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Early recruitment responses to interactions between frequent fires, nutrients, and herbivory in the southern Amazon

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Abstract Understanding tropical forest diversity is a long-standing challenge in ecology. With global change, it has become increasingly important to understand how anthropogenic and natural factors interact to determine diversity. Anthropogenic increases in fire frequency are among the global change variables affecting forest diversity and functioning, and seasonally dry forest of the southern Amazon is among the ecosystems most affected by such pressures. Studying how fire will impact forests in this region is therefore important for understanding ecosystem functioning and for designing effective conservation action. We report the results of an experiment in which we manipulated fire, nutrient availability, and herbivory. We measured the effects of these interacting factors on the regenerative capacity of the ecotone between humid Amazon forest and Brazilian savanna. Regeneration density, diversity, and community composition were severely altered by fire. Additions of P and N + P reduced losses of density and richness in the first year post-fire. Herbivory was most important just after germination. Diversity was positively correlated with herbivory in unburned forest, likely because fire reduced the number of reproductive individuals. This contrasts with earlier results from the same study system in which herbivory was related to increased diversity after fire. We documented a significant effect of fire frequency; diversity in triennially burned forest was more similar to that in unburned than in annually burned forest, and the community composition of triennially burned forest was intermediate between unburned and annually burned areas. Preventing frequent fires will therefore help reduce losses in diversity in the southern Amazon's matrix of human-altered landscapes.

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Introduction

Diversity in tropical forests exceeds by several times that of temperate forests (Longman and Jeník 1974), and anthropogenic global change is affecting the interactions that generate diversity in tropical forests (Tylianakis et al. 2008) before they are fully understood. Among the most important of these global change variables in dry tropical forests is increasing fire frequency resulting from agricultural burning and stronger and more frequent droughts (Cochrane and Laurance 2002; Moreira de Araújo et al. 2012; Wooster et al. 2012).

As fire frequency is increasing in the tropics, it is important to understand its interactions with other factors related to forest diversity, such as nutrients and herbivory (Fine et al. 2004; Laurance et al. 2010; Terborgh 2012), which can also be altered by fire. Soil nutrient availability has been shown to be strongly correlated with both alpha (Bartels and Chen 2010; Laurance et al. 2010) and beta (Gentry 1988; Pitman et al. 2008; Fine et al. 2010) diversity in mature tropical forests. P is considered the most limiting resource for plant growth in the Amazon (Vitousek 1984), and large amounts of P and N are lost with repeated fires (Kauffman et al. 1995). Frequent fire may therefore affect diversity in tropical forests by reducing plant growth and recruitment due to reduced nutrient availability.

Changes in nutrients and fire both interact with herbivory, which has been shown to be important in determining tropical forest diversity (Dyer et al. 2010; Swamy and Terborgh 2010; Alvarez-Loayza and Terborgh 2011). The Janzen-Connell hypothesis postulates that herbivores create patterns of negative density dependence by selectively feeding on aggregated groups of conspecific seeds or seedlings (Janzen 1970; Connell 1971). Herbivores, however, may affect diversity differently in burned and intact forests depending on the interacting species and availability of recruits (Massad et al. 2013). Herbivores also respond to changes in nutrient conditions, generally by increasing consumption when soil nutrient availability is enhanced (Massad and Dyer 2010; Santiago et al. 2012). Changes in herbivory after fire may also be due to an increased abundance of herbivores after burning (Fredericksen and Fredericksen 2002; Carvalho 2008).

Understanding the effect of changes in fire activity is particularly important in the cerrado (savanna) and seasonally dry forests of Brazil. Over the last decade, pervasive forest clearing using fire in this area has led to substantial burned-over forest fragments (Moreira de Araújo et al. 2012). From 1999 to 2010, the amount of understory area

that burned within 500 m of a deforestation event ranged from 25 to 46 % during years with high deforestation rates (Morton et al. 2013). Models suggest that fire amplifies edge effects in fragmented forest, accelerating degradation more rapidly than expected from fragmentation alone (Cumming et al. 2012). The Xingu River headwaters region of Brazil that surrounds the present study site encompasses many of these factors. The region naturally comprises Amazon rainforest, cerrado, and transitional forest between them. High deforestation rates in this region are driven by the conversion of forest to vast soybean farms and cattle ranches (Stickler et al. 2009). Models indicate that a continuation of business-as-usual land-use change in the region, coupled with climate change, will lead to an estimated 140 % increase in area burned by 2050 (Soares-Filho et al. 2012). Fire frequency is also increasing in other regions of the Amazon, and areas that burned once are more likely to suffer from additional fires in the future (Alencar et al. 2011). Understanding the effects of increased fire frequency in this diverse and threatened region will therefore contribute to conservation and improved understanding of ecological interactions under global change.

