processes on tropical forest ecosystem services. Our specific objectives were to quantify the effects of anthropogenic edges on three different ecological values of conservation concern: tree alpha-diversity, tree species composition, and aboveground carbon storage.

Study Area

Southeastern Madre de Dios Department, Peru, is in southwest Amazonia at 200–260 m asl. Mean annual temperature is 25° C, and mean annual rainfall is 2200–2400 mm with 3–4 months receiving <100 mm (Malhi et al. 2002). This level of seasonality is comparable to locations farther to the northeast, where edge effect research has concentrated, but is more intense than that of the northwestern quadrant of Amazonia. The natural vegetation of lowland Madre de Dios is humid, lowland, tropical forest, with generally more fertile soils, faster turnover, and lower wood density than forests farther to the northeast. Dominant tree families include the palms (Arecaceae), legumes (Fabaceae), and Moraceae, but the biota are very diverse, with more than 1000 tree species known from our study area (Phillips et al. 2003a) and with individual sites having world records for species totals of birds and insect groups (e.g., Pearson 1984; Lamas 1994; Parker et al. 1994). Some dominant tree taxa are ubiquitous (Pitman 1999), but there is also soil-determined compositional differentiation (Phillips et al. 2003a; Tuomisto et al. 2003).

The region has a long history of human immigration and migration both forced and voluntary, which has generated a complex cultural mix (e.g., Lawrence et al. 2005). Timber and extraction of Brazil nuts represents a major source of income, but subsistence in the area depends heavily on small-scale farming and to a lesser extent extraction of natural products from mature forest. For example, more than 20 tree species are used in house building (Phillips et al. 1994). Deforestation is concentrated along one road and the major rivers of the region. More than 90% of Madre de Dios is still in old-growth forest, reflecting a low overall population density (0.90 persons/km² in 1996, estimated to be increasing by 3–4% annually since [cf. Institución Nacional de Investigación y Extensión Agraria: <http://www.inei.gob.pe/home.htm>]). Densities are somewhat higher in our study region (province of Tambopata, which includes our area, averaged 1.42 persons/km² in 1996 and approximately 3 persons/km² in

the communities we worked in [O.L.P. et al., unpublished data]).

Late twentieth century land-use patterns in the region are complex and have shifted with changing cultural, economic, zoning, and infrastructural environments. Current land-use within the study area includes urban development, cattle ranching, shifting subsistence agriculture, settled subsistence agriculture, commercial fruit plantations, logging camps and tractor trails, gold-mining, ecotourism camps, and degraded abandoned pastures (together comprising in 1998 7% [898 km²] of a 110 × 110 km Landsat Thematic Mapper image that spans the study area), regenerating secondary forests (1%), and land-use activities in the mature forest itself, including extractive zones for Brazil nuts and other nontimber forest products (NTFPs), areas with selective harvesting of timber species, ecotourism reserves, and national conservation units.

The pace of clearance of mature forest has varied, with the largest pulse from the late 1970s to early 1990s. Since the early 1990s until the date of fieldwork (1998, 1999), land-use patterns had been relatively stable (e.g., Alvarez & Naughton-Treves 2003) because of reduced political and economic incentive for deforestation and better recognition of territories of native and immigrant communities and zoning decisions that favor ecotourism and extraction over wholesale clearance. In one community (La Torre), we traced the history of land use in the 1990s independently of local reports by comparing an Ikonos image from 2001 with ground-truthed Landsat thematic mapper images from 1991 to 1998. The 1998 and 2001 images reveal the areas burned since the previous dry season and show that 5–10% of the originally deforested area is recut annually. Comparison of the area deforested up to 1991 (reported in Phillips et al. 1994) with the later images, however, shows little deforestation of mature forest during the intervening period in this community.

Methods

General Approach and Sample Units

The study area is defined as a circle with a radius of 50 km centered on the regional capital of Puerto Maldonado. We included 10 of the 11 legally recognized indigenous and Andean migrant communities that have substantial access to mature forest (i.e., covering >50% of their territory). Samples were taken in mature forests in three protected areas and the community territories (Fig. 1) (cf. Appendix 1 in Phillips et al. 2003a) and were stratified by geomorphology on the basis of the 1998 Landsat image, ground-truthed with local residents. Within each community we inventoried mature forests with a range of human impacts in consultation with our community collaborators in areas without plant extraction for at least 20 years (zero-impact

