Effects of Geomorphology and Primary Productivity on Amazonian Leaf Litter Herpetofauna

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ABSTRACT

The Amazon Basin, representing the largest expanse of intact tropical rain forest on the planet, harbors the largest diversity of amphibians and reptiles in the world. Limited elevation and climate differences across the Basin belie one major division of upland forests – geomorphological soil age and induced nutrient levels. We hypothesized that secondary consumers in the leaf litter herpetofauna community on ancient soils of Central Amazonia would exhibit reduced biomass compared with those found on younger soils of Western Amazonia, and that population densities on ancient soils could be driven below viable thresholds, reducing species richness. We found overall herpetofauna abundance, biomass and richness on young soils in Ecuador were significantly greater than those on ancient soils in the Brazilian Amazon. Separately, amphibians were only slightly more abundant, but their biomass on younger soils was twice that on ancient soils. Even more impressive was the variation exhibited by lizards: abundance was not significantly different, but biomass was five times greater on younger soils. Diversity of both taxa was greater on young soils. The most important driver of differences in herpetofauna biomass, abundance and possibly diversity across Amazonia may be the underlying geomorphologic differences. Reduced primary productivity on ancient soils appears to reverberate up the food chain, leaving fewer resources for higher trophic levels. We suggest that conservation initiatives must compensate for reduced biomass on ancient soils through increased reserve size, especially as forest fragmentation escalates. This study highlights the importance of including biomass as a standard measure in herpetofauna sampling.

Key words: amphibians; biomass; Brazil; Ecuador; reptiles; soil age; trophic cascade.

RELATIVE TO THE REST OF SOUTH AMERICA, the Amazon Basin appears to be a homogeneous expanse of forest, but closer observations reveal a very different picture. The geomorphology of Amazonia has shaped historical differences in productivity and composition of the lowland forests.

Across the Basin, weathering and mineralization cause leaching of soil nutrients, the extent of which is associated with the age of the soils (Sombroek 2001). Much of Central and Eastern Amazonia lies on ancient, low nutrient Oxisols (Van Wambeke 1992). These soils originated in the Guiana Shield and the Brazilian Highlands (> 300 mya) and have no remaining weatherable mineral reserves (Sombroek 2000). On the other hand, a large extent of Western Amazonia lies on much younger soils, mainly Ultisols (Valencia *et al.* 2004a), having eroded from the Andean uplift which began *ca* 30 mya and continues to this day (Gregory-Wodzicki 2000).

The paucity of available mineral nutrients in Central and Eastern Amazonia should affect primary productivity. In fact, forests in Western Amazonia have been shown to support 50 percent higher course woody productivity (Malhi *et al.* 2004) and have lower wood density (Malhi *et al.* 2006) than slow-growing forests on older soils in Central and Eastern Amazonia. Furthermore, tree turnover in Western Amazonia is twice as high as tree turnover in the Central part of the Basin (Phillips *et al.* 2004), indicating faster regeneration and higher mortality. Differences in soil age also affect floristic composition. For

example, tree species composition depends, at least in part, on soil fertility (Terborgh & Andresen 1998) and the major gradient in tree composition across Amazonia and the Guiana Shield emulates the gradient in soil age (Ter Steege *et al.* 2006). These differences in primary productivity due to soil age should cascade through higher trophic levels as well (Dyer & Letourneau 2003).

Although our understanding of tropical forest productivity has increased dramatically over the last few years, little is known about the implications of productivity on the fauna within the forests (but see Kay *et al.* 1997, Radtke *et al.* 2007, Peres 2008). Substantial data show that leaf litter herpetofauna abundance varies in rain forests across the globe (Scott 1976, Inger 1980, May 1980). Abundances of litter frogs and lizards in Central America are an order of magnitude greater than at SE Asian sites (Scott 1976, Inger 1980). Within the Neotropics, litter frog abundances in the Brazilian Amazon (Allmon 1991) may be low relative to the Peruvian Amazon and Central America (Scott 1976, Toft 1980). These results strongly suggest that plant productivity may play a crucial role in herpetofaunal biomass; however, all these studies documented numbers of individuals, but not biomass. Furthermore, sampling methodologies varied from study to study so site to site comparisons may be biased. Other research has also shown general trends of increased animal abundances in areas with younger soils (Emmons 1984, Becker *et al.* 1991, Peres & Dolman 2000), but once again, these studies compared sites differing in a number of confounding factors such as climate, disturbance, fragmentation and/or hunting pressure.

