

TROPICAL FOREST COMMUNITY ECOLOGY

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Chapter 21

SOIL FERTILITY AND ARBOREAL MAMMAL BIOMASS IN TROPICAL FORESTS

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OVERVIEW

Tropical forests have been characterized across a wide range of primary plant productivity, which is partly dependent on soil properties. Yet the relationships between soil fertility and plant productivity and herbivore biomass remain poorly understood in tropical forests. Here I review the evidence regarding the relationship between soil fertility and mammal assemblage biomass from the perspective of primates spanning a wide dietary spectrum. I also present new data based on a comprehensive compilation of available community-wide estimates of neotropical primate biomass density in Amazonian and Guianan forests. A composite index of soil fertility, based on both chemical and physical properties of soils, explained 37% of the variation in total diurnal primate biomass in a set of 60 undisturbed Amazonian forest sites that had not been affected by hunting pressure and anthropogenic habitat disturbance. I discuss the mechanisms by which tropical forest soil nutrient availability may constrain bottom-up trophic cascades from green plant producers to primary and secondary consumers. These include edaphic effects on the quality and amount of resources produced by individual food plants, as well as wholesale changes in floristic composition. Measures of soil fertility and other environmental gradients affecting forest productivity can serve as an efficient framework for predicting the diversity and population sizes of vertebrate species that can be protected by potential reserve polygons.

INTRODUCTION

Early perceptions that evergreen tropical forests must be sustained by fertile soils (Wallace 1853) – which is reinforced by the paradoxical high phytomass supported by highly efficient nutrient capture and cycling in nutrient-poor soils – have been unequivocally demystified by a vast body of evidence on the limited agropastoral potential of the humid tropics (Goodland and Irwin 1975, Irion 1978, Sioli 1980). Yet the physical and chemical properties of unfertilized tropical forest soils are remarkably variable (Projeto RADAMBRASIL 1972–1978, Sanchez 1981, Uehara and Gilman 1981, Cochrane and Sanchez 1982, Vitousek and Sanford 1986,

Jordan 1989, Furley 1990, Richter and Babbar 1991). The local to regional scale heterogeneity in soil age, texture, drainage, depth, parent materials, pH, and macro- and micronutrient content therefore presents a highly diverse set of consequences to forest primary productivity.

Most soils in the humid tropics are highly weathered and relatively nutrient poor (Irion 1978, Uehara and Gilman 1981). Tropical forest plants are often able to prevent nutrient loss through leaching and herbivory using a number of above- and below-ground strategies. However, retention of scarce nutrients may be less imperative in fertile soils that can replace nutrients lost through leaching and herbivory. Given the fundamental laws of thermodynamics,

bottom-up constraints on green plant producers often reverberate via successive nodes in a food chain onto the size and dynamics of herbivore and carnivore populations, and through the structure of whole forest ecosystems. Yet the role of soil fertility as a factor regulating vertebrate populations remains poorly investigated. In particular, the diverse relationships between soil nutrient limitation and forest composition, forest phytochemistry, and ultimately the amount and quality of digestible resources available to invertebrate and vertebrate consumers have been poorly explored in tropical forests (but see Janzen 1974, McKey *et al.* 1978, Coley *et al.* 1985, Chapin *et al.* 1986, Vitousek and Sanford 1986, Oates *et al.* 1990, Coley and Aide 1991). If rainfall and light are not limiting, food quality for herbivores will depend on the rate of nutrient uptake by food plants, which is ultimately a function of soil fertility and the underlying geological parent material.

Soil texture and nutrient status have major effects on the distribution and abundance of plant communities in terms of both understory shrubs and herbs (Tuomisto and Poulsen 1996, Tuomisto *et al.* 2003, Costa *et al.* 2005) and trees (Huston 1980, Gentry 1988, Clark *et al.* 1999, Givnish 1999, Potts *et al.* 2002, Phillips *et al.* 2003). The composition and density of food plants, the productivity and growth rate of preferred food items, and foliage levels of defensive secondary metabolites may therefore be more favorable to herbivores in higher fertility soils (Coley *et al.* 1985, Chapin *et al.* 1986, Vitousek and Sanford 1986, Waterman and Mole 1989). In more fertile soils, this may lead to higher folivore and frugivore densities as documented in tropical forests of South America (Emmons 1984, Peres 2000a), central Africa (Barnes and Lahm 1998), and northern Australia (Kanowski *et al.* 2001), as well as in tropical savannas (Bell 1982, du Preez *et al.* 1983, Runyoro *et al.* 1995, Augustine *et al.* 2003) and temperate regions (Jones and Hanson 1985, Pastor *et al.* 1993, Recher *et al.* 1996). In Amazonian forests, studies on the relationship between soil chemistry and wildlife abundance strongly suggest that population densities of large vertebrates can be depressed under conditions of low fertility (Emmons 1984, Peres 1997a,b, 1999a,b,

2000a,b, Peres and Dolman 2000, Haugaasen and Peres 2005a,b, Palacios and Peres 2005).

In general, species richness should increase with the size of the resource base because higher population densities result from greater energy availability, thereby enabling more species to attain viable population sizes within a given area (Wright 1983, Rosenzweig and Abramsky 1993). This species-energy relationship predicts that the species richness of an area will be positively correlated with the aggregate population density of all taxa (but see Srivastava *et al.* 1998, Mittelbach *et al.* 2001), although this correlation can also emerge from other mechanisms (Evans *et al.* 2005). If soil nutrient availability limits primary consumer population sizes, and therefore species richness, one would expect that, at regional scales, not only will there be a positive relationship between soil fertility and species richness, but these species should have greater biomass densities in high productivity areas.