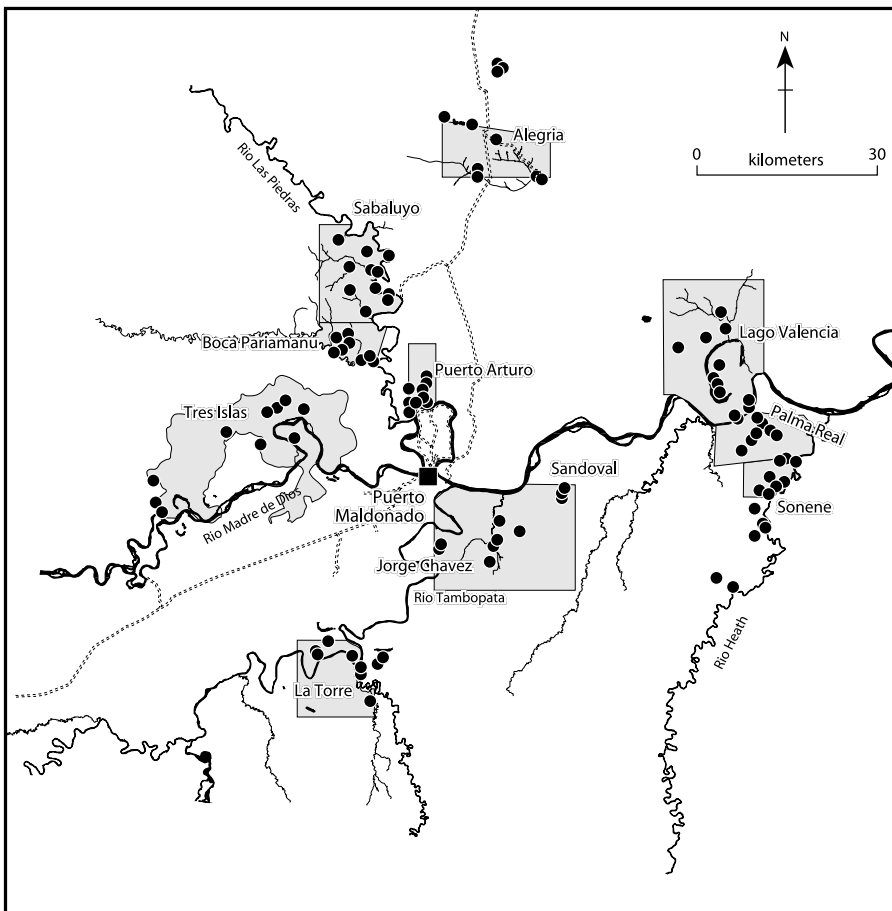


Figure 1. Map of the study area, showing approximate location of each sample, the community boundaries, and principle geographic features. Note the scale and the fact that samples are clustered by community but distributed over an area of approximately 10,000 km².

sites), sites with some NTFP extraction within the last 10 years (low-impact sites), and sites with extraction of major timber species and NTFPs (medium-impact sites). Further methodological details and maps are available at <http://www.geog.leeds.ac.uk/projects/pbc/method.html>.

Constructing precise harvest histories was not possible, but observations in protected area sample plots and of timber harvesting suggests a typical one-time cut of at most two emergent trees/ha. The level of impact broadly reflects the distance from the edge of the forest to a clearing (median distance to anthropogenic edge: zero-impact sites, 2.46 km; low-impact sites, 0.69 km; medium-impact sites, 0.30 km; $\chi^2 = 23.4$, $df = 2$, $p < 0.001$, Kruskal-Wallis test). Patches of advanced secondary forest were ignored, so our distance to edge represents the distance to open habitat. For some communities we needed to sample zero-impact forest in the nearest protected area, randomizing site selection by sampling within 5 km of a randomly chosen river access point. In all, we completed 96, 0.1-ha floristic and soil samples, with distance from plot center to the nearest anthropogenic edge ranging from 50 m to 14.3 km. We focused on human impacts on the dominant terra firme forests, so we excluded all samples in swamp forests and successional floodplains from

the analysis and four for which soil samples were lost. The remaining core data were composed of 88 samples.

Our 0.1-ha inventories are modified versions of the Gentry method (Gentry 1982; Phillips & Miller 2002). Elsewhere we describe our protocols in detail (<http://www.geog.leeds.ac.uk/projects/pbc/>; Phillips et al. 2003a, 2003b); here we emphasize the key aspects.

We sampled forests at each location in 1998 and 1999 in ten 2 × 50 m subplots, totaling 0.1 ha located within a 100 × 180 m sampling grid so as to systematically subsample 1.8 ha of forest, in which all subplots were oriented in the same randomly chosen direction so as to minimize possible sampling biases. Each nonclimbing plant rooted within the transect area and with diameter at breast height of ≥2.5 cm was included. Where necessary, diameters were measured above buttresses and other stem irregularities. Every plant was identified or recorded as a unique “morphospecies.” We collected voucher specimens for each species and whenever there was any uncertainty to identity. Repeated collections of sterile plants were frequently needed to reliably distinguish morphospecies. A full duplicate set is deposited in Peru at the Herbario Vargas in Cusco, where we cross-referenced vouchers among samples and communities and identified them in consultation with specialists worldwide. A partial set was also

deposited at the herbarium of the University of San Marcos (USM).

At every plot we also assessed topography and sampled soil (0–15 cm below the organic material layer). Methodologies and results are reported in Phillips et al. (2003a). A geographic information system (ArcView, ESRI, Redlands, California) was developed for the area, based on the geo-referenced 1998 Landsat image and digitized community maps indicating land tenure, land-use history, extractive zones, trails, protected areas, and precise locations of our samples. In the geographical information system, we computed straight-line distances from sample center to (1) nearest edge, (2) nearest access point for motorized extraction of forest products, and (3) center of the nearest community. Clearings ranged from approximately 2 ha (the smallest size considered) to as large as approximately 14 km² (i.e., 1400 ha) in one community (Alegria). When classified by the size of the nearest clearing as recorded in the 1998 image, of the samples that were within 1000 m of an artificial clearing, 2 samples were nearest to a deforested area of <10 ha, 16 were nearest to a deforested area of 10–100 ha, 29 were nearest to a deforested area of 100–1000 ha, and 6 were nearest to a deforested area of >1000 ha.

Analyses

For aboveground biomass (AGB) and diversity analyses, we included records of unidentified morphospecies but removed them before floristic analysis to ensure that any inconsistency in cross-referencing of vouchers would not bias the results. We applied our analyses to all non-scan-dent plants in our 88 sample data set, including some shrubs, arborescent palms, and a few coarse woody herbs. For simplicity, we use the term *trees* to describe the plants we sampled.

