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Herbivory and habitat association of tree seedlings in lowland evergreen rainforest on white-sand and terra-firme in the upper Rio Negro

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Background: It has been proposed that the interaction between herbivory and soil nutrient availability drives habitat association of tree species in Peruvian Amazonia. Nevertheless, there is no empirical evidence that this interaction holds across other Amazonian regions.
Aims: We address this knowledge gap by testing whether the interaction between herbivory and soil nutrient contributes to habitat association of tree species in white-sand and terra-firme forests in the upper Rio Negro, Brazil.
Methods: We conducted a reciprocal transplanting field experiment in which we controlled for the presence of herbivores. We tested for differences in tree-seedling growth and herbivory among seven white-sand and seven terra-firme habitat-specialist species. Additionally, we assessed whether tree seedlings differed in their functional traits.
Results: We found no empirical evidence that an interaction between herbivory and soil nutrients shapes habitat association in white-sand and terra-firme forests of the upper Rio Negro. Tree seedlings showed higher mortality when growing in their non-typical habitat. Growth and herbivory were similar regardless of the presence or absence of herbivore protection and type of soil.
Conclusions: We suggest that the overall differences in soil nutrient status between white-sand and terra-firme forests in the upper Rio Negro are insufficient to trigger an interaction between herbivory and soil nutrient availability.

Keywords: Amazonia; interaction between herbivory and soil nutrient availability; habitat association of trees; herbivory; seedling traits; terra-firme forests; tree seedlings; upper Rio Negro; white-sand forests

Introduction

Amazonian rainforests harbour the Earth's most diverse tree communities. The beta-diversity of these tree communities, i.e. the change in tree species composition across space, is partially driven by the association of tree species with distinct habitats (Phillips et al. 2003). This habitat association of tree species results from long-term species' adaptation to the physical conditions of their habitats as well as the interactions among co-existing species. Recent research has shown that habitat association of tree species can be determined by an interaction between resource availability and herbivory. Fine et al. (2004, 2006) showed that habitat-specialist species developed growth and defence strategies that were tightly linked to the differing resource availability in their typical habitat. For instance, low soil nutrient availability may favour tree species that grow slowly and invest in herbivore defence, whereas habitats with high soil nutrient availability may support the occurrence of tree species that are fast growing while investing little in herbivore defence (Wright and Westoby 1999).

Habitat association of tree species is a well-known feature in the white-sand and terra-firme forests of Amazonia (Fanshawe 1952; Anderson 1981; Dezzeo et al. 2000; ter Steege et al. 2000; Boubli 2002; Stropp et al. 2011). White-sand forests grow on non-flooded extremely nutrient-poor sandy soils, and host tree communities that differ in their species composition from those found on nutrient-richer clayey soils in terra-firme. Habitat association of tree species in these two forests has been explained by the physiological adaptation of species to soil nutrient and water availability as well as to soil acidity (Cuevas and Medina 1988; ter Steege 2000; Baraloto et al. 2006; Luizão et al. 2007). In addition to soil properties, an interaction between soil nutrients and herbivory has been proposed to reinforce habitat association of tree species in these forests (Fine et al. 2004, 2006). By conducting a reciprocal transplanting field experiment, these authors found that seedlings of tree species associated with terra-firme forests, when protected from herbivores and planted in white-sand soils, grew faster than seedlings of tree species associated with white-sand forests. Fine et al. (2004, 2006) provided empirical support for the resource-availability hypothesis (Coley et al. 1985) and suggested that the link between resource availability, plant growth and herbivore defence was a major factor that drove habitat association in white-sand and terra-firme forests in Peruvian Amazonia, hereafter referred to as western Amazonia. However, no additional field experiments to test if the resource-availability hypothesis explained habitat association of tree species in white-sand and

terra-firme forests have been carried out in other regions of Amazonia.

We investigated if an interaction between soil nutrient availability and herbivory contributed to habitat association of seven white-sand and seven terra-firme tree species in the upper Rio Negro, north-western Amazonas State, Brazil. This region harbours the largest area of white-sand soils in Amazonia (Quesada et al. 2011). We assessed tree seedling mortality, growth and herbivore damage as well as seedling functional traits in a reciprocal transplanting field experiment. We addressed the following questions and the corresponding predictions:

(1) Do tree seedlings of white-sand and terra-firme species show differences in mortality when transplanted into their non-typical soil type? We expected seedlings to show higher mortality when growing in their non-typical soil type, thus showing habitat association.