In this chapter, I review the relationship between soil fertility and mammal biomass in tropical forests. I explore this relationship from the perspective of arboreal mammals based on community-wide estimates of platyrhine primate biomass in Amazonian and Guianan forests. Finally, I discuss the mechanisms by which tropical forest soil nutrient availability may constrain bottom-up trophic cascades from green plant producers to primary and secondary consumers.

SOIL INFERTILITY IN TROPICAL FORESTS

The structure of any community may be largely determined by its primary productivity (Fretwell 1977, Hunter and Price 1992, Power 1992, Rosenzweig 1995), although this claim remains contentious against much empirical evidence (e.g., Crête 1999, Howe and Brown 1999, Seagle and Liang 2002). Primary productivity in moist tropical forests is often constrained by a limited supply of nutrients and trace elements in low pH soils, which tend to be poorer than those in the temperate zone due to a long and repeated history of intensive leaching and weathering (Hacker 1982, Jordan 1989). A low soil pH may

result in increased toxicity caused by H⁺, Al, and Mn and a reduced uptake of most nutrients (Marshner 1991).

If tropical lowland forests are nutrient limited, one might predict that they would respond to nutrient enrichment treatments which could result in higher vegetative or reproductive productivity, litterfall, and soil organic matter accumulation. Although responses to fertilization experiments have been variable, most tropical forest plots fertilized on a meaningful scale show increased above-ground net primary production, radiation conversion efficiency, leaf area index, and nutrient content of leaf litter (Harrington *et al.* 2001). Other studies in primary forests have shown that tree girths, litterfall mass, and litter nutrient content increase in fertilized plots (e.g., Tanner *et al.* 1998, Mirmanto *et al.* 1999). In regenerating secondary forests, tree biomass can increase significantly following N-only and N + P treatments (Davidson *et al.* 2004), indicating that secondary productivity and recovery of above-ground biomass is often constrained by soil fertility and texture across regions and soil types within a region (Chazdon 2003). Crucially, quantitative allocation to reproductive plant parts – that are important to consumers of flowers, nectar, and whole unripe/mature fruits or seeds – also appears to increase. In a Sumatran forest, production of leaf litter and fruit increased along a natural gradient of increasing soil fertility (van Schaik and Mirmanto 1985). Nutrient enrichment enhances allocation to reproduction in other tropical ecosystems like dwarf mangrove stands in Panama (Lovelock *et al.* 2004). But as far as I am aware, the only experimental fertilization study in a tropical forest where litterfall was fractioned into both leaf litter and reproductive components (at Barito Ulu, central Kalimantan, Borneo) shows a significant increase in reproductive parts (flowers and fruits) in most tree species within fertilized plots (Mirmanto *et al.* 1999, J. Proctor, personal communication). Further studies are however necessary to confirm whether nutrient enrichment augments plant reproductive productivity at the community level in a range of soil types.

Only 7% of the soils under forest or agriculture in the Amazon basin show no sign of

fertility limitation (Cochrane and Sanchez 1982), and most of Brazilian Amazonia consists of nutrient-poor, acidic soils that are often associated with aluminum toxicity (Nicholaides *et al.* 1984). Agricultural production is severely constrained by nitrogen, phosphorus, potassium, and calcium deficiency in 62–90% of the Amazon. In much of the basin, soil nutrients exported through leaching and runoff are replaced not so much from weathering of the parent material but from long-range export of approximately 40 million tons year⁻¹ of atmospheric dust particles and dissolved material carried by wind and rainfall from the Sahara alone (Swap *et al.* 1992, Koren *et al.* 2006). Exogenous nutrient inputs from rainfall at a remote site in the state of Amazonas are in the order of 0.34, 0.9, 0.3, and 1.32 kg ha⁻¹ year⁻¹ for P, K, Mg, and Ca, respectively (Williams and Fisher 1997). In fact, water flowing out of crystal-clear forest streams in many upland parts of the basin is more distilled and may contain only half of the elemental concentrations (e.g., P, Ca, and Mg) of rainwater, obviously attesting to the net efficiency with which nutrients are retained by the vegetation (Irion 1978, Furch 1984, Bruijnzeel 1991).

However, all regional-scale soil maps available for the Amazon show a diversity of pedological processes and a highly variable macromosaic of soil types of varying fertility (Sombroek 1966, EMBRAPA 2002). While vast upland tracts of lowland Amazonia consist of highly weathered soils of ancient pre-Cambrian origin, young soils along white-water rivers are mainly Quaternary (Pleistocene and Holocene) deposits that are renewed annually by a prolonged flood pulse (Junk 1997). Most of central Amazonia both north and south of the Amazon River consists of the so-called Barreira formation characterized by extremely low clay fractions of key inorganic nutrients which were radically impoverished during the formation of the kaolinitic topsoil. Total amounts of sodium, calcium, magnesium, and potassium are often in the range of 100–300 ppm and the cation exchange capacity barely exceeds 5 mval 100 g⁻¹ (Irion 1978). By contrast, the Cretaceous to Tertiary fine-grained sediments that formed much of the soils of southwestern Amazonia are often relatively fertile.