Here we investigate the effect of soil age, a known determinant of forest productivity (Malhi *et al.* 2004, Phillips *et al.* 2004, Ter Steege *et al.* 2006), on the biomass, abundance and species richness of secondary consumers in the leaf litter community of large, undisturbed tracts of wet tropical forest, using a standardized methodology for sampling herpetofauna. Moreover, we chose sites that share similar climates, the same latitude, the same elevation and limited hunting pressure.

We predict that differences in forest productivity caused by soil age will reverberate up through higher trophic levels, resulting in lower biomass and abundance of secondary consumers in the herpetofauna community on ancient soils. Biomass is a better measure of energy flow in an ecosystem than abundance, which simply reflects the raw number of individuals (Saint-Germaine *et al.* 2007). For this reason, we expect biomass to display a stronger response to differences in soil age than abundance. We also expect that reptiles may exhibit more pronounced responses to differences in soil age than amphibians. Amphibians and reptiles share similar roles in the litter ecosystem as secondary consumers. However, because most amphibians undergo an aquatic life stage, often as herbivores or omnivores, reptiles spend a larger portion of their lives as predators on the forest floor. Finally, we predict that reductions in density and biomass may push populations below minimum viable thresholds, resulting in fewer species in regions with ancient soils (Wright 1983, Evans *et al.* 2005).

METHODS

STUDY SITES.—We selected three sites on ancient soils and two sites on young soils (Sombroek 2000). The ancient soil sites are located in the reserves of the Biological Dynamics of Forest Fragments Project (BDFFP), which is a joint effort of the Instituto Nacional de Pesquisas da Amazônia and the Smithsonian Tropical Research Institute. Surrounded by several million hectares of continuous tropical lowland rain forest, the BDFFP, located *ca* 120 km north of Manaus, Brazil (2°24′ S, 59°44′ W), comprises many reserves scattered over 1000 km^2 that include both continuous forest and isolated forest fragments. We sampled continuous forest in three reserves within the BDFFP: Dimona, Cabo Frio and KM41. Cabo Frio is located in the middle, with Dimona *ca* 25 km to the west and KM41 17 km to the east. The soils underlying the area were

classified by Sombroek (2000) as Eastern Sedimentary Uplands (ESU), derived from pre-weathered crystalline parent material originating from the Guyana Shield. The ESU are well drained and contain no remaining mineral reserves (Laurance *et al.* 1999, Sombroek 2000).

The young soil sites sampled are Tiputini Biodiversity Station and Yasuní Research Station, located within or adjacent to the Yasuní Biosphere Reserve in Eastern Ecuador. Tiputini Biodiversity Station (0°37′ S, 76°10′ W) is a 650 ha reserve established in 1995 by the Universidad San Francisco de Quito and Boston University. Yasuní Research Station (0°40′ S, 76°24′ W) is managed by the Pontificia Universidad Católica de Ecuador. The two sites are located *ca* 30 km from one another and are surrounded by extensive (> 900,000 ha) continuous tropical lowland rain forest. This area was classified as Western Sedimentary Uplands by Sombroek (2000) with soils derived from the Andean Uplift. They characteristically hold much more weatherable mineral reserves and have higher cation-exchange capacities than the ESU.

Floristic composition varies among sites, but forest structure is similar with emergent trees reaching between 45 and 55 m (Laurance *et al.* 1998, Valencia *et al.* 2004b) and species richness exceeding 250 tree species ≥ 10 cm dbh/ha (Rankin-de Merona *et al.* 1992, Valencia *et al.* 1994, de Oliveira & Mori 1999). All sites are similar in latitude, elevation, rainfall and seasonality but differ in the geologic age of the soils (Table 1). Each site was sampled during its rainy season to avoid potential biases resulting from natural temporal fluctuations in herpetofauna population densities. We sampled quadrats in Ecuador from April to May 2005 and again from February to March 2006. Plots in Brazil were sampled from February to May 2007. Sampling years exhibited normal rainfall for each of the sites.