(2) Do tree seedlings of white-sand and terra-firme species differ in their relative height growth rate (RHGR), relative leaf area growth rate (RLAGR), herbivore damage and physical defence against herbivores (analysed as leaf punch strength (LPS)) when transplanted to their non-typical soil type? Following the resource-availability hypothesis, we expected that seedlings of white-sand species would show a conservative growth strategy and thus a lower growth rate than terra-firme species on both soil types. By contrast, we expected terra-firme species to show higher growth rates than white-sand species on both soil types when protected from herbivores (Fine et al. 2004). Furthermore, we predicted that white-sand species would suffer less herbivore damage than terra-firme species in both habitats due to their higher investment in anti-herbivore defence.

(3) Do tree seedlings of white-sand and terra-firme species differ in their functional traits? Seedling functional traits are indicative of the growth and

defence strategy of tree species. Typically, species growing in habitats with limited resources tend to share functional traits, which reflect slow growth, such as long-lived and tough leaves. If resource availability increases, species tend to share traits, which mirror fast growth, e.g. high leaf turnover and high specific leaf area. We expected that white-sand and terra-firme species would differ in their functional traits, indicating adaptations to soil nutrient availability. We hypothesised that white-sand species would show traits that indicated slow growth and high investment in anti-herbivore defence, caused by the low soil nutrient availability of their typical habitat (see Wright et al. 2004). If this hypothesis held, one would expect that terra-firme species would have, for instance, a higher leaf nutrient concentration and lower LPS than white-sand species (Table 1).

Materials and methods

Study site

The research was carried out on non-flooded areas of the 'Terra Indígena do Alto Rio Negro' (1.52° N; 68.66° W), along the middle Içana River, north-western Amazonia, Brazil (hereafter referred to as upper Rio Negro). In this region, soils of white-sand (podzols) and terra-firme (ferrasols) derive from the weathering of crystalline Precambrian bed rocks ca. 2500 Ma BP (Bezerra et al. 1976); these soils can be considered extremely nutrient poor (Quesada et al. 2011). White-sand forests on sandy podzols occurring in non-flooded areas dominate the vegetation of our study site and occur alongside terra-firme forests, which are present on non-flooded areas of ferrasols (Cabalzar and Ricardo 2006). Previous tree inventories indicated little overlap in tree species composition between the two forest types (Abraão et al. 2008; Stropp et al. 2011). The climate is aseasonal with mean annual precipitation of 3000 mm and a mean monthly precipitation >100 mm in all months of the year (Sombroek 2001).

Table 1.   Functional traits, their role in plant growth and prediction according to the habitat of the species investigated in the upper Rio Negro, Brazil.

Traits	Abbreviation	Unit	Role	Prediction
Leaf area	LA	cm^2	Resource capture	High in terra-firme
Specific leaf area	SLA	$cm^2\,g^{-1}$	Resource capture	High in terra-firme
Leaf area ratio	LAR	$cm^2\,g^{-1}$	Resource capture	High in terra-firme
Leaf mass fraction	LMF	$g\,g^{-1}$	Resource capture and defence	Uncertain
Leaf punch strength	LPS	$N\,mm^{-2}$	Defence	High in white-sand
Leaf nitrogen concentration	LNC	$mg\,g^{-1}$	Resource capture	High in terra-firme
Leaf phosphorus concentration	LPC	$mg\,g^{-1}$	Resource capture	High in terra-firme
Leaf potassium concentration	LKC	$mg\,g^{-1}$	Resource capture	High in terra-firme
Root length	RL	cm	Resource capture	High in white-sand
Root mass fraction	RMF	$g\,g^{-1}$	Resource capture	Uncertain
Root:shoot ratio	RS		Resource capture	Uncertain
Stem density	SD	$g\,cm^{-3}$	Stem transport, structure and defence	High in white-sand
Stem mass fraction	SMF	$g\,g^{-1}$	Structure	High in white-sand
Total seedling biomass	BIOM	g		Uncertain