BASIN-WIDE PATTERNS OF PRIMATE BIOMASS

Primates are ideal candidates for a regional-scale test of bottom-up effects of soil fertility because (1) they represent one of the most important biomass components of arboreal vertebrate assemblages; (2) they consume a significant but unknown proportion of the primary vegetative and reproductive productivity of neotropical forests (Eisenberg 1980, Terborgh 1983, Peres 1999a, 2000a, Haugaasen and Peres 2005b); (3) they are strictly arboreal and therefore have priority of access to food items produced in the forest understory and canopy before they fall to the ground and become available to terrestrial vertebrates; (4) they often form highly conspicuous and observable groups, and are amenable to highly standardized population surveys that can be replicated in any tropical forest (Peres 1999c); and (5) they consequently have attracted a disproportionately large amount of interest from field ecologists and behavioral biologists,

resulting in a strong cadre of primatologists in most habitat-countries.

I compiled data on the population density and biomass for all diurnal primate species from 96 spatially independent undisturbed forest sites in lowland Amazonia and the Guianan shield (Figure 21.1). This excludes only night monkeys (*Aotus spp.*), which are rarely censused by primatologists. Over half of these sites ($N = 52$) resulted from our own long-term series (1987–2004) of standardized line-transect censuses of mid-sized to large-bodied vertebrate assemblages throughout lowland Amazonia (Peres 1997a, 2000a,b, Peres and Dolman 2000, Haugaasen and Peres 2005b, Palacios and Peres 2005, Peres and Nascimento 2006, Peres and Palacios 2007). Data compilation for all other sites was updated from Peres (1999b) and included an exhaustive survey of published and unpublished reports of primate population densities obtained through line-transect census techniques. However, I excluded from the final dataset any study that either failed to report densities for one or more diurnal

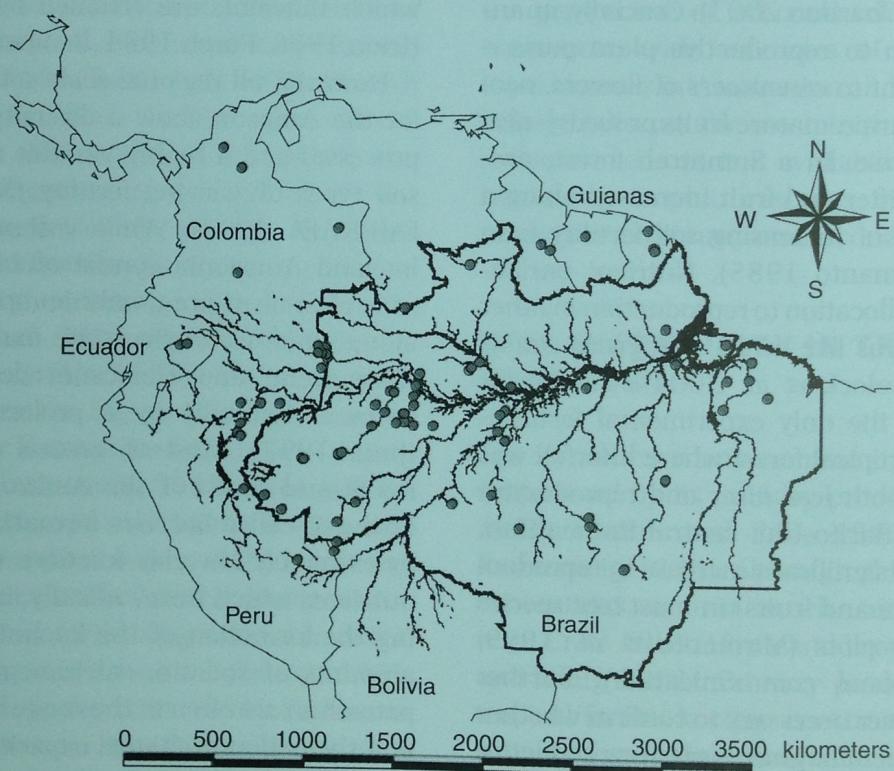


Figure 21.1 Location of 96 forest sites within eight South American countries where community-wide primate surveys considered in this analysis were conducted. The boundary polygon of Brazilian Amazonia is indicated by a thick line.

primate species occurring at a given site, or was considered to be based on an insufficient census effort (<100 km of census walks). All survey sites were part of continuous tracts of primary forest that may have been selectively hunted to a varying extent but otherwise had not been subjected to structural habitat disturbance due to selective logging, slash-and-burn agriculture, surface wildfires, and forest fragmentation. In most of the analyses, I excluded sites that had been hunted to a moderate or persistent extent (see Peres and Palacios 2007) because subsistence game hunting profoundly affects the size structure and aggregate biomass of Amazonian primate assemblages (Peres 1990, 1999b, Peres and Dolman 2000). Non-hunted and lightly hunted sites, on the other hand, showed no significant differences in total biomass and size distribution of the primate assemblage, and were therefore pooled together. Conversions of population density to biomass estimates relied on mean body mass values for adult males and females available from the literature, which were then corrected using a factor of 0.8 to account for juveniles in the population (see Peres 2000a). Descriptive details on all but the most recently surveyed study areas (2001–2004), forest site classification according to levels of hunting pressure, and procedures used during line-transect censuses and data analysis can be obtained elsewhere (Peres 1999b, 2000a, Peres and Palacios 2007 and references therein) or from the author.