Fire can change the composition and diversity of forests by altering interactions among nutrients, herbivores, and seedlings. We examined the effects of these factors in a field experiment in which we manipulated fire, nutrient availability, and herbivory. We assessed the impact of these variables on woody species' regeneration and survival, diversity, and community composition. The results reported here build on long-term research in the area, testing the hypothesis that repeated fires may push forests to a tipping point beyond which they are converted to savanna-like ecosystems (Balch et al. 2008, 2011; Brando et al. 2012; Massad et al. 2013). This work extends the findings of Massad et al. (2013) which reported on regeneration during the first 6 months of seedling establishment after repeated fire. In that work we found a combination of P or N additions following fire and herbivory led to increased diversity. To assess the robustness of these results, we expanded the experiment to capture a full year of recruitment after another experimental burn and to compare the effects of fire frequency on early forest recovery.

We tested the following hypotheses:

1. Fire frequency (annual versus triennial burns) changes recruitment, species diversity, and community composition.
2. Nutrient additions can offset the negative effects of frequent fire on regeneration by replacing N and P typically lost after burning.
3. Herbivory enhances diversity, particularly in burned forest with nutrient additions because seedlings grow more vigorously and are thus more apparent to

herbivores. These seedlings may therefore suffer greater herbivore-driven mortality and be replaced by recruits of other species.

4. Herbivory intensifies the negative effect of fire on the composition of recruiting communities, so that communities suffering from fire and herbivory will be less similar to undisturbed communities.

Materials and methods

Study site

This work took place in seasonally dry forest on the Fazenda Tanguro in the southern Amazon in Mato Grosso, Brazil (13°04′35.39″S, 52°23′08.85″W). The fazenda comprises 30,000 ha of soy fields and 50,000 ha of preserved forest. The ecosystem forms the transition between the cerrado and Amazon rainforest. Most species produce fruits between November and January. Soils at the site are infertile Oxisols. The study area was divided into three 500 × 1,000-m plots that border soy fields on their northern sides and extend 1 km into the forest. The cerrado begins about 20 km south of the fazenda [see Balch et al. (2008) for an extensive description of the site and more details on how the controlled burns were conducted].

Experimental design

The results presented here are from a long-term, large-scale burn experiment designed to examine the effects of fire on multiple aspects of forest functioning (Balch et al. 2008). Controlled burns were conducted annually in the western-most 50-ha plot between 2004 and 2010 with the exception of 2008. The center plot has been burned every 3 years since 2004 (2004, 2007, and 2010). The eastern plot is unburned. Fires were set every year at the end of the dry season (August). During experimental burns, flame heights, which reflect fire intensity (Rothermel and Deeming 1980), varied between 25 and 38 cm in the annually burned plot.

In March 2009, we added a fertilization treatment to the experiment. Subplots (30 × 40 m) were placed 500 or 750 m from the forest edge in the control and annually burned plots. Three subplots received 100 kg N ha^{-1} (urea), three received 50 kg P ha^{-1} (superphosphate), and three received both N and P in the same amounts as in the single nutrient subplots. The same nutrient additions produced marked differences in tree growth on Oxisols in Amazonian secondary forest (Davidson et al. 2004). An additional three subplots served as unfertilized controls. Fertilizer was added to these subplots again in April and October 2009 and directly after the controlled burn in September 2010. This resulted in a total of 12 nutrient treatment subplots

in both the unburned and burned areas (Supplementary Fig. 1).

In February 2010, an additional treatment was added to test for interactions between annual fire, nutrient availability, and herbivory on regeneration. Paired plots (2 × 1 m) were located in each fertilizer by burn treatment plot; one excluded all crawling herbivores and the other (control) allowed herbivore access. The exclosures were made of 75-cm-high transparent plastic walls buried 10 cm into the soil and painted with a strip of glue to keep crawling insects from feeding on regeneration inside the plots. There was one set of paired regeneration plots in each of the 12 nutrient plots in the unburned and annually burned areas. Light intensity inside and outside the plots was measured with a LI-COR 250 light meter, and light did not differ statistically (paired t-test, $P = 0.3$). Plots were removed from the burned area in August 2010 prior to the final fire treatment and then immediately replaced. Three additional sets of plots (open/closed to herbivores) were set up in the triennially burned area at the time of peak germination in February 2011 to measure the effects of fire frequency and herbivory on regeneration.