Soil

To account for potential edaphic controls on AGB and diversity, we used principal components analysis (PCA) to describe the major gradients in normalized and standardized soil variables and then tested the effects of these gradients with multiple regression. To account for potential edaphic controls on composition, we used the transformed soil variables because our aim was to model compositional differences by the more complex technique of multiple regression on distance matrices. Interpreting the ecological meaning of among-site distances in soil parameters is more intuitive than interpreting distances in PCA factors.

Biomass and Diversity

The AGB was estimated for each tree on the basis of diameter (D) and wood specific gravity (ρ), following a new tropical tree allometric model based on all available pantropical allometric data for lowland moist forests (Chave et al. 2005):

$$\text{AGB} = \rho \exp\{-1.499 + 2.148(\log_e D) + 0.207(\log_e(D)^2) - 0.0281(\log_e(D)^3)\}. \quad (1)$$

The ρ for each tree was estimated from Neotropical data (J. Chave et al., unpublished data). Where there were no species-level data for individual stems we allocated generic- or family-level mean values, following Baker et al. (2004a, 2004b). We used the overall species-level mean (0.62 g/cm³) for a few stems with no taxonomic information and for families for which no information on specific gravity was available. Biomass of larger trees is very sensitive to tree height, and because Eq. 1 is parameterized on few large trees, there is a risk of systematic errors in biomass estimates. Therefore, for trees with $D \geq 70$ cm, we adopted the recommended model of Chave et al. (2005) that incorporates height (b), such that

$$\text{AGB} = 0.059\rho(b)(D)^2. \quad (2)$$

We estimated height (b) with a region-specific height/diameter allometry calculated from 48 trees ≥ 70 cm in permanent plots within the same study region (T. Baker et al., unpublished data), where

$$b = 6.6342 \log_e(D) - 0.8251. \quad (3)$$

We applied Eq. 1 to our palms, in the absence of a model for arborescent Neotropical palms. For bamboos of the genus *Guadua*, we used an allometric model based on *G. angustifolia* from premontane Colombia (Riaño et al. 2002).

We used Fisher's alpha to assess within-community diversity, because this measure is robust to the effects of varying the number of individuals (Condit et al. 1996). To assess how AGB and diversity vary as a function of the environment and with anthropogenic edge effects, we first computed the linear correlation of AGB and Fisher's alpha with soil variables and PCA factors and with \log_e distance to the following anthropogenic landscape features: distance to a forest edge, to a trail or river for extraction, or the distance to the community center. Candidate multiple regression models were identified by a best subsets exploratory analysis, followed by examination of potential multicollinearity (variance inflation). Coefficients with variance inflation factors >4 indicate their confidence intervals are more than twice as wide as they would be for an uncorrelated predictor, leading us to reject that particular model.

Floristic Composition

We examined compositional differences among samples by accounting for (1) known environmental differences between sites (i.e., soil differences), (2) differences that could be explained solely by geographic distance (i.e., "distance decay" resulting from spatially structured but

ecologically stochastic processes such as recruitment limitation), and (3) compositional differences that can be related to anthropogenic factors. Earlier (Phillips et al. 2003a) we quantified relationships between plant species composition and soil and geographic distance between sites. This approach is the basis for our question here: How much variation can anthropogenic effects explain? Thus, we briefly describe the core procedure used in Phillips et al. (2003a).

Construction of Distance Matrices

Distance metrics were calculated for each of three classes of variables (plant species composition, 15 soil variables, geographical distance among sites), to produce a dissimilarity matrix between all possible sample pairs for each variable. We measured floristic distance between sample pairs by the Sørensen (Bray-Curtis) similarity index. Distance matrices of soil characteristics (exchangeable Ca, K, Mg, Na extracted with 1-M ammonium acetate, sum of base cations, exchangeable Al extracted with 1-M KCl, ECEC [effective cation exchange capacity], Al/ECEC, Bray P, pH, LOI, sand, silt, clay, fraction <0.063 mm) and geographical distances were based on Euclidean distance (i.e., the difference in the values of each sample pair). Before calculating distances we transformed variables with Tukey's ladder of powers to correct positively skewed distributions and ensure that absolute differences between low values receive greater weight than differences between high values. This reflects environmental and spatial differences experienced by tropical plants better than the use of raw variables would (cf. Condit et al. 2000).

Analyses with Distance Matrices

We used the distance matrices in two different analyses to assess how composition varies with spatial, environmental, and anthropogenic factors. First we applied Mantel's test on matrix correlation (Mantel 1967) to test for interdependence among variables, and second we used multiple regression on distance matrices (Legendre et al. 1994) to model the full floristic variation. The Mantel test involves computing the correlation coefficient between two matrices (Smouse et al. 1986) and applying a Monte Carlo procedure to estimate the probability of error. We distinguished a 0.1% probability of error by comparing observed distributions of r against the distribution of random values generated by permuting one matrix and recalculating r 999 times. We used a partial Mantel test to evaluate how correlations between floristic composition and environmental variables changed after controlling for the effect of geographical distance. Mantel tests were performed for all pairwise variable combinations with PC-ORD and with the R-Package (Legendre & Vaudor 1991). In the multiple regression method on distance matrices, variation in the dependent matrix is expressed in terms of variation in a set of independent matrices. The com-

putational procedure mimics that of normal multiple regression, except that parameter significance is estimated by Monte Carlo permutation. We modeled the variation of the floristic data in terms of environmental and spatial factors by performing multiple regression of the floristics distance matrix against the variable matrices. Both forward- and backward-elimination methods were used.