SOIL FERTILITY

I used a classification of the agricultural potential of the Amazon basin based on key physical and chemical indicators of soil fertility. These data are based on a 1:3,000,000-scale digital soil map of Brazilian Amazonia that was produced in the 1970s by the Soils Division of the Brazilian Institute for Agricultural Research (EMBRAPA 2002). This is regarded as the best available soil map for the Amazon (Laurance *et al.* 2002), containing 17 major soil types that are further subdivided into over 100 subtypes, using the Brazilian soil taxonomy (cf. Beinroth 1975). The different soil

subtypes were classified using published sources (especially Sombroek 1984, 2000).

The index of soil fertility ranged from 1 (poorest soils) to 5 (best soils) with nine class-intervals of 0.5. Although soil chemistry was considered, a slightly greater weight was given to physical properties of the soil (e.g., soil depth, texture, stoniness, waterlogging) that cannot be easily enhanced by agricultural inputs. Soil fertility classes 4.0–5.0 have the highest agricultural potential. These include nutrient-rich alluvial soils in várzea forests (seasonally inundated by white-water rivers of Andean origin), terra roxa soils (nutrient-rich, well-structured upland soils formed on base-rich rock), eutrophic Cambisols (young, relatively unweathered soils with high activity clay and high nutrient status), and Vertisols (clay soils with high activity clay minerals and high nutrient content). These soil types collectively encompass only 1.8% of the Brazilian Amazon (EMBRAPA 2002). Soil classes 2.5–3.5, comprising 53.4% of the Brazilian Amazon, have some agricultural potential but also important limitations, such as high acidity, low nutrient availability, shallowness, waterlogging, and concretionary status. Soil classes 1.5–2.0 are suitable mainly for cattle pasture or undemanding tree crops, and encompass 34.8% of the Brazilian Amazon. They include the intensively weathered Xanthic Ferralsols of central Amazonia, very stony and shallow soils, nutrient-poor waterlogged soils, and Plinthosols (soils that become hardened laterite when exposed to wetting and drying cycles). Soil class 1 encompasses 7.8% of Brazilian Amazonia, has no potential for agriculture, and largely consists of very sandy soils, including podzols and quartz sands, some of which are waterlogged. Because 31 of the 96 sites were located outside Brazilian Amazonia, I assigned fertility classes based on available soil-type information and applied the same criteria used in the EMBRAPA soil map.

EDAPHIC DETERMINANTS OF PRIMATE BIOMASS

The assemblage biomass of all sympatric primate species, estimated for 60 non-hunted to lightly

hunted forest sites and 36 moderately to heavily hunted sites, was highly variable. In non-hunted to lightly hunted sites, it ranged from as low as 20.1 kg km^{-2} to as high as 953.1 kg km^{-2} (mean \pm SD = 248.6 ± 156.7). The lowest biomass estimates were very similar across major levels of hunting pressure (20.1 versus 26.3 kg km^{-2}) but the highest estimate in moderately to heavily hunted sites was 626.8 kg km^{-2} (mean \pm SD = 148.1 ± 127.7), and there was a significant difference in primate biomass between hunted and non-hunted sites ($t = 3.25$, d.f. = 94, $P_{adj} = 0.002$). By contrast, there was no significant difference in the total primate density between non-hunted to lightly hunted sites (mean \pm SD = 106.4 ± 66.9 ; range = $9.9 - 355.2 \text{ ind. km}^{-2}$) and moderately to heavily hunted sites (mean \pm SD = 106.6 ± 75.1 ; range = $13.1 - 357.8 \text{ ind. km}^{-2}$; $t = -0.014$, d.f. = 94, $P_{adj} = 0.989$), partly because of density compensation in hunted sites by small-bodied species (Peres and Dolman 2000).

Considering only non-hunted to lightly hunted sites, primate biomass tended to increase away from the equator towards the Guianan and Guaporé shield (north and south of the Amazon, respectively), but especially towards seasonally dry parts of southwestern Amazonia (Figure 21.2). Soil fertility alone explained one third of the variation in the log-transformed estimates of total primate biomass ($R^2 = 0.368$, $F_{1,58} = 31.4$, $P < 0.001$, $N = 60$; Figure 21.3a). This is roughly equivalent to a mean primate biomass increment of 47 kg km^{-2} across consecutive classes of soil fertility, or a nearly six-fold increase in biomass from the least to the most fertile soils. Soil fertility also had an appreciable effect on the overall primate density in non-hunted sites ($R^2 = 0.342$, $F_{1,58} = 30.19$, $P < 0.001$, $N = 60$), but not on the mean individual body mass of all co-occurring species ($R^2 = 0.002$, $P = 1.0$), which ranged from 1436 to 4874 g (mean \pm SD = 2469 ± 781 g, $N = 60$). There was no significant interaction between levels of hunting pressure and soil fertility, and combining these two variables further improved a minimum regression model explaining nearly half the total variation in primate biomass across all sites ($R^2 = 0.452$, $F_{2,93} = 38.4$, $P < 0.001$, $N = 96$).