Study species

We selected first-year tree seedlings of seven white-sand and seven terra-firme habitat specialists, hereafter referred to as white-sand species and terra-firme species, respectively. The selection of habitat-specialist species was based on (1) species lists from tree inventories carried out in the upper Rio Negro (Dezzeo et al. 2000; Boubli 2002; Abraão et al. 2008; Stropp et al. 2011) and (2) advice from local indigenous experts (Table S1). When collecting seedlings in their original habitat, we found adult trees and seedlings of *Chamaecrista adiantifolia* (Spruce ex Benth.) H.S. Irwin & Barneby (Fabaceae), *Macrolobium angustifolium* (Benth.) R.S. Cowan (Fabaceae), *Aspidosperma araracanga* Marcondes-Ferreira (Apocynaceae), *Scleronema* cf. *micranthum* (Ducke) Ducke (Malvaceae), *Haploclathra* cf. *paniculata* (Mart.) Benth. (Clusiaceae) and *Micrandra sprucei* (Müll. Arg.) R.E. Schultes (Euphorbiaceae) only in white-sand forests; whereas adult trees and seedlings of *Eperua purpurea* Benth. were found in both forest types, but with a much higher abundance in white-sand forests. For the terra-firme habitat-specialist species, adult trees and seedlings of *Clathrotropis macrocarpa* Ducke (Fabaceae), *Monopteryx uaucu* Spruce ex Benth. (Fabaceae)*, Swartzia* cf. *tomentifera* (Ducke) Ducke (Fabaceae)*, Tetragastris panamensis* (Engl.) Kuntze (Burseraceae), *Virola calophylla* (Spruce) Warb. (Myristicaceae) and *Micropholis guyanensis* (A. DC.) Pierre (Sapotaceae) were only found in terra-firme forests, while *Mouriri ficoides* Morley (Melastomataceae) was found in both forest types but with a higher abundance in terra-firme forests. The number of selected species belonging to Fabaceae reflects their higher abundance in the study area as compared to other families (57% in white-sand and 35% in terra-firme forests (ter Steege et al. 2006; Stropp et al. 2011)). We refrained from restricting our selection to pairs of co-generic species partially because, as indicated by previous botanical inventories, it is rare to have co-generic species that are habitat specialists in white-sand or terra-firme forests in the upper Rio Negro. When they occur, species have a low abundance, making it difficult to find a sufficient number of seedlings. Controlling for co-generic species, and thus phylogeny, would have therefore substantially reduced the number of suitable species for our study. Our choice of species implies that both species history and present-day ecology contribute to explaining our results (see Westoby 1995).

Our criteria for identifying first-year tree seedlings were: (1) absence of leaf scars on the seedling stem and (2) indications of recent masting on the harvest sites (e.g. seed and/or fruit still remaining on the ground). We selected seedlings of a similar developmental stage and collected a maximum of seven seedlings per mother tree. We collected approximately 750 seedlings from June to July 2007. Before starting the experiment, we kept the seedlings in plastic nursery bags filled with soil from their typical forest type. The bags were placed with a minimum distance of 30 cm from each other on the forest floor of their typical forest type, without any protection against herbivores, for up to four weeks.