DATA COLLECTION.—We sampled a total of 465 quadrats across five primary forest terra firme sites. To establish a quadrat, we measured out a 5 × 5 m area and raked a 1 m border around it. Plot selection was haphazard and based on the following criteria: quadrats were located at least 200 m from any permanent body of water, at least 100 m from the edge of a plateau, at least 200 m from a forest edge, did not contain any excessively large trees (occupying over 1/4 of the space in the plot), and had no standing water. Within each plot, we measured eight microhabitat variables: the number of trees

TABLE 1. *Climate data for sampled sites on young (Tiputini and Yasuní) and old (BDFFP) soils.*

Site	Latitude	Elevation (m)	Temperature (°C)[a]	Rainfall (mm)	Length of rainy season (# months)	Months w/ < 100 mm precipitation[a]
BDFFP	2°24′ S	100	26	2651[a]	7[c]	0
Tiputini	0°37′ S	200	27	2740[b]	7[b]	0
Yasuní	0°40′ S	200	25	2826[a]	7[b]	0

[a]Radtke *et al.* (2007).

[b]Karubian *et al.* (2005).

[c]Gascon & Bierregaard (2001).

> 10 cm dbh, number of logs > 10 cm diam, percent canopy cover, leaf area index, litter depth, ambient temperature and humidity and elevation. These are variables traditionally measured in studies of leaf litter herpetofauna (Scott 1976, Inger 1980, Allmon 1991). Plots were searched by teams of two to four individuals. All amphibians and reptiles encountered in the quadrats, with the exception of turtles and venomous snakes, were captured by hand and placed in zip-lock bags until the plot was completely sampled. Captured individuals were identified to species and photographed from dorsal, ventral and lateral views. The snout vent length (SVL) was measured with calipers to the nearest 0.01 mm and all animals were weighed on a top-loading field balance (Ohaus Scout Pro) to the nearest 0.01 g. Individuals were released after processing. For observed individuals that escaped capture, the approximate SVL was noted and the mass was estimated using SVL/mass regression equations (Deichmann *et al.* 2008). Biomass per plot was calculated as the sum of the actual and estimated mass of all individuals encountered in the plot. We excluded only nonsecondary consumers and nonleaf litter species from the analyses.

DATA ANALYSES.—Unless otherwise noted, we used SAS 9.1.2 (Cary, North Carolina) to conduct all statistical analyses. We used multiple regression (PROC REG with stepwise selection and Akaike Information Criterion [AIC]) to test for significant effects of microhabitat variables on the abundance and biomass of herpetofauna found in the plots both for young soil sites in Ecuador and ancient soil sites in Brazil. $P < 0.15$ was used as the criterion for inclusion of independent variables in the model.

To test for differences in abundance and biomass of amphibians and reptiles, separately and combined, we used PROC MIXED. To assure no differences between sites within areas of similar soil age and to support our grouping of sites, we first tested for differences between all sites sampled by using site nested in soil age as an effect. We then tested for differences between soils of different ages. Because the territory size of most tropical leaf litter frogs and lizards is small ($< 50 \text{ m}^2$) and our quadrats were spaced at least 10 m apart, we are confident not only that all our sites are independent, but also that our quadrats represent independent samples (Schoener & Schoener 1982, Wells 2007).

We estimated species richness using Estimate S (Colwell 2006). Individual based rarefaction curves with 95% CIs were calculated for amphibians, lizards and the two groups combined.

Our hypotheses about differences in leaf litter herpetofauna between ancient and new soils are based in ecology, but if such differences exist they could simply reflect differences in phylogeographic histories of herpetofaunas of Ecuador and Brazil. We used two approaches to tease out any potential effects of phylogeny. First, we compiled species pools of all frog and lizard species that are known to inhabit the leaf litter on ancient soils in the reserves at the BDFFP and on young soils at Tiputini and Yasuní, including species we did not find in our own sample plots. Using the literature, we determined the average adult size for males and females of each species of frog, and because lizard size is less well documented, we found the average size of each lizard species irrespective of sex.