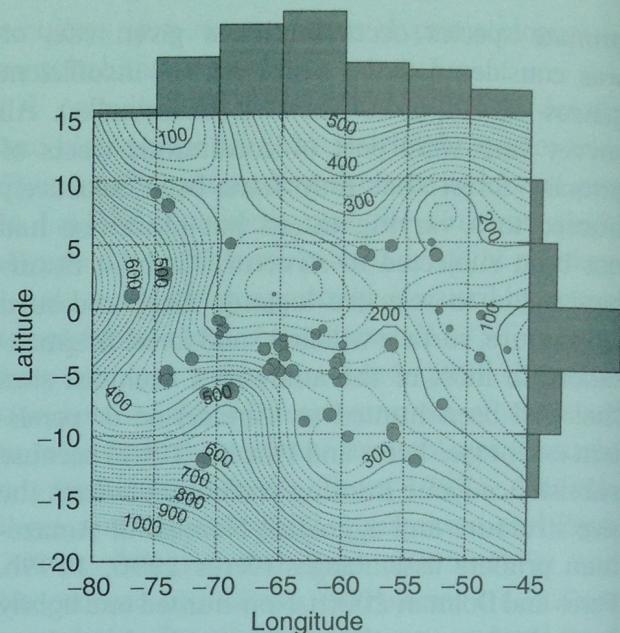


Figure 21.2 Geographic patterns of primate biomass in Amazonian and Guianan forests. Sizes of shaded circles are scaled according to the \log_{10} total diurnal primate biomass estimates whereas contour lines indicate interpolations of untransformed biomass values. Border histograms indicate the total number of non-hunted to lightly hunted sites within 5-degree bands for which data are available. Solid line represents the equator.

Once the effects of hunting pressure and soil fertility were taken into account (in an analysis of covariance), the total primate biomass was still affected by the local primate species richness, which ranged from 2 to 13 species (mean \pm SD = 7.87 ± 2.67 species, $N = 96$). I therefore examined the effects of different environmental variables on the mean primate biomass per species co-occurring at any given site. Soil fertility again had a significantly positive effect on the primate biomass per species richness, explaining 43% of the variation in this ratio considering only the 60 non-hunted and lightly hunted sites (Figure 21.3b).

None of the other environmental variables associated with each forest site, including total rainfall and strength of the dry season, had a significant effect on primate biomass. Rainfall gradients are often closely correlated with levels of soil fertility because cumulative leaching and runoff of soil and plant nutrients are more likely if ancient

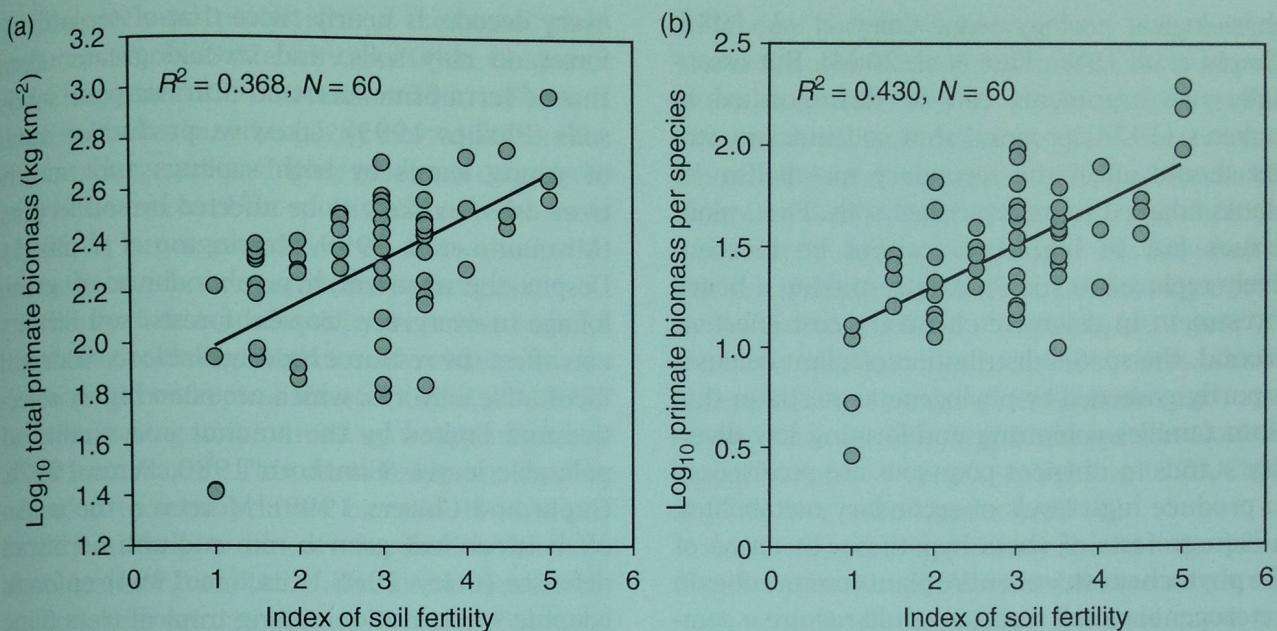


Figure 21.3 Relationships between a composite index of soil fertility and (a) the aggregate biomass density (kg km^{-2}) and (b) the mean biomass density per co-occurring species of all diurnal primate species in non-hunted to lightly hunted forest sites of Amazonia and the Guianan shield. R^2 values of each relationship are indicated in each plot.

soils have been subjected to a long and repeated history of heavy rainfall. For the 96 forest sites considered here, there was a significantly negative correlation between total annual rainfall and soil fertility ($r = -0.434, P_{adj} < 0.001$), so this relationship appears to hold at a pan-Amazonian scale despite the wide mesoscale variation in soil fertility within regions sharing the same rainfall regime. However, rainfall alone was a very weak correlate of total primate biomass ($r = -0.079, P_{adj} = 1.0$) or the primate biomass per species ratio ($r = -0.118, P_{adj} = 0.906$).