Our aim was two fold: (1) to model the compositional variation *potentially* attributable to the measured anthropogenic factors and (2) to evaluate the *most likely* contribution of human factors to floristic pattern within the landscape having accounted for natural factors. Therefore, for (1) we report results of Mantel tests on matrix correlations between composition and, in turn, each environmental, spatial, and anthropogenic variable. For (2) we generated and selected models as follows: We built the largest model possible in which each factor contributes significantly ($p < 0.05$). We then eliminated independent environmental variables with negative b coefficients until all remaining environmental b coefficients were positive (negative b coefficients are meaningless, implying that as samples become more similar their compositional differences become greater). Finally, we applied backward elimination with Bonferroni-corrected probability levels estimated from 999 permutations to decide eliminations for three different models: (1) the best overall model, (2) the best model in which all anthropogenic, environmental, and spatial factors were included, and (3) the best model in which anthropogenic and environmental factors were included. Multiple regressions on distance matrices were performed with Permute! 3.4 (Legendre et al. 1994).

Results

Soils varied substantially among the 88 plots but within-sites soil variables were highly intercorrelated. A PCA showed that half the soil variation was accounted for by one axis describing a gradient from sites with high clay and cation content to those with high sand and low cation content. Smaller amounts of variation were described principally by variation in Al and pH (axis 2), silt (axis 3), and P (axis 4).

Biomass as a Function of Environmental Effects and Anthropogenic Effects

$\log_e(\text{AGB})$ was only marginally correlated with one transformed soil variable, CEC ($r = 0.211$, $p < 0.10$ after Bonferroni correction), and was not correlated with any PCA factor. No correlation was detectable between $\log_e(\text{AGB})$ and any anthropogenic factor. Thus, biomass was invariant with distance to edge (Fig. 1). Biomass was also invariant with respect to our a priori impact classes (mean AGB zero-impact forest was 368.3 t, for low-impact forest

Table 1. Aboveground biomass (ABG) in 0.1-ha samples of mature forest as a function of the natural and human environment.

Variable	b, partial regression coefficient	p in final model	Variance inflation factor	Effect of removing variable on the whole model, (Δr^2 ,%)
Natural environmental effects only ^a				
AI ^{0.5}	-0.039	0.002	2.3	-9.1
log ₁₀ (Mg)	-0.473	0.002	3.6	-9.3
-CEC ^{-0.5b}	4.098	0.004	2.4	-4.7
log _e (clay)	0.366	0.012	2.5	-5.9
Natural and anthropogenic effects together ^c				
AI ^{0.5}	-0.0380	0.004	2.4	-8.5
log ₁₀ (Mg)	-0.4188	0.013	4.2	-6.0
-CEC ^{-0.5b}	4.462	0.004	2.6	-8.9
log _e (clay)	0.309	0.048	2.9	-3.4
log _e (edge)	-0.0214	0.682	1.9	+0.9
log _e (access)	0.0466	0.402	1.8	-0.3
ln (community)	0.0364	0.654	1.9	+0.9

^aModel that maximizes adjusted r^2 and has acceptable variance inflation: $\log_e(\text{AGB}) = 6.39 - 0.0393(\text{AI})^{0.5} - 0.473 \log_e(\text{Mg}) - 4.1(\text{CEC})^{-0.5} + 0.366 \log_e(\text{clay})$; $r^2 = 16.6\%$; $r^2(\text{adj}) = 12.6\%$; $F_{4,87} = 4.12$, $p = 0.004$.

^bCation exchange capacity.

^cNatural effects model plus all anthropogenic variables: $\log_e(\text{AGB}) = 6.38 - 0.0380(\text{AI})^{0.5} - 0.419 \log_e(\text{Mg}) - 4.46(\text{CEC})^{-0.5} + 0.309 \log_e(\text{clay}) + 0.036 \ln(\text{community}) + 0.047 \ln(\text{access}) - 0.021 \ln(\text{edge})$; $r^2 = 17.7\%$; $r^2(\text{adj}) = 10.5\%$; $F_{7,87} = 2.46$, $p = 0.025$. Key: edge, distance to nearest edge; community, distance to the community center; access, distance to the nearest access point for motorized extraction of forest products.

373.3 t, and for medium-impact forest 386.0 t; $F = 0.08$, $p = 0.92$.

In multiple regression models with edaphic variables, greater adjusted r^2 values were achieved with several transformed soil variables than with the composite PCA eigenvectors, but soil variables still only explain a small portion of the variance in biomass (Table 1). When anthropogenic variables are taken into account, none add significantly to this model, and the adjusted r^2 declines (Table 1). No combination of anthropogenic factors and natural factors improved on the four-variable soil factor model for AGB (i.e., increased fit was only attainable at the price of unacceptable variance inflation).

Diversity as a Function of Environmental Effects and Anthropogenic Edge Effects

Fisher's alpha was weakly but significantly correlated with a number of transformed soil variables, including pH ($r = -0.305$, $p < 0.01$), dry matter ($r = 0.250$, $p < 0.05$), and silt ($r = 0.280$, $p < 0.02$) (after Bonferroni corrections). Correlations with PCA factors were weak and were only significant for PCA factor 3 ($r = 0.250$; $p < 0.05$). No correlation was detectable between Fisher's alpha and any anthropogenic factor. Thus, diversity was invariant with distance to edge (Fig. 3). Diversity was also invariant with respect to our a priori impact classes (mean Fisher's alpha zero-impact forest was 55.6, for low-impact