We then compared the size of frogs and lizards in the two species pools (species from young soils in Ecuador vs. ancient soils in Brazil) using a two sample Kolmogorov–Smirnov comparison. Second, we considered the average biomass contributed to the samples by genera which occur in both species pools (young soils at sites in Ecuador and ancient soils at sites in Brazil; 'in common') and those that are not common to both pools (not in common). Genus was used as the criterion for commonality instead of species because of the 54 total secondary consumer herpetofauna species encountered in litter plots on young and ancient soils, only four were common to both samples, whereas 10 of 26 genera of frogs and lizards were found in our plots on both young and ancient soils (Table S1). We used a factorial analysis of variance to test for an effect of the interaction between soil age and commonality in the biomass of frogs and lizards at sites on young and ancient soils.

RESULTS

ENVIRONMENTAL VARIABLES.—Of the eight microhabitat variables measured, canopy cover, leaf litter depth and number of trees in the quadrat best predicted reptile and amphibian abundance ($F_{3, 255} = 4.50$, $P = 0.004$). Even so, these variables account for only 5 percent of the variance in herpetofauna abundance. For young soils, elevation was the only variable that predicted abundance ($F_{1, 195} = 3.33$, $P = 0.069$), but once again, very little variance in herpetofauna abundance was explained ($R^2 = 0.017$). None of the measured microhabitat variables predicted herpetofauna biomass at either ancient or young soil sites. The multiple regression models given here were selected as the best-fit by both the stepwise and AIC selection methods.

ABUNDANCE AND BIOMASS.—Statistical analyses revealed no differences in abundance ($F_{3, 460} = 0.76$, $P = 0.520$) or biomass ($F_{3, 460} = 0.85$, $P = 0.468$) among sites within ancient or young soil regions. These results confirmed our grouping of sites within each soil region for comparison between regions.

Amphibians and reptiles were more abundant on young soils than on ancient soils ($F_{1, 460} = 7.39$, $P = 0.007$; Fig. 1). We found an average of 4.94 ± 0.75 herpetofauna/100 m^2 (mean $\pm$ 95% CI) at ancient soil sites and 6.38 ± 0.96 at young sites. Separately, amphibians were less abundant on ancient soils (3.88 ± 0.62) than on young soils (5.20 ± 0.78; $F_{1, 460} = 8.70$, $P = 0.003$). Lizard abundance was not different between ancient and young soils (1.03 ± 0.27 and 1.06 ± 0.33, respectively; $F_{1, 460} = 0.00$, $P = 0.996$).

The biomass of litter herpetofauna was greater on young soils ($11.4 \pm 3.8 \text{ g}/100 \text{ m}^2$) than on ancient soils ($4.25 \pm 1.84 \text{ g}/100 \text{ m}^2$; $F_{1, 460} = 37.0$, $P < 0.001$). Amphibians had more than twice as much biomass on young soils as on ancient soils (9.83 ± 3.77 and $3.99 \pm 1.85 \text{ g}/100 \text{ m}^2$, respectively; $F_{1, 460} = 26.8$, $P < 0.001$). Lizard biomass on young soils greatly exceeded that on ancient soils (1.41 ± 0.85 and $0.27 \pm 0.17 \text{ g}/100 \text{ m}^2$, respectively; $F_{1, 460} = 16.72$, $P < 0.001$).