Experimental design and implementation

We selected 20 sites, 10 of which were located in white-sand forests and 10 in terra-firme forests with similar light conditions. The minimum and maximum distance between the sites was 0.3 km and 9 km, respectively. At each of the 20 sites, we established a paired plot: one protected from insect herbivores (protected plots) and one unprotected control plot. Protected plots consisted of cages of $3 \times 3 \times 2$ m (length, width, height) completely covered with nylon mosquito net ($\varnothing = 1$ mm). The unprotected plots were composed of cages of the same dimensions as the protected plots but with the mosquito net covering only the top in order to create similar light conditions as in the protected plots. Because we were interested in the effect of only insect herbivores on plant performance, we laterally covered the unprotected plots with wire mesh ($\varnothing = 5$ cm), thereby avoiding damage from medium and large mammal herbivores, e.g. Dasyproctiae, Cervidae and *Tapirus terrestris*. At each site, the protected and unprotected plots were located ca. 5 m apart from each other. All litterfall and lichens growing on the nylon netting were removed every second week during the experiment. In total, 560 seedlings were transplanted (14 species (seven white-sand species and seven terra-firme species) × two soil types (sandy white-sand podzols and clayey terra-firme ferrasols) × two herbivore treatments (protected and unprotected) × 10 replicates per soil type). One seedling for each of the 14 species was planted in each plot. Before transplanting the seedlings, we carefully removed soil matter from the roots of the seedlings. Seedlings were placed in all the plots following the same sequence at a distance of 0.5 m from each other. During the experiment, plots of one site located in white-sand forests had its mosquito net removed. We excluded this site from the analysis. One month after the transplanting, seedling mortality was 6% (i.e. 32 out of 532 seedlings of the nine plots retained for analysis (560 minus 14 seedlings of the excluded site). As we did not replace these seedlings, our analysis considers 500 tree seedlings. We set up the experiment in June 2007 and harvested the seedlings in August 2008.

Light and soil measurements

We quantified the canopy openness of the 20 sites by taking four hemispherical photographs of the canopy for each plot (eight per site) using a camera with a fish-eye lens. The photographs were taken once at the end of the experiment. The camera was placed perpendicularly to the forest floor with a fixed orientation to the north. Afterwards, we estimated the percentage of canopy openness using WinPhot version 5.0 (ter Steege 1986, Tropenbos-Guyana Programme, Guyana).

Table 2.   Mean and standard errors of the content of sand, silt, clay, total phosphorus, nitrogen and carbon as well as canopy openness of nine white-sand and 10 terra-firme sites in the upper Rio Negro, Brazil.

Parameter	White-sand Mean ± SE	Terra-firme Mean ± SE	Df	Soil type effect		Block effect	
				F	P	F	P
Sand (g kg^{-1})	947 ± 3	744 ± 3	1	0.33	0.6	0.33	0.6
Silt (g kg^{-1})	34.5 ± 2.5	89.1 ± 1.4	1	0.01	0.9	0.01	0.9
Clay (g kg^{-1})	18.9 ± 0.6	166.5 ± 3.1	1	0.46	0.5	0.46	0.5
Phosphorus (mg kg^{-1})	7.5 ± 1.4	54.4 ± 6.7	1	2.62	0.12	2.62	0.12
Nitrogen (mg g^{-1})	0.4 ± 0.1	1.1 ± 0.1	1	0.48	0.5	0.48	0.5
Carbon (mg g^{-1})	6.6 ± 1.0	16.2 ± 1.3	1	0.43	0.52	0.43	0.52
Canopy openness (%)	8.2 ± 2.7	7.8 ± 2.6	1			0.72	0.4

Sand = 0.05–2.00 mm, silt = 0.002–0.05 mm, clay <0.002 mm. F and *P* values are from analysis of variance. SE: standard deviation; df: degrees of freedom.

We collected soil samples from all 19 sites included in our analysis. Each soil sample was composed of eight soil cores (four from protected and four from unprotected plots), collected to a depth of 30 cm after removing the litter layer. Soil samples were oven-dried at 80 °C for 12 h before being transported to the laboratory. We determined the soil texture of the white-sand and terra-firme sites (Table 2). Soil samples were also analysed for their total soil phosphorus content by digestion with H_2SO_4 + H_2O_2 (Tiessen and Moir 1993); nitrogen and carbon were determined in an automated C/N analyser (Vario Max, Elementar Instruments, Germany). Drying soil samples at 80 °C may cause losses of nitrogen due to volatilisation. This methodological shortcoming does not affect the comparisons between soils of white-sand and terra-firme forests. However, caution is needed when comparing the values presented here with values presented elsewhere. All soil samples were analysed at the Instituto Nacional de Pesquisas da Amazonia (INPA), Brazil (see Quesada et al. 2010 for a more detailed description). We applied an ANOVA to assess the effect of soil type and block on the environmental variables (canopy openness, soil texture and soil nutrient) (Table 2).