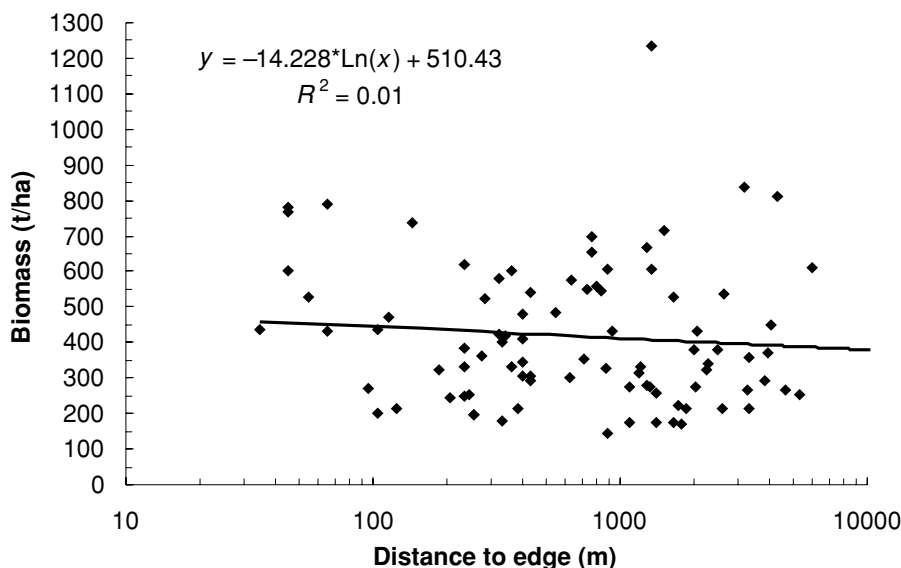


Figure 2. Biomass of samples as a function of distance from anthropogenic edge. Best-fit models were selected, but there was no evidence for a relationship at any spatial scale.

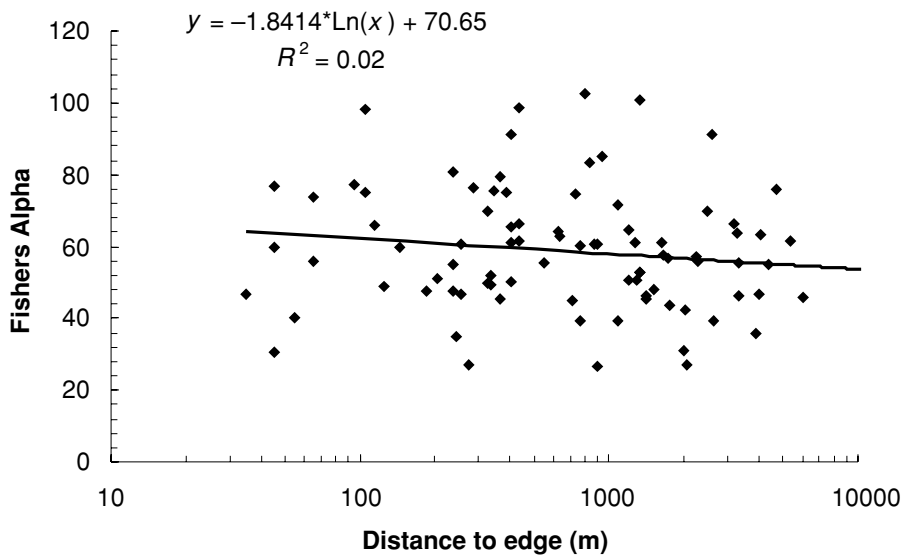


Figure 3. Fisher's alpha of samples as a function of distance from anthropogenic edge. Best-fit models were selected, but there was no evidence for a relationship at any spatial scale.

forest 60.0, and for medium-impact forest 60.4; $F = 0.61$, $p = 0.55$).

In multiple regression models with only edaphic variables, greater r^2 values were achieved with transformed soil variables than with composite PCA eigenvectors. The best model (maximizing adjusted r^2 while keeping variance inflation acceptable) included pH, K, Al/CEC, and particle size variables (Table 2) but, again, when anthropogenic variables were taken into account, none added significantly to this model (Table 2). There was, however, a weak tendency for samples close to edges to have slightly higher alpha diversity ($t = -1.49$, $p = 0.14$). The

model that best accounted for natural and anthropogenic effects (not shown) was indistinguishable from that in Table 2 (natural and anthropogenic effects together), except that distance to community was eliminated.

Floristic Composition as a Function of Environmental and Geographic-Distance Effects and Anthropogenic Effects

Individual Mantel tests on matrix correlations between composition and other measured factors (Table 3) showed high correlations with some soil variables (notably cations) and a weak correlation with geographic distance. Composition was unrelated to two of the three measured

Table 2. Tree diversity in 0.1-ha samples of mature forest as a function of the natural and human environment.

Variable	b, partial regression coefficient	p in final model	Variance inflation factor	Effect of removing the variable on r^2 of whole model (Δr^2 , %)
Natural environmental effects only ^a				
-(pH-3.2) ⁻¹	-11.1	0.01	2.3	-5.5
(silt) ²	-0.00410	0.002	2.8	-8.3
Al/CEC ^b	-16.8	0.07	2.9	-2.4
log _e (K)	-15.9	0.004	1.3	-7.2
fraction of particles < 0.063 mm	0.275	0.04	3.6	-3.1
Natural and anthropogenic effects together ^c				
-(pH-3.2) ⁻¹	-12.8	0.004	2.5	-7.5
(silt) ²	-0.00307	0.03	3.4	-3.7
Al/CEC	-20.3	0.04	2.9	-3.2
log _e (K)	-16.9	0.002	1.5	-8.5
fraction of particles < 0.063 mm	0.267	0.05	3.8	-2.9
log _e (edge)	-2.6	0.14	1.9	-1.2
log _e (access)	+2.5	0.20	1.8	-0.7
log _e (community)	-0.7	0.81	2.1	+0.9

^a Model that maximizes adjusted r^2 and has acceptable variance inflation: Fisher's alpha = $113.4 - 11.1 - (\text{pH}-3.2)^{-1} - 0.00410(\text{silt})^2 - 16.8(\text{Al}/\text{CEC}) - 15.9 \log_e(\text{K}) + 0.275(\text{fraction} < 0.063 \text{ mm})$ ($r^2 = 26.3\%$; $r^2 [\text{adj}] = 21.8\%$; $F_{5,87} = 5.84$, $p < 0.001$).