All seedlings and sprouts (hereafter collectively termed "regenerating stems") that were observed after the August 2010 fire were tagged and identified to species or morphospecies and censused in November 2010, February 2011, and August 2011. Analyses did not separate seedlings from sprouts (see Balch et al. 2013 for an analysis of seedling vs. sprout regeneration in the study site). Height, basal diameter, leaf area, and percent herbivory were measured on all regenerating stems at each sampling date. Leaf area and herbivory were measured using transparent grids with 0.25-cm^2 cells. Percent herbivory was calculated as the amount of leaf area lost to herbivores divided by the total leaf area (area present plus area consumed). When entire leaves were missing but the petiole was still present, the average area of the leaves directly above and below the missing leaf was used to estimate herbivore damage. If seedlings had more than 30 leaves, an average of ten leaves was used for these calculations.

Data analysis

Regeneration density, species richness, the Shannon-Wiener index (H'), and Simpson's index (D) were analyzed with split-split plot repeated-measures analyses of covariance starting with fully crossed mixed models examining the interacting effects of annual fire, nutrient additions, and percent herbivory as fixed effects; time was also included as a fixed effect. Lower values of D indicate greater community evenness. Split-split plot analyses were used because the fire treatment was not replicated at the 50-ha scale. The repeated measurements included data from February, the

time of peak germination, and August, the end of the dry season and the end of the experiment. Because animals and falling trees often damaged the regeneration plots, plot-level log-transformed percent herbivory values were included as a covariate rather than using the exclosures as a categorical treatment. The fertilizer subplots and the regeneration plots were included as random effects in the analysis; interactions between random effects and sampling dates were tested and maintained when significant. Non-significant interactions were removed when they did not significantly change the fit of the model. Models were run using the lmer function in R and proc mixed in SAS (SAS/STAT 9.1). The significance of removing terms from the model was determined by comparing hierarchical models with the ANOVA function in R; individual terms were selected for removal based on their F- and P-values calculated in SAS. Denominator df for these calculations were estimated using the Satterthwaite approximation in SAS. All response variables except H' were log transformed for normality. Significant contrasts in least squares means (LSM) between levels in significant interactions were determined with SAS proc glimmix's slicediff function with a Bonferroni correction. The slicediff function calculates differences in one factor of an interaction while holding other factors constant (SAS/STAT 9.2).

Similarly, models were constructed to compare all three levels of the burn treatment and the herbivory treatment. These models included only the plots without fertilizer in the control and annually burned areas because the triennially burned site did not receive fertilizer. D, species richness, and abundance were log transformed for normality. Best-fit models are presented.

Community similarity was compared between annually burned and unburned plots with and without herbivore exclosures in February and August of 2010 using the Morisita similarity index (MSI) for comparisons between multiple communities. Morphospecies were omitted (see Supplementary Information for details). The three levels of the burn treatment were likewise compared for community similarity. The data were bootstrapped 200 times (Chao et al. 2008). Analyses were performed using SPADE (Chao and Shen 2010).

Regeneration survival between February and August was evaluated using stepwise selection logistic regressions including the fire and fertilizer treatments, early herbivory (in February; log transformed), recruit size in February (log-transformed height and basal diameter), and plot-level density and diversity (based on H' and D) as possible predictors. Variables significant at the 0.05-level were maintained. The best-fit model had the lowest Akaike information criteria score, and the model's fit is described by the Hosmer–Lemeshow goodness-of-fit test. These analyses were performed in SAS (SAS/STAT 9.1).

Results

Overall, the number of regenerating stems and all diversity metrics point to greater and more diverse recruitment in unburned, unfertilized plots. Heavy losses in the number and richness of recruits occurred over the dry season in both burned and unburned forest. There were no clear rescue effects associated with nutrient additions, although richness losses over time were less severe in burned forest where P or N + P were added, and evenness increased slightly in August in plots with N or P. Early herbivory (at the time of peak germination) had strong negative effects on the numbers of recruits and on richness, and it was related to an increase in species evenness in unburned but not burned forest. Specific responses are described below.