SPECIES RICHNESS.—Species accumulation curves showed significantly greater richness at young soil sites, with no overlap of 95%
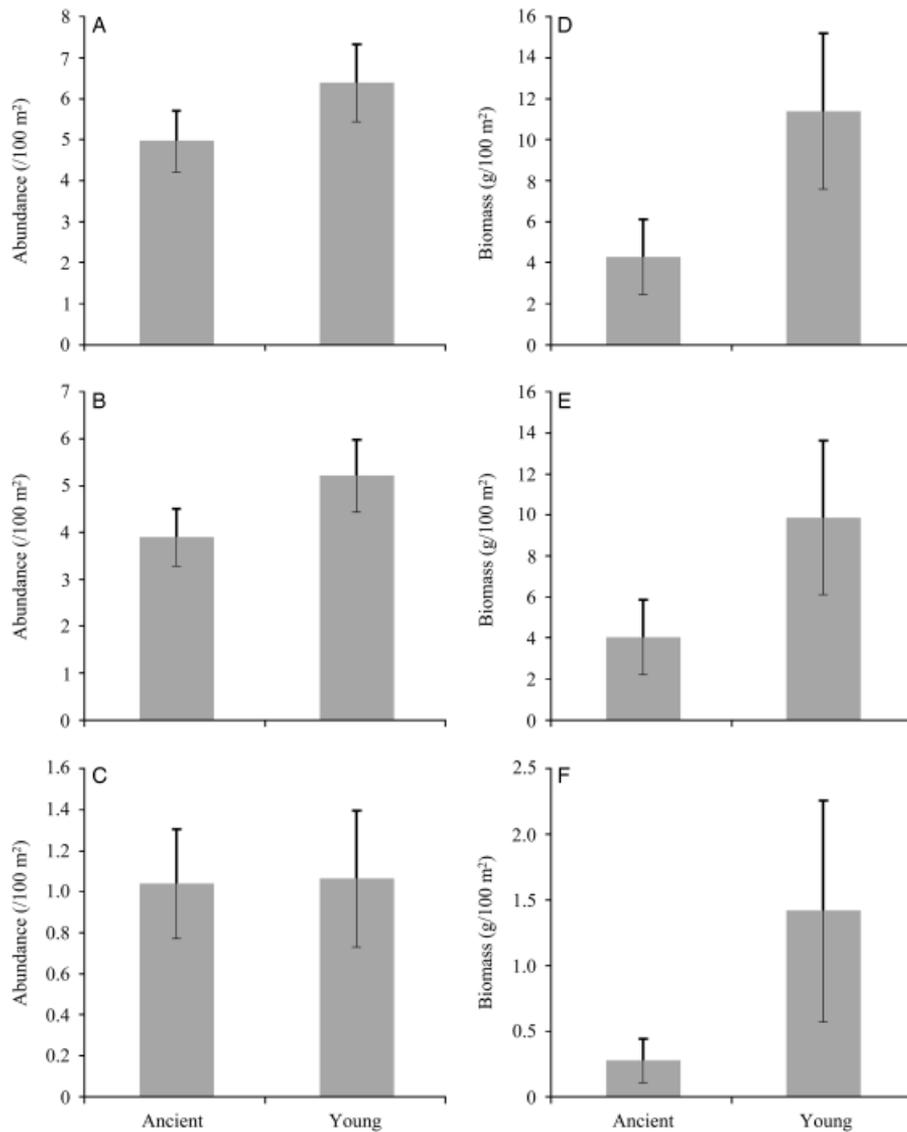
FIGURE 1. For secondary consumers, abundance of (A) all reptiles and amphibians, (B) only amphibians and (C) only lizards and biomass of (D) all reptiles and amphibians, (E) only amphibians and (F) only lizards on ancient and young soils. Error bars represent 95% CIs.

CIs, for overall herpetofauna as well as amphibians and lizards separately (Fig. 2).

PHYLOGEOGRAPHIC CONSIDERATION.—We found no significant differences in literature-derived size distributions of male or female frogs from the species pool at our sites on young soils in Ecuador and the pool on ancient soils in Brazil (males: $P = 0.694$; females: $P = 0.909$), nor did we find significant differences in literature-derived lizard size distributions ($P = 0.793$). We also confirmed that the size of the individuals we encountered in our samples did not differ appreciably from the sizes reported in the literature. Finally, we found no effect of the interaction between soil age and commonality of genera on frog biomass ($F_{1,925} = 1.85$, $P = 0.175$) or lizard biomass ($F_{1,925} = 2.06$, $P = 0.152$).