^b Cation exchange capacity.

^c Natural effects model plus all anthropogenic variables: Fisher's alpha = $110.3 - 12.8 - (\text{pH}-3.2)^{-1} - 0.00307(\text{silt})^2 - 20.3(\text{Al}/\text{CEC}) - 16.9 \log_e(\text{K}) + 0.267(\text{fraction} < 0.063 \text{ mm}) - 2.6 \log_e(\text{edge}) + 2.5 \log_e(\text{access}) - 0.7 \log_e(\text{community})$. Key: edge, distance to nearest edge; community, distance to the community center; access, distance to the nearest access point for motorized extraction of forest products ($r^2 = 26.3\%$; $r^2 [\text{adj}] = 21.8\%$; $F_{5,87} = 5.84$, $p < 0.001$).

Table 3. Individual Mantel tests on matrix correlations between tree species composition and, in turn, each soil, spatial, and anthropogenic variable.

Variable	Distance matrix*	Correlation (p)	Correlation accounting for space (p)	Correlation of space versus predictor variable (p)
Soil, physical parameters	frac63	0.331 (<0.001)	0.331 (<0.001)	0.056
	clay	0.129 (<0.01)	0.145 (<0.01)	-0.025
	sand	0.032	0.034	-0.001
	silt	0.007	0.007	0.000
	drainage	0.321 (<0.001)	0.337 (<0.001)	0.005
Soil, chemical parameters	dry matter	0.106 (<0.05)	0.109 (<0.05)	0.011
	Al/ECEC	0.521 (<0.001)	0.546 (<0.001)	0.011
	log _e (Al)	0.283 (<0.001)	0.289 (<0.001)	0.027
	log _e (Ca)	0.608 (<0.001)	0.639 (<0.001)	0.008
	log _e (ECEC)	0.495 (<0.001)	0.521 (<0.001)	0.002
	log _e (K)	0.168 (<0.001)	0.189 (<0.001)	-0.035
	log _e (Mg)	0.506 (<0.001)	0.535 (<0.001)	-0.003
	log _e (Na)	0.352 (<0.001)	0.334 (<0.001)	0.116 (<0.05)
	log _e (P)	0.208 (<0.001)	0.231 (<0.001)	-0.033
	loss on ignition	0.254 (<0.001)	0.141 (<0.01)	0.064
	pH	0.338 (<0.001)	0.366 (<0.001)	-0.029
	Distance parameter	space	0.140 (<0.05)	n/a
Anthropogenic parameters	log _e (edge)	-0.001	-0.078	0.224 (<0.001)
	log _e (access)	0.083 (<0.05)	0.071	0.048
	log _e (community)	0.049	-0.019	0.212 (<0.001)

*Key: ECEC, effective cation exchange capacity; space, straight-line distance between samples; edge, distance to nearest edge; community, distance to community center; access, distance to the nearest access point for motorized extraction of forest products.

anthropogenic factors but was marginally related to access distance for resource extraction. Nevertheless, once geographic distance was accounted for the relationship became nonsignificant, and the other two anthropogenic factors (distance to edge and distance to local population centers) were themselves weakly spatially structured across the region, correlating with geographic distance among sites. By themselves these results suggest that forest composition in the landscape was strongly controlled by the edaphic environment, but they do not totally exclude the possibility of an anthropogenic effect, perhaps masked by covariation with geographical distance.

The multiple regression on distance matrices provided further insight (Table 4). The best model included four soil variables and geographic distance. In the second model, in which all environmental and spatial factors were accounted for, the intersite anthropogenic distance effect factors provided a small increase in explanatory value (0.7%), but the factors either made no significant difference or the partial regression coefficient was negative, indicating there was no detectable anthropogenic effect on composition. In the final model in which only environmental factors were accounted for, of the anthropogenic factors only distance to edge added explanatory value but again the coefficient was meaningless.

Discussion

In our study area in southwestern Amazonia, anthropogenic edge effects had no detectable effect on above-

ground biomass, tree alpha diversity, or floristic composition. We had relatively few plots (eight) within 100 m of the edge, so we could not eliminate the possibility of impacts here. Nevertheless, our samples included typical regional impact regimes, short of intensive logging and deforestation, and, within these constraints, showed no impact on tree biomass or diversity. A simplistic interpretation of these results would be that the forests of the region are mostly so resilient to human impacts that conservationists need not be especially concerned by recent levels of selective logging, forest product extraction, and edge effects, at least in the context of the relatively low population densities here. Or, more positively, we could infer that (1) low-intensity extractive activities should be encouraged because they generate income and subsistence value for local people (Lawrence et al. 2005) without substantial plant biodiversity or carbon cost and (2) that all mature forest here may have equivalent conservation value almost regardless of whether it is close to an edge or in a remote wilderness area.