Herbivory

Herbivore exclosures limited herbivory overall, but their effect was not consistent due to damage to several of the exclosures. Herbivory was consistently higher in the burned area (12.5 ± 2.6 %) than in the unburned area (5.5 ± 1.5 %; Supplementary Table 1). Examination of the unfertilized plots in all three levels of the burn treatment showed herbivory was highest in the triennially burned forest (17.7 ± 3.0 %), followed by the annually burned forest (11.0 ± 4.0 %) and the unburned forest (3.3 ± 1.3 %; Supplementary Table 2).

Comparisons between annually burned and unburned forest, nutrient additions, and herbivory

Recruitment

At the time of peak germination, recruitment was higher in the unburned plots. By the end of the dry season, the difference in the number of recruits in unburned and burned forest only persisted in unfertilized plots. More recruits survived in unfertilized plots in both the burned and unburned areas (burned area = 7 ± 3.7, unburned area = 29.2 ± 12.0; Table 1; Fig. 1a), but the fertilizer effect was only significant in unburned plots (all LSM contrasts unburned/unfertilized–unburned/fertilized, $P < 0.01$; all burned/unfertilized–burned/fertilized, $P > 0.1$). Recruits were lost from burned and unburned forest as seedlings passed through the dry season, although the loss was not significant in burned plots with N + P or P additions. Early herbivory in February (the time of peak germination) significantly limited recruitment while herbivory just 6 months later was less strongly correlated with recruitment (Fig. 1c).

Table 1 Results of mixed-model ANOVA showing the effects of burning, herbivory, nutrient additions, and time on recruitment, species richness, and two measures of diversity

	Recruitment (AIC = 203.7, −2 LL = 149.7)			Species richness (AIC = 114.9, −2 LL = 76.9)			Shannon-Wiener index (AIC = 156.0, −2 LL = 110.0)			Simpson's index (AIC = 141.0, −2 LL = 93.0)		
	F	df	P	F	df	P	F	df	P	F	df	P
Burn treatment	33.7	1/50.8	****	36.4	1/47.2	****	29.5	1/43.5	****	14.2	1/64.9	0.0004
Percent herbivory	10.5	1/75.9	0.002	4.5	1/75.1	0.04	4.9	1/79.5	0.03	4.6	1/50	0.04
Nutrient treatment	4.6	3/80.6	0.005	4.9	3/43.9	0.005	3.6	3/77.4	0.02	0.8	3/58.6	0.5
time	6.9	1/71.9	0.01	37.9	1/38.2	****	18.4	1/37.9	****	4.6	1/58.3	0.04
Burn × nutrient	0.9	3/50.5	0.4	0.6	3/44	0.6	0.2	3/43.2	0.9	1.8	3/57.7	0.2
Burn × time	5.1	1/52	0.03	9.9	1/40.8	0.003	8.4	1/42.4	0.006	_a	_a	_a
Burn × herbivory	_a	_a	_a	_a	_a	_a	_a	_a	_a	19.0	1/52	****
Nutrient × time	4.5	3/71.5	0.006	0.2	3/39.1	0.9	0.9	3/37.2	0.4	3.5	3/34.7	0.03
Nutrient × herbivory	0.5	3/74.4	0.7	_a	_a	_a	2.1	3/77.2	0.1	4.7	3/53.1	0.006
Time × herbivory	0.2	1/73.3	0.7	_a	_a	_a	_a	_a	_a	6.0	1/60.1	0.02
Nutrient × time × herbivory	4.6	3/72.7	0.005	_a	_a	_a	_a	_a	_a	_a	_a	_a
Burn × nutrient × herbivory	_a	_a	_a	_a	_a	_a	_a	_a	_a	3.6	3/51.7	0.02
Burn × nutrient × time	3.0	3/49.6	0.04	4.4	3/39.2	0.009	3.9	3/39.7	0.02	_a	_a	_a

df were estimated using the Satterthwaite approximation in SAS

AIC Akaike information criterion, *LL* log likelihood

**** $P \leq 0.0001$

[a] Interactions without statistics in final, best-fit models

Diversity

Species richness declined the least in unburned, unfertilized plots between peak germination and the end of the dry season (just two species were lost; Table 1). These plots also had the highest average species richness at the end of the experiment (7.5 ± 1.1; LSM contrasts of unburned/unfertilized plots with all other treatment combinations, $P \leq 0.01$). Nutrient additions did not help maintain richness in unburned plots. Similar to the numbers of recruits, in the burned area species richness declined the least through the dry season where N + P or P were added. However, in burned plots the highest overall richness occurred in unfertilized subplots (Fig. 1b). Herbivory was significant as a main effect, and average richness declined as herbivory increased across plots (Fig. 1d).