All sites surveyed had a full complement of terrestrial and aerial predator species, which are known to affect herbivore abundance (Hairston *et al.* 1960, Dyer and Letourneau 1999, Halaj and Wise 2001). However, primate biomass was considerably higher in nutrient-rich forests despite the concomitant higher abundance of predators that habitually or occasionally take primates, such as harpy eagles, ornate hawk eagles, and a range of scansorial mammalian carnivores (Peres unpublished data). Arboreality does not necessarily confer immunity to predation, and none of the primate species surveyed grow to a complete

size refuge. Indeed, predation pressure shapes a range of behavioral adaptations and the ecology of group living in Amazonian primates (Terborgh and Janson 1986, Peres 1993, Isbell 1994). However, natural predators do not appear to play a major role in limiting primate population density along the productivity gradient experienced by undisturbed Amazonian forests. Moreover, human predation (hunting) of medium- to large-bodied primate species tends to be heavier in nutrient-rich forests, but is unlikely to significantly mitigate the impact of natural predation through predator control. These lines of evidence suggest that regulation of primate abundance, at least in vast tracts of continuous Amazonian forest, is primarily a bottom-up rather than a top-down process.

SOIL NUTRIENT LIMITATION AND HABITAT PRODUCTIVITY

The importance of soil nutrient limitation on the cost-effectiveness of a plant's anti-herbivore arsenal has become fairly well established in plant

physiological ecology (e.g., Coley *et al.* 1985, Chapin *et al.* 1986, Fine *et al.* 2004). But essentially two arguments can be distinguished in Janzen's (1974) proposal that soil nutrient status should affect the secondary metabolism of plants adapted to impoverished soils. First, plant tissues lost to herbivores cannot be inexpensively replaced in such habitats, making a heavy investment in defensive chemistry cost effective. Second, the spatial distribution of plant defenses is partly governed by phylogenetic inertia in that plant families colonizing and forming low diversity stands in nutrient-poor soils are predisposed to produce high levels of secondary metabolites. Adequate tests of these hypotheses in terms of the phytochemistry of entire plant communities in heterogeneous soil mosaics would require a comprehensive analysis of biochemical profiles and to a large extent this has not been done. However, there appears to be a fairly tight relationship between soil nutrient availability, plant chemistry and digestibility, and the abundance of mammalian herbivores in undisturbed tropical forests (McKey *et al.* 1978, Waterman and McKey 1988, Waterman *et al.* 1988, Chapman and Chapman 1999, Chapman *et al.* 2002, but see Oates *et al.* 1990) and tropical savannas (Bell 1982). Nutrient-deficient environments often lead to an emphasis on secondary metabolites derived from "carbon-overflow" pathways, whereas nutrient-rich environments are often characterized by a greater production of nitrogen-based metabolites or enhanced growth rates (Waterman and Mole 1989).

Levels of plant reproductive investment (e.g., production of flowers, fruits, and seeds) relative to somatic investment (e.g., energy storage, survival, and morphological or chemical defense) is also likely to be determined by the uptake of macronutrients and trace elements. Higher per capita investments into large crop sizes of reproductive parts (flowers, fruits, or seeds), of higher densities of large-crowned trees that can afford to produce large fruit crops would favor nectivores, frugivores, and seed predators. In Madre de Dios, Peru, for example, the annual yield of fresh edible fruits in nutrient-rich alluvial soils ($592 \text{ kg ha}^{-1} \text{ year}^{-1}$), that are replenished by a flood pulse from the Tambopata River once

every decade, is nearly twice that of terra firme forest on clay soils, and six-fold greater than that of terra firme forest on nutrient-poor sandy soils (Phillips 1993). Likewise, production rates of young leaves by both saplings and mature trees are also likely to be affected by soil fertility (Mirmanto *et al.* 1999, Harrington *et al.* 2001). Despite the apparent hyperabundance of green foliage in evergreen tropical forests, soil fertility can affect the resource base available to strict and facultative folivores, which are often highly selective and limited by the amount and quality of palatable leaves (Ganzhorn 1980, Peres 1997b, Gupta and Chivers 1999). Moreover, the trade-off between leaf growth rate and anti-herbivore defenses (Coley 1988, Kitajima 1994) enforces edaphic specialization among tropical trees (Fine *et al.* 2004), further increasing community-wide differences in foliage quality between nutrient-rich and nutrient-poor soils.

MAMMAL BIOMASS AND SOIL FERTILITY IN TROPICAL FORESTS

The positive effects of soil fertility on the total output and quality of plant food items may seem obvious, especially if light and moisture are not limiting. However, few tropical forest studies have demonstrated this relationship despite over 30 years of mammal surveys following Janzen's (1974) seminal discussion on this topic. The multitrophic consequences of soil nutrient limitation to vertebrate communities are even less well understood, and no tropical forest study has been able to demonstrate a direct link between soil fertility and mammal biomass at regional scales. I have shown that key indicators of soil fertility, including soil chemistry and texture, can affect the biomass of primate assemblages in Amazonian forests, and that this relationship is significant even when differences in species richness are taken into account.