Our negative results pose interpretational difficulties, however. Failure to reject the null hypothesis is not equivalent to disproving the hypothesis. We did not detect anthropogenic effects, but there may (indeed there must) still be some human impact on forest carbon storage and biodiversity. We did not attempt to measure the impact of hunting in these forests, which our anecdotal observations suggest is substantial. In addition, the fact that we did not detect harvesting impacts on biomass or plant composition and diversity may owe at least as much to relatively light harvesting intensities within this region

Table 4. Multiple-regression models of floristic variation based on environmental, spatial, and anthropogenic factor distance matrices (see text for details).

Variable ^a	b, partial regression coefficient	p in final model	Effect of removing the variable on the whole model (Δr^2 , %)
Best model for floristic variation ^b			
drainage	0.147	<0.001	-2.0
log _e (Ca)	0.323	<0.001	-0.8
log _e (ECEC)	0.148	<0.001	-11
Al/ECEC	0.178	<0.001	-26
log _e (space)	0.311	<0.001	-10
Model for floristic variation that maximizes r^2 while including all anthropogenic factors ^c			
drainage	0.191	<0.001	
log _e (Ca)	0.520	<0.001	
Al/ECEC	0.087	0.018	
log _e (space)	0.311	<0.001	
log _e (access)	-0.069	0.009	
log _e (edge)	-0.076	0.007	
log _e (community)	0.058	0.073	
Model for floristic variation that maximizes r^2 while excluding geographic distance and including one or more anthropogenic factors ^d			
drainage	0.191	<0.001	
ln (Ca)	0.485	<0.001	
Al/ECEC	0.109	0.011	
ln (edge)	-0.023	0.269	

^a Key: ECEC, effective cation exchange capacity; space, straight-line distance between samples; edge, distance to nearest edge; community, distance to community center; access, distance to the nearest access point for motorized extraction of forest products.

^b Total $r^2 = 50.9\%$.

^c Total $r^2 = 51.6\%$.

^d Total $r^2 = 41.0\%$.

as it does to the forests' intrinsic resilience. This calls into question the extent to which our data are suitable for detecting anthropogenic edge effects and the extent to which we can state there is some effect size, x , that is not exceeded in this system.

The relationship between anthropogenic edge effects and biomass and diversity in this landscape can be assessed by comparison with known effects detected elsewhere. For example, a long-term study of forests in central Amazonia has quantified biomass decline with proximity to anthropogenic edge. Laurance et al. (1997) report that permanent plots within 100 m of edges lost 3.5 ± 4.1 Mg/ha/year during the first 10–17 years after fragmentation, and fit the loss rate to an exponential model such that over this period the annual decline in AGB since an edge was cut = $9.58 - (22.47 \times 3 \times e^{-0.28 \times \log(\text{distance to edge})})$, where distance to edge is measured in meters. Most biomass loss occurs in the first 4 years after edge creation. We used this relationship and assumed that the nearest edge to our forest samples to fields, pasture, or secondary vegetation was established by clearing at least 4 years prior to our fieldwork, and adjusted the results by the ratio between our mean whole data set biomass

(416 Mg/ha) and that from the central Amazonian landscape (356 Mg/ha) (Laurance et al. 1999). At the same proportional-loss rate as central Amazon forests our edge samples would lose substantial biomass (e.g., at 50 m approximately 69 Mg/ha), but this would decline rapidly with distance to edge. For distances >1000 m the exponential model actually predicted a nonsignificant increase in biomass; for these distances we made no adjustment to our biomass.

We then asked whether our data would be capable of detecting the same effect as reported in central Amazonia. Results of a subsequent study in the same central Amazonian landscape (Nascimento & Laurence 2004) showed no significant difference in AGB in plots within 100 m of an anthropogenic edge and AGB in plots >100 m from the edge, presumably because natural variability in the environment was much stronger than the edge effect. When the effects of natural variability were removed (by subtracting the final from the original prefragmentation biomass in each experimental plot), a highly significant edge-related decline of AGB was apparent. This underlines the importance of accounting for the natural variability within a data set of once-off inventories when attempting to quantify the impact of an experimental treatment such as an anthropogenic edge effect. Our regression approach (Table 1) already explicitly accounts for the impacts of soil-related variation, but it cannot account for other random environmental noise, and, additionally, thin samples such as ours may be subject to unavoidable human error (a sampling edge effect). We therefore accounted for the impact of environmental and sampling noise on our analysis by randomly allocating each of our sample AGB values to each of their distance-to-edge measurements (sampling without replacement), subtracting the biomass lost under central Amazon expectations from each value, and applying a Monte Carlo procedure to estimate the probability of error, by computing the correlation coefficient between the 88 biomass values (log_e AGB) and the 88 distance-to-edge values (log_e distance) for 1000 permutations. We are not aware of a landscape-scale tropical study that has determined the extent to which tree diversity changes in proximity to anthropogenic edge, so we lack an appropriate comparison.

The actual correlation coefficient, r , between log_e (AGB) and log_e(distance) was -0.108 . There is less than a one in one hundred chance of obtaining a less positive score in our data set based on the sampled variation in biomass and the biomass decline function. This suggests that forest response to anthropogenic edges here is different from forest response near Manaus. The actual Fisher's alpha versus log_e(distance) correlation was -0.155 .

We then modified our approach, and asked, at what lower level of postulated impact would we no longer be able to detect an effect? To determine this, we repeatedly weakened the effect by altering the exponential term and then permuted predicted log_e(AGB) and Fisher's alpha with respect to distance to edge, until we reached

such an effect where $\geq 5\%$ of attribute versus distance values were less positive than those we actually observed. For biomass, this level was attained for AGB decline = $151.1 - (354.5 \times e^{-0.34 \times \ln(\text{distance})})$, which translates to approximately 50% of the central Amazon function at 100-m distance and zero effect at approximately 320 m. We conclude that the anthropogenic edge effects on biomass in our landscape were probably no stronger than half of those in the central Amazon landscape. For diversity this level was attained for Fisher's alpha decline = $7.7 + 4.75 \times \ln(\text{distance})$, which by comparison would equate to 23% of the central Amazon AGB decline function at 100-m distance and zero effect at approximately 190 m.