H' was highest at the time of peak germination and declined over the course of the dry season (Table 1). H' was 1.0 ± 0.15 in the unburned area but just 0.63 ± 0.13 in the burned site at the end of the experiment. Herbivory was negatively correlated with H' (Fig. 2a), and by the end of the dry season nutrients had no effect on H' in burned or unburned forest (Fig. 2b; Supplementary Fig. 2).

Fire reduced community evenness (D). Evenness increased with herbivory in the burned forest but tended to decrease with herbivory in unburned forest (Table 1). A significant interaction between burning, nutrients, and herbivory showed decreased evenness in burned plots with herbivory, although less so where P was added. In contrast, evenness increased the most with herbivory where P was added in unburned plots, suggesting herbivory was most strongly related to increased evenness when P was present (Fig. 3a, b; note a decrease in D signifies an increase in evenness). Early herbivory again had the most important effect, with an overall positive correlation between evenness and herbivory (Fig. 3c).

In sum, fire, herbivory, and nutrients interacted to affect recruitment and diversity in multiple ways. Overall, fire reduced recruitment and diversity. Many recruits were lost over the course of the dry season in both burned and unburned forest. Early herbivory, at the time of peak germination, had the strongest negative effects on recruitment and diversity. Herbivory was negatively related to evenness in burned forest but positively related to evenness in unburned forest. Nutrients did not have consistent effects across response variables, but fewer recruits and species were lost from the burned forest during the dry season when P or N + P were added to the plots.

Community composition in annually burned and unburned forest

Beyond changes in richness and diversity, the composition of the communities recruiting in unburned and burned plots
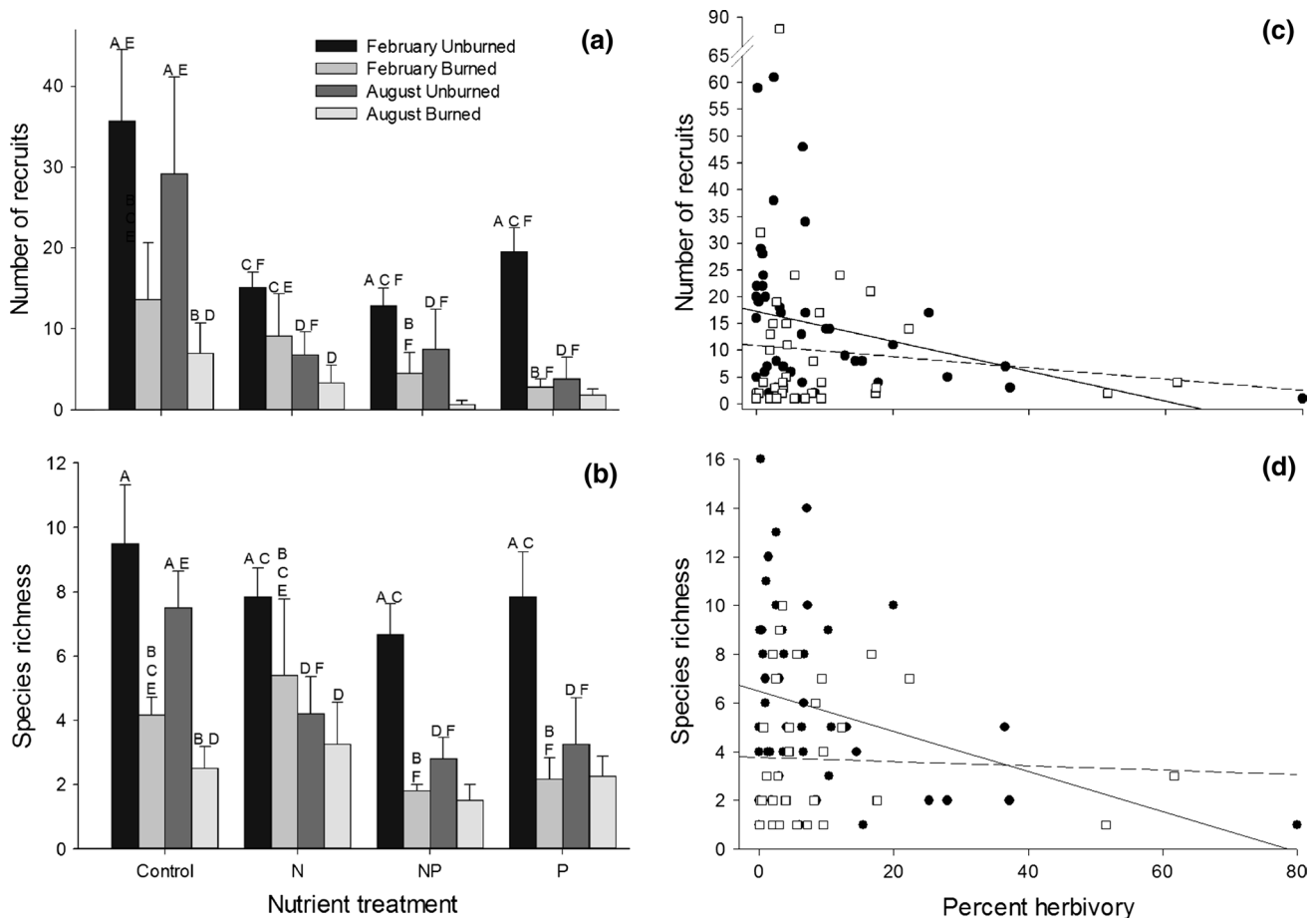
Fig. 1 Effects of fire and nutrients on **a** the number of recruits and **b** species richness in February (the time of peak germination) and August. *Bars* show mean ± SE (*n* = 6). *Letters above the bars* indicate significant differences between least squares means determined by Bonferroni corrected contrasts (A–B = differences between fire regimes, C–D = differences between February and August, E–F = differences between nutrient additions). Relationships between plot-level herbivory and **c** the number of recruits and **d** species richness at the time of peak germination (February) and August in unburned and burned plots combined