The relatively strong bottom-up effect of soil fertility on primate biomass is quite remarkable given the variation in other environmental variables that can also affect primate abundance, including forest type, forest structure, floristic composition, total fruit production, and

the density and patch size of keystone plant resources (Peres 1997a, 1999b, 2000c, Chapman and Chapman 1999, Stevenson 2001). Some of these variables may be partly nested within the effects of large-scale edaphic gradients considered here but a more robust multivariate model could explain a larger proportion of the variation in primate abundance over such a vast region.

Primary forest productivity in terms of total litterfall is a strong predictor of primate species richness in neotropical forests (Kay *et al.* 1997), both increasing with rainfall up to approximately 2500 mm year⁻¹. This relationship can now be extended to total primate biomass in that soil fertility is likely to be correlated with the total above-ground turnover of the forest biomass. In general, both primate species richness (Peres and Janson 1999) and forest biomass turnover (Malhi *et al.* 2004) increase from eastern to western Amazonian forests, and this geographic pattern also holds for total primate biomass and primate biomass per species. Above-ground coarse wood productivity in Amazonian forests increases with soil fertility, particularly towards the eastern flanks of the Andes (Malhi *et al.* 2004), which mirrors the geographic pattern of primate biomass. I predict that the relationship between forest productivity (e.g., as indexed by litterfall) and the biomass of a group of primary consumers such as primates would be even tighter if flower and fruit production were considered separately, but few studies distinguish the vegetative and reproductive fractions of litterfall. I also predict that mammal biomass in tropical forests is a strong positive correlate of the above- to below-ground ratio in forest phytomass, and that this relationship will hold at most meso- to large scales, depending on the extent to which wide-ranging mammals integrate local edaphic constraints at the landscape scale.

Fittkau (1973, 1974) was one of the first to show a severe deficiency of some nutrients essential to plant growth in central Amazonia, particularly calcium, phosphorus, nitrogen, potassium, and a number of trace elements. He attributed the paucity of snails and mussels to the notorious calcium deficiency of Amazonian forest streams. Both terrestrial and aquatic food webs are affected by regional

differences in geochemistry and soil fertility. The net productivity of Amazonian nutrient-rich white-water lakes can be 15- to 19-fold greater than that of nutrient-poor black-water lakes, where fish can show signs of severe nutrient deficiency in their vertebrae (Geisler and Schneider 1976, Smith 1979). For example, the fish production of sediment-rich rivers of Andean origin such as the Madeira or the Purús ($52 \text{ kg ha}^{-1} \text{ year}^{-1}$) is much greater than that of rivers draining primarily nutrient-poor podzols and spodosols such as the Negro–Casiquiare–Guainía ($6.6\text{--}13.2 \text{ kg ha}^{-1} \text{ year}^{-1}$; Goulding 1979, Clark and Uhl 1987, Goulding *et al.* 1988).

Previous studies had already shown large differences in total primate biomass between eutrophic soils in seasonally inundated Amazonian várzea forests and mesotrophic or oligotrophic soils in upland terra firme forests (Peres 1997a,b, 1999b, Peres and Dolman 2000). These patterns are consistent with those found for Amazonian assemblages of small canopy mammals (Malcolm *et al.* 2005), large terrestrial and arboreal mammals (Emmons 1984, Haugaasen and Peres 2005), and mid-sized to large-bodied vertebrates (Peres 2000a,b). Primate communities in seasonally flooded and terra firme forests consistently show a reverse abundance–diversity relationship with high biomass, species-poor assemblages occurring in the most nutrient-rich soils (Peres 1997a). Variation in primate biomass throughout the western Amazon can also be explained by regional differences in soil types and geochemistry. Primate densities in southeastern Colombia, eastern and southern Peru, western Brazilian Amazonia, and northern Bolivia are consistently higher in white-water than black-water drainages (Freese *et al.* 1982, Peres 1997a, Palacios and Peres 2005), despite sediment overflow from white-water rivers to adjacent black-water drainages in exceptionally high inundation years. For example, primate biomass along the black-water Rio Nanay, upriver of Iquitos, Peru, tends to be particularly low (Freese *et al.* 1982), reflecting the nutrient-poor status of the soils in this region (Kauffman *et al.* 1998). On the basis of 300 km of census effort conducted at seven Amazonian forest sites of varying productivity, Emmons (1984) suggested that mammal abundance in Amazonian forests

is largely a function of soil fertility. She noted that densities of non-volant mammals gradually decreased from forests on fertile alluvial or volcanic soils in western Amazonia, through those on upland latosols, to very nutrient-poor white sands of the Guianan shield. Abrupt declines in population densities of howler monkeys (Peres 1997b) and other arboreal folivores (Peres 1999a) can be observed throughout Amazonian forests and across a gradient of soil fertility from annually flooded várzea forests, to supra-annually flooded floodplain forests, to Paleovárzea forests, to mesotrophic terra firme forests, and finally oligotrophic terra firme forests. The present analysis confirms the positive effect of soil fertility on mammal biomass on a much larger scale. Salovaara (2005) also showed that primate and ungulate biomass in a non-flooded forest landscape of eastern Peruvian Amazonia was considerably higher in more fertile soils. In this study, major soil formations were classified using estimates of soil cation content (Ca^+ K^+ Mg^+ Na) based on the composition of pteridophyte species (ferns and allies) with known optimal cation requirements (Salovaara *et al.* 2004).