A different approach to help interpret our failure to detect an anthropogenic effect is to conduct a formal test of equivalence. A test of equivalence has hypotheses $H_0: |\Theta| \geq \bar{\Theta}$ versus $H_1: |\Theta| < \bar{\Theta}$, where $\bar{\Theta}$ is an effect size of scientific importance (Lenth 2001). Schuirman (1987) suggests H_0 can be rejected at significance level α if the $100(1 - 2\alpha)\%$ confidence interval for Θ lies entirely within the interval $(-|\bar{\Theta}|, +|\bar{\Theta}|)$. Deciding on an effect size that is "important" is clearly a subjective matter. Here we propose that a 20% decline in biomass and diversity within 100 m of an edge constitutes a serious concern. When the plots at ≤ 100 m were compared with plots > 100 m from an edge, H_0 was rejected for both biomass and diversity anthropogenic impacts: any effect close to the edge must therefore be relatively modest. If our concern, however, was for a weak effect that penetrated farther into the forest, say a 5% decline in biomass and diversity reaching 300 m into the forest, we could not be so sanguine: here we would be unable to reject the null hypotheses.

Floristic composition is a multidimensional parameter, so assessing the ability of our data to detect anthropogenic distance effects is more problematic. Instead we interpret our results by comparing them with the known environmental effects on composition. Most compositional variance was explained by soil factors (40.8%), less by spatial autocorrelation (10.1%), and least by anthropogenic effects (0.7%). Therefore anthropogenic distance effects are unlikely to be responsible for more than $0.7 / (0.7 + 10.1 + 40.8) = 1.4\%$ of the total compositional variation. Furthermore, because the small portion of variance attributed to anthropogenic factors was mostly associated with negative, and therefore meaningless, parameters, their overall effects on tree composition were clearly negligible.

Why are anthropogenic edge effects here apparently so weak? Our leading explanation is that trees in western Amazonian forests are naturally faster growing and more adapted to canopy disturbance than trees in the east (Phillips et al. 2004), perhaps as a result of richer soils (Malhi et al. 2004) and more vigorous fluvial dynamics (Salo et al. 1986). Other things being equal, more productive and dynamic landscapes may generally be more

resilient to human impacts such as NTFP harvesting, selective logging, and edge formation.

Several caveats need emphasizing. First, we have relatively few plots (eight) within 100 m of the edge, which is where the greatest impacts were shown in central Amazonia, and we have not monitored the biomass of edge plots over time. In this sense our study cannot provide the same insight into edge processes as the long-term experimental setup in central Amazonia. Our results are still entirely consistent with a modest anthropogenic effect near the edge, or a small one penetrating further in. Second, our landscape is not heavily fragmented or extensively cleared. Our results therefore do not address the issue of fragmentation impacts on forests, which are known to include the potential collapse of floral and faunal communities once tropical forests become isolated as small islands (e.g., Terborgh et al. 2001; Laurance 2004). Compared with our study region, the Biological Dynamics of Forest Fragments Projects experimental landscape has very few, very large cleared areas (most of the cleared area is in five deforested blocks of 10 km² or more each), and the majority of plots studied are in fragments, both of which could help explain the different findings of the two studies. Third, we did not evaluate animal populations. Fourth, there may yet be a long-term extinction debt among our plant species: we did not evaluate population structures to assess whether severe compositional changes are simply slowing down the anthropogenic disturbance. There is clear evidence from our region that a few heavily logged species such as mahogany have declined (Lawrence et al. 2005) and throughout southwestern Amazonia a major NTFP species, brazil nut, is not regenerating successfully possibly because of overharvesting of seeds (Peres et al. 2003). Intensive harvesting of timber species undoubtedly has an impact on the long-term carbon storage potential of the landscape, as shown, for example, by simulations of species extirpations in a Neotropical forest (Bunker et al. 2005). Finally, we caution against overinterpreting our results. This is one case study and cannot be used to draw dogmatic conclusions about the impacts of human beings on tropical ecosystems.

Acknowledgments

This work was funded by grant ERP-196 from the U.K. Department for International Development, and by a Research Fellowship to O.P. from the U.K. Natural Environment Research Council. We thank colleagues for field assistance, especially F. Cornejo, C. Chacón, A. Farnan, W. Galeano, M. Lopez, W. Ramirez, and A. Reategui. We thank Peruvian Safaris S.A., Bahuaja Lodge, and the people of the communities of La Torre, Palma Real,

Alegria, Tres Islas, Sandoval, Jorge Chávez, Loero, Sonene, Puerto Arturo, Lago Valencia, Boca Pariamanu, and Sabaluyo for their generous hospitality. We acknowledge help from M. Yli-Halla (soil analysis, Agrifood Research Finland), R. Kendall (GIS technical assistance), D. Appleyard (graphics), J. Chave (permission to use unpublished allometric equations), and T. Baker (access to his unpublished Amazon tree allometry data). We benefited from helpful discussions with T. Baker, A. Lawrence, S. Lewis, and J. Lloyd, and from the constructive comments of W. Laurance, F. Putz, and two anonymous reviewers. Instituto Nacional de Recursos Naturales provided permits for conducting the work and Universidad Nacional San Antonio Abad de Cusco and its herbarium (CUZ) supported us logistically.

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