differed dramatically, and the presence of herbivores also contributed to these differences. The MSI was calculated to compare community composition between burned and unburned forest with and without herbivores at the time of peak germination and at the end of the dry season. The overall similarity value was low (0.42 ± 0.02 SE). At the time of peak germination communities were quite similar, but differences were already apparent between burned and unburned forest, and the effects of herbivores were also apparent in burned forest. By the end of the dry season, recruiting communities in burned and unburned forest were distinct (pairwise comparisons <0.15), and this difference was even stronger in burned forest when herbivore presence was manipulated (Supplementary Table 3).

The effect of herbivores is related to the loss of dominant species in burned forest. For example, eight species were lost between February and August in plots open to herbivores, and one of these was the most dominant

species in February, *Amaioua guianensis* (Rubiaceae). In herbivores exclosures, there was a loss of six species over time, and these did not include the most abundant species. In addition, by the end of the dry season, the most abundant species in the burned, open plots was represented by three individuals, whereas the most abundant species in the burned, closed plots had 23 individuals (*A. guianensis*).

Effects of fire frequency

These analyses compare all three levels of the fire treatment and include only unfertilized plots from the annually burned and control areas because no fertilizer treatment was applied in the triennially burned site. Unburned plots had the highest recruitment (29.2 ± 12.0) and species richness (7.5 ± 1.2) followed by triennially burned (recruitment = 13.2 ± 3.8, richness = 5.8 ± 1.5) and finally annually burned (recruitment = 7.0 ± 3.7, richness = 2.5 ± 0.7)
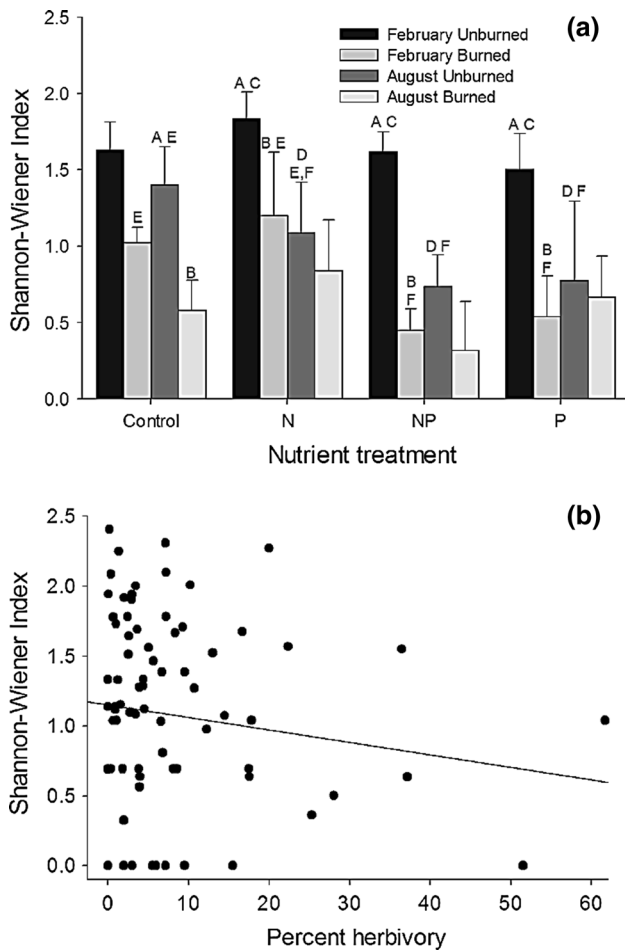
Fig. 2 Effects of fire and nutrients on **a** Shannon-Wiener index values in February (the time of peak germination) and August. *Different letters* indicating significant differences among treatments are as in Fig. 1. **b** Overall relationship between plot-level herbivory and the Shannon-Wiener index

plots. Herbivory was not significant in any of these analyses (Table 2).

D did not differ with fire or herbivory, but H' was significantly affected by fire (Table 2). The unburned area and the area burned every 3 years had similar levels of H' (1.4 ± 0.2 and 1.3 ± 0.2, respectively), but the annually burned area had less than half those values (0.6 ± 0.2).

Community composition in annually burned, triennially burned, and control forest

When final community composition was compared across the three levels of the fire treatment (herbivory was not included because it was not significant in other analyses), large differences were detected (MSI $= 0.07 \pm 0.04$ SE). Triennially burned forest was intermediate in similarity relative to the unburned and annually burned plots (Supplementary Table 4). Some of the same, very common species
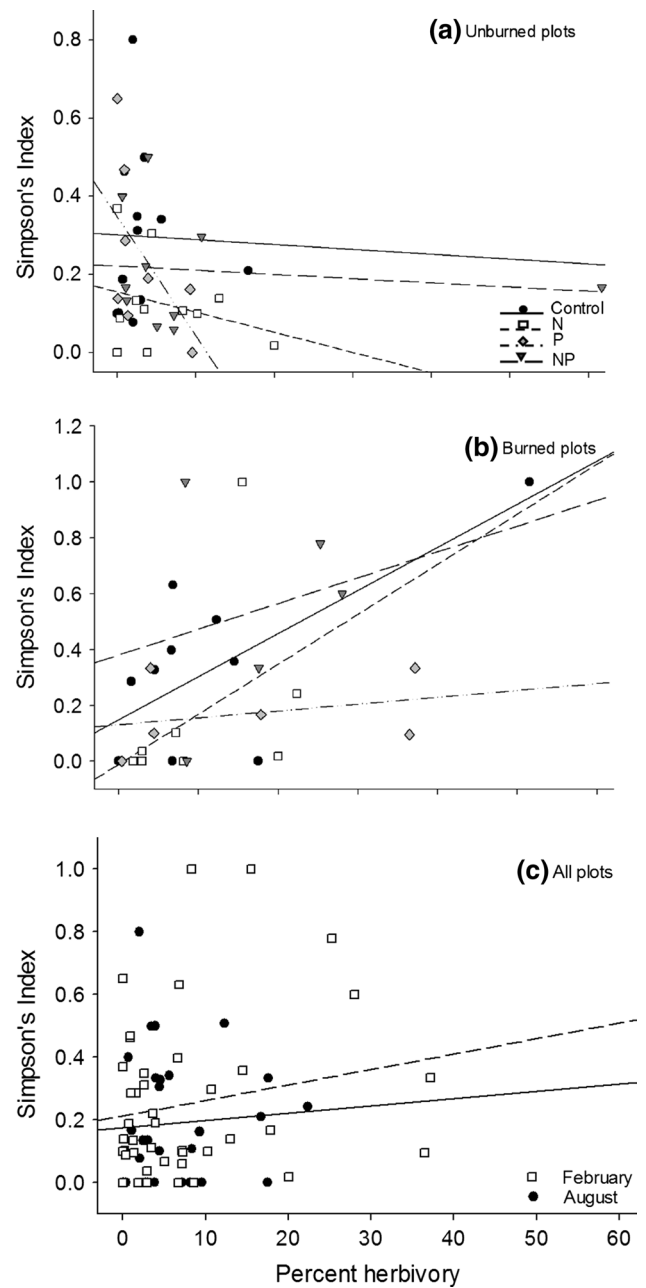
Fig. 3 Response of Simpson's index to fire, nutrient additions, and herbivory in **a** unburned forest and **b** burned forest. **c** Effects of early (February) and later (August) herbivory on Simpson's index