The relationship between large vertebrate population abundance and soil fertility can be generalized to other continental mammal faunas. Once the effects of altitude were taken into account, the combined abundance of folivorous marsupials in Australian rainforests was significantly higher in sites on nutrient-rich basalts than in those on nutrient-poor acid igneous or metamorphic rocks (Kanowski *et al.* 2001). Barry (1984) showed that infertile podzol soils in rainforest sites of southeast Queensland supported significantly fewer small mammals than fertile krasnozem soils. There is also conclusive evidence that the richest and most abundant Australian vertebrate (or mammal) faunas occur in sites with the greatest degree of soil fertility (Barry 1984, Recher *et al.* 1996, Woinarski *et al.* 1999, Claridge and Barry 2000), although these studies may be confounded by the effects of rainfall.

Although the high species richness of the large mammal fauna of East Africa may be largely due to the sheer size of its savanna biome (Cristoffer and Peres 2003), the exceptionally high native ungulate biomass (e.g., Runyoro *et al.* 1995,

Caro 1999) can be largely attributed to the rich volcanic soil originating from the Great Rift. Low concentrations of essential mineral elements may limit the distribution of some species. The spectacularly large mixed-species herds of East African ungulates have been spatially correlated with high concentrations of Na, Mg, and P in grasses (McNaughton 1988). This is consistent with the striking differences in large mammal biomass between savannas on fertile and infertile soils (East 1984, Fritz and Duncan 1994), a pattern that can be extended to North American savannas and forests (Jones and Hanson 1985). The distribution of elephant and rhinos in Borneo may be limited by mineral-rich soils in salt licks (Davies and Payne 1982). Conversely, the remarkably low mammal biomass sustained by even relatively undisturbed South American savannas of the Brazilian cerrado (Marinho-Filho *et al.* 2003, personal observations) can be partly attributed to its highly weathered latosols that are particularly poor in key plant nutrients, especially P and Ca. Although large mammal assemblages of the cerrado were far more species rich in the Plio-Pleistocene (Simpson 1980), there is no evidence to suggest that the megafaunal abundance of this biome was ever analogous to extant nutrient-rich African or Asian savannas.

Low biomass of folivorous lemurs in Malagasy evergreen forests has been attributed to the relatively high fiber content of mature leaves (Ganzhorn 1992), which in plants on nutrient-poor soils tends to be associated with slower growth rates and higher leaf replacement costs (Janzen 1974, McKey *et al.* 1978, Coley *et al.* 1985). In central African forests, both the biomass of wild herbivores and densities of humans exploiting them increase steeply in sites characterized by medium to high soil nutrient availability primarily due to greater deposits of sediments from volcanic, marine, and sedimentary rocks (Barnes and Lahm 1998). Compared with most upland Amazonian forests, central African forests of the Congo basin are more nutrient rich and in general can usually sustain a much higher biomass of diurnal primates and game vertebrates (Fa and Peres 2001), and these differences do not take into account the more prominent nocturnal African primate fauna which is rarely censused. In fact,

from an intercontinental perspective, mammal biomass in a typical undisturbed terra firme forest of central Amazonia is more analogous to that of nutrient-poor forests of central Borneo where primate and ungulate densities can be extremely low (Bodmer *et al.* 1991, McConkey 1999).

CONCLUDING REMARKS

The effect of soil fertility on the geographic variation in terrestrial vertebrate biomass at different spatial scales is a reminder of the powerful influence of bottom-up forces regulating the structure of tropical forest communities. Baseline densities of wildlife populations can be properly investigated only in continents and regions that remain relatively unadulterated by large-scale anthropogenic disturbance, including structural habitat changes and direct or atmospheric inputs of industrial fertilizers. There is no reason why this relationship should not apply to temperate forests and other biomes, but sadly the opportunities to understand the distribution and movements of large vertebrates in pre-agricultural Europe and North America are no longer with us. Several questions remain wide open for future investigation, including the consequences of soil fertility on the availability of vertebrate-mediated seed dispersal services to plant taxa bearing fleshy fruits, which may have a positive feedback effect on the density of fruiting plants in nutrient-rich soils. Large-scale edaphic constraints on tropical forest habitat productivity should also be explicitly considered in increasingly overhunted landscapes because productivity–abundance relationships are likely to affect the size, recovery rate, and source–sink dynamics of game vertebrate populations (Joshi and Gadgil 1991). For example, sustainable harvest rates of different vertebrate prey species in Amazonian forests are profoundly affected by soil fertility largely because this boosts standing population densities of game birds and large mammals (Peres 2000b). Finally, edaphic constraints on habitat productivity should be considered in regional-scale conservation planning, particularly in terms of the size of herbivore populations that can be sustained in forest polygons to be set aside as nature reserves. Yet few

community ecologists have linked soil processes to vertebrate populations and assemblages at large spatial scales in the tropics. It is to be hoped that our understanding of soil–productivity–abundance–diversity relationships will improve while they can still be unraveled in the world's remaining tracts of relatively undisturbed tropical forests.

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