DISCUSSION

Sites on young soils support higher biomass, abundance and species richness within the leaf litter herpetofauna community than sites on ancient soils. The measured microhabitat variables did not play a role in determining the community differences displayed in these regions. Appropriate models show independent variables explained only 5 percent of the variation in abundance on ancient soils and 2 percent of abundance on young soils. Furthermore, no combination of the measured environmental variables explained the differences in biomass at ancient or young soil sites. This result is no surprise given that they rarely prove to be good predictors of herpetofauna densities, despite being measured in most litter plot studies (e.g., Fauth et al. 1989, Whitfield & Pierce 2005). This study is the first to demonstrate that soil age is a much better
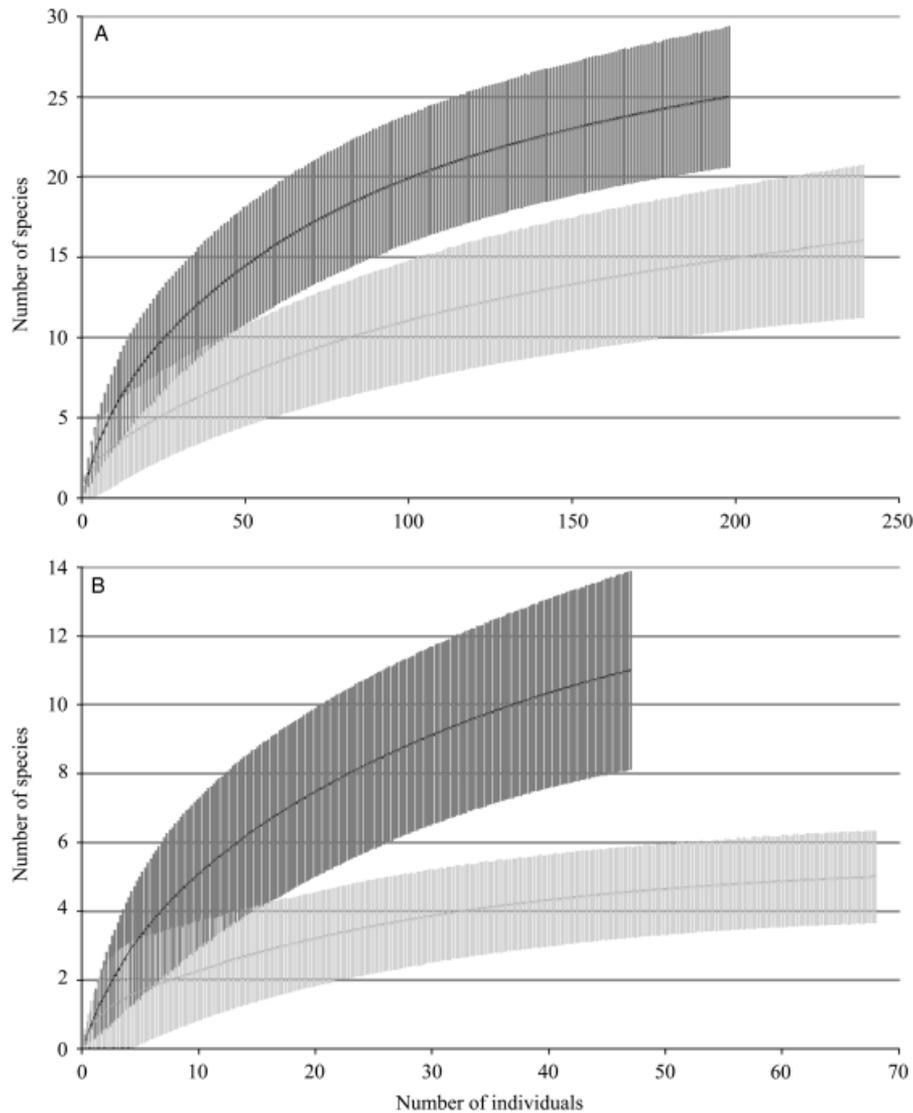
FIGURE 2. Rarefaction curves with 95% CIs for (A) amphibians and (B) lizards encountered in quadrats from young soils (black lines) and ancient soils (gray lines).

predictor of the leaf litter herpetofauna community than the microhabitat variables at the scale of our study.