were found across levels of the fire treatment, such as the liana, *Hippocratea* sp. (Hippocrateaceae), and the trees, *Protium guianense* and *Trattinnickia* spp. (Bursuraceae). In terms of differences, many lianas were lost from the frequently burned area; eight species of lianas were identified in the unburned forest, six were found in the triennially burned forest, and only two were present in the annually burned forest. A greater percentage of species was represented by just one individual in burned forest; 50 %

herbivory did not increase diversity in the burned area, indicating the dynamic nature of relationships between insect herbivores and the composition of regenerating communities. For Janzen-Connell effects on richness or H' to manifest themselves, herbivore-related seedling mortality of common species should be accompanied by recruitment of rare species [community compensatory effect (Connell et al. 1984)]. In August 2010, evidence suggested this could be happening in burned forest where H' increased with herbivory and D decreased (indicating both a greater contribution of rare species to diversity and higher evenness). In 2011, herbivory was instead negatively correlated with evenness in burned forest. This result emphasizes several important points. First, the ability of herbivores to increase diversity depends on local conditions, which vary with time. An increase in H' was detected in burned forest in 2010 likely because there was a sufficient diversity of species to recruit into burned plots. In 2011, this was not the case, and overall richness was in fact reduced (richness in burned plots in August 2010 = 3.0 ± 0.5, richness in burned plots in August 2011 = 1.7 ± 0.4).

It is also important to note that positive relationships between herbivory and diversity are based on more than the number of recruiting species. Community composition also mediates the relationship between herbivory and diversity, and the selectivity of herbivores as well as the tolerance of seedlings to herbivory influence the herbivory-diversity relationship (Jactel and Brockerhoff 2007; Barton 2013; Loranger et al. 2014).

Lastly, the total amount of herbivory was not responsible for differences in results in burned forest over time. Herbivory in burned plots averaged 12.5 % in 2010 and 13.5 % in 2011. Herbivory was higher in unburned forest in 2011 (8.9 vs. 5.5 % in 2010), however, which may partly account for the appearance of a positive correlation between herbivory and species evenness there. Similar to the variable effects of herbivory on diversity recorded in this work, patterns of negative density dependence also changed over time in seedling communities recovering from a hurricane (Comita et al. 2009).

Multiple factors affected seedling survival. First, an increase in mortality in plots with higher seedling densities during the peak germination period indicates competition may limit survival in this forest. A separate logistic regression analyzing survival in only the unburned plots further showed mortality increased with recruit density in February (unpublished results). This contrasts with work concluding interspecific competition is not important for seedling survival in other tropical forests (Paine et al. 2008; Alvarez-Loayza and Terborgh 2011). The length and severity of the dry season at our study site distinguishes it from these other forests, indicating competition may become important for tropical seedlings when moisture is scarce. Plot diversity was related

to increased seedling survival, which suggests having heterospecific neighbors is beneficial, fitting with the resource concentration hypothesis (Tahvanainen and Root 1972; Barbosa et al. 2009). Another useful result was the consistent finding that early herbivory had the strongest effects on survival, richness, and diversity. Measuring herbivory in the weeks following germination may therefore best elucidate the role that herbivores play in shaping forest diversity.

As communities are redesigned by climate and land use, species interactions will both respond to (Stireman et al. 2005; Menendez et al. 2008; Tylianakis et al. 2008; de Sassi et al. 2012) and interact with abiotic factors to influence community composition and diversity (Massad et al. 2013). More integrative studies are therefore needed to accurately understand ecosystem responses to global change as abiotic and biotic drivers will not operate in isolation.

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