A number of hypotheses have been put forth to explain the well-documented differences in leaf litter herpetofauna abundances between Central America and SE Asia (Scott 1976, Inger 1980). Some of these pose potential alternatives to our productivity hypothesis. For example, perhaps an increased number of predators or competitors in Brazil relative to Ecuador could explain lowered herpetofauna abundances on ancient soils. Another alternative hypothesis is that increased accumulation of leaf litter at the Ecuadorian sites could lead to higher herpetofauna densities through augmented habitat structure for shelter and oviposition sites. Although both these hypotheses may provide reasonable explanations for the differences between SE Asian and Central American litter herpetofauna abundances, they do not explain the differences seen in our study. For example, we found more snakes on young soils, although the number of snakes was low at all sites.

Similarly, spider abundances were greater in plots on young soils (J. L. Deichmann, unpubl. data). These data indicate that predator and competitor densities are likely higher in Ecuador, and therefore cannot account for the herpetofauna differences on young and ancient soils. Furthermore, we found no difference in depth of litter in Ecuador and Brazil, providing no basis for increased habitat structure on young soils.

Primary productivity differences between the ancient and young soils have come to light in recent studies on forest dynamics (Malhi et al. 2004, Phillips et al. 2004, Ter Steege et al. 2006), thus confirming Sombroek's (2000) view that the ancient soils of the Amazon are extremely poor in weatherable minerals. Such a difference at the base of the food chain portends differences at higher trophic levels, but how such differences are mediated is unknown. We propose two mechanisms by which energy is transferred up the food chain, thereby influencing leaf litter herpetofauna abundance and biomass. First, the allocation of energy by plants to growth and

reproduction is nonlinear. Where productivity is limited, reproduction may be minimal or delayed until sufficient resources have been accumulated. In contrast, where productivity is enhanced, there may be a disproportionate shift toward reproduction as the needs of growth have all been met and excess production is channeled into flowers and fruits. It is the flowers, fruits and seeds that provide the most nutritious resources for herbivores and subsequently, consumers of herbivores. The actual differences in 'productivity' recorded in recent studies of forest dynamics across the Amazon were measured as differences in vegetative growth without regard for reproductive effort. Quite probably, differences in production of flowers and fruits could have been even more exaggerated. For example, Kaspari *et al.* (2008) recently reported no increase in litter fall of leaves and twigs, but a 43 percent increase in reproductive litter from a long-term soil fertilization experiment in Panama.

Second, declines in primary productivity may result in local extinction of species at higher trophic levels. If so, then a given percent decline in primary production may trigger a greater decline in secondary production. The relationship between productivity and species richness is largely unexplored in tropical taxa; however, such bottom-up effects imply that large vertebrates with small population sizes may be subject to extirpation where productivity reduces population density below a viable minimum threshold (Wright 1983). Within the conservative parameters of 95% CIs (Payton *et al.* 2003), our data illustrate a striking difference in species richness of secondary consumers (frogs and lizards) between sites of differing productivity. Therefore, even at this lower trophic level, the difference in productivity generated species richness differences. Data comparisons for primates (Kay *et al.* 1997, Peres & Dolman 2000), mammals (Emmons 1984) and fishes (Henderson & Crampton 1997), all also strongly suggest that reduced primary productivity in the Central and Eastern Amazon causes declines in species richness, although these studies failed to control for confounding site factors. Here we used standardized measurements of litter herpetofauna biomass with a common methodology in undisturbed primary forest tracts of at least a million hectares that share a comparable climate, the sites differing primarily in landform, as defined by Sombroek (2000).

A plausible alternative to our hypothesis that differences in primary productivity drive species richness differences in leaf litter herpetofauna between ancient and young soil sites is that proximity to the Andes of the western Amazonian sites drives up species richness through refugia and speciation (Haffer 1969, Vanzolini 1970). The Andes are considered an area of active speciation (Fjeldsa 1994), and as such, may provide a species source to the proximal Amazonian lowlands, which could explain species richness differences across the Basin. Cohn-Haft *et al.* (1997), however, found that once habitat heterogeneity differences were accounted for, bird species richness did not differ between western and central Amazonia. We were careful not to sample across habitat types, yet still found higher species richness at young soils sites.

In the only other study to use standardized methodology in a comparison of fauna on ancient vs. young soils, Radtke *et al.* (2007) found no difference in species richness of dung beetles between

Ecuador and Brazil. However, dung beetle biomass, which is a proxy for mammal biomass, exhibited a threefold increase on young soils (Radtke *et al.* 2007). A recent meta-analysis of primate biomass over a range of Amazonian soil fertilities confirmed a fivefold increase between the least and most fertile soil sites examined (Peres 2008). If dung beetles (detritivores), primates (herbivores and omnivores) and leaf litter herpetofauna (insectivores) are all affected by differences in soil fertility, then primary productivity imposes control on the biomass of many guilds across multiple trophic levels.

While the biomass of amphibians on young soils was twice that on ancient soils, lizard biomass was nearly five times greater on young soils. This difference in response strength may reflect ontogenetic differences in these taxa with lizards spending their entire lives dependent on the leaf litter ecosystem, whereas many amphibians do not begin their lives feeding in the litter. Tropical frogs use a variety of habitats for reproduction that temperate frogs do not (Duellman & Trueb 1986). Just a few of these include the use of arboreal phytotelmata, creation of terrestrial foam nests with nonfeeding tadpoles, and terrestrial or arboreal nests with direct developing eggs (Crump 1971, Duellman & Trueb 1986, Hödl 1990). Among tadpoles that do feed, some are carnivorous or oophagous, but most tropical larval anurans are herbivorous, feeding primarily on algae and detritus in the water column (Dutra & Callisto 2005). Consequently, tadpole survival is generally independent of litter arthropods on the forest floor.

Overall herpetofauna biomass was nearly three times greater on young soils, far exceeding the difference exhibited by abundance. Biomass reflects energy movement through a system and is more responsive to plant productivity than raw numbers of individuals. For this reason, it should be no surprise that biomass demonstrates a stronger response to differences in soil age than abundance. This phenomenon is even more pronounced in lizards, which showed no difference in abundance, but greatly increased biomass on young soils. The majority of the aforementioned studies showing trends of increased densities on younger soils focused on differences in abundance and disregarded biomass. Our study suggests that important community differences may be overlooked when focusing exclusively on abundance and that the noted differences may be even more drastic when biomass is taken into account.

We cannot ignore the possibility that the biomass variation seen within the leaf litter herpetofauna community may be due to phylogeography. Our analyses, however, suggest that although the species pools differ at sites on ancient and young soils, there is no difference in the size distributions from these pools and hence, no phylogenetic constraints on size. Frog and lizard species on ancient soils in Brazil attain the same SVL as species on young soils in Ecuador, as evidenced by size data from the literature. Additionally, the average biomass contributed to our actual sample by in-common and not-in-common frog and lizard genera to the total biomass sample is consistent between countries, suggesting again that phylogeny is not a confounding factor in this study.

Biomass and productivity are often neglected components of conservation ecology because their roles in species preservation and community dynamics remain clouded. Our results, however, clearly imply that proportionally larger tracts of land on ancient

soils of Amazonia may be required to maintain biomass and abundance of herpetofauna comparable to smaller tracts of land in the young Amazon. This area effect will become exaggerated as forest fragmentation intensifies: for a given sized fragment there will be lower population sizes on ancient Amazonian soils than on young ones. Therefore, reduced productivity is equivalent to smaller fragment sizes in that population sizes are reduced. Likewise, vertebrate territory sizes may be larger on less productive soils, as shown for Amazonian birds (Stouffer 2007). Increased territories or home ranges may lead to increased extinctions if vertebrates suffer mortality at the edges of reserves (Woodroffe & Ginsberg 1998). Such large-scale edge effects have been postulated by Laurance (2000) and demonstrated for large cats and pigs in Malaysia (Ickes & Williamson 2000). Clearly, extreme variation in productivity needs to be incorporated into the conservation equation in order to develop practical and responsible management of litter herpetofauna as well as other vertebrates in the Amazon Basin.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Abundance and biomass of each species found in litter plots at sites on young soils in Ecuador and ancient soils in Brazil.*

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