Tree seedling measurements

One month after the experiment had been set up (July 2007) we measured the number of surviving seedlings, stem height, total leaf area and total leaf damage of the 560 seedlings. We regarded these measurements as the initial conditions (t_0). After 13 months (August 2008, t_1), we harvested the seedlings and measured the same parameters as at the beginning.

To calculate total leaf area and total leaf damage at t_0 and t_1, we took photographs of fresh leaves placed over a flat white board with a 0.5 × 0.5 cm grid. Afterwards, total leaf area and total leaf damage were calculated by digitising the contour of each leaf and, if present, the damaged or missing areas. We calculated leaf area with the program Image J (version 1.38 (Rasband 2007)). To calculate total leaf area, we summed up the area of individual leaves attached to each seedling. Based on measurements

of stem height and leaf area, we calculated the RHGR and the RLAGR as follows:

$$RHGR = \frac{\ln S_{t_1} - \ln S_{t_0}}{\Delta t} \qquad (1)$$

$$RLAGR = \frac{\ln LA_{t_1} - \ln LA_{t_0}}{\Delta t} \qquad (2)$$

where *S* represents the stem height (cm), *LA* represents the total leaf area (cm^2) and Δt the duration of the experiment in number of days ($t_1 - t_0$).

We calculated the proportional damage for each seedling by dividing the total area of leaf damage at t_1 by the total leaf area at t_1.

After harvesting in August 2008, we dissected each seedling into roots, stem, petioles, leaves and cotyledons, if present. Based on the fresh material, we measured the length of the main root (RL), stem volume and LPS. We calculated stem volume as:

$$V = \frac{\pi L}{12} \left(D_{top}^2 + D_{top} D_{base} + D_{base}^2 \right) \qquad (3)$$

where *V* represents stem volume, *L* stands for stem length (cm), D_{top} for the diameter at the top of the stem just under the growth meristem and D_{base} for the diameter at the base of the stem just above the root. We measured LPS (N mm^{-2}) of three fresh leaves of every seedling by using a field penetrometer. The field penetrometer consisted of a needle with a flat tip of 4.98 mm^2 attached to a plastic Erlenmeyer flask. The needle was held straight by a plastic casing connected to a tripod. A leaf was placed between two acrylic plates, both containing a 6 mm diameter hole. The holes were positioned exactly above each other, creating an opening for the needle to touch the leaf (see Aranwela et al. 1999; Onoda et al. 2011). We calculated the LPS based on the volume of water in the Erlenmeyer flask necessary to penetrate a leaf. We considered the average LPS of three leaves of each individual seedling as one observation (Cornelissen et al. 2003).

After conducting the measurements on the fresh material, all seedlings were dried in a field oven at ca. 80 °C for

48 h on the same day they were harvested. In the laboratory, they were re-dried in an oven at 60 °C for 48 h. Dry weight of total roots, stem, petioles, leaves and cotyledons, if present, were used to determine the biomass of each section and of the total seedling. Additionally, we determined the nitrogen, phosphorus and potassium concentration of the leaves with a continuous flow analyser (Skalar, the Netherlands) after Kjeldahl digestion.

We calculated the specific leaf area (SLA: leaf area per unit of dry leaf mass), leaf area ratio (LAR: leaf area per unit of dry plant mass), leaf, stem as well as root mass fractions (LMF, SMF, RMF: leaf, stem and root dry mass per unit of dry plant mass, respectively) and stem density (SD: dry stem mass per unit of stem volume). All traits were calculated for individual seedlings. In total, we analysed 14 morphological traits, which were considered to respond to the nutrient availability of the habitat and/or to tolerance to herbivore damage.

Statistical analyses

Tree seedling performance. We estimated the probability of a seedling dying as a function of treatment, i.e. herbivory, soil type and species origin, and interaction between treatments by applying a general linear mixed model (GLMM) considering the binomial distribution of the response variable. We included species identity as a random effect nested within species origin. We backwards eliminated the terms and interactions that were non-significant in the original model. For the GLMM, we used the function lmer of the R package lme4 (R Development Core Team 2011; Bates et al. 2012). We attempted to apply a GLMM to analyse the effect of treatment and interaction between treatments on RHGR, RLAGR, proportional damage and LPS; this nonetheless proved to be inappropriate because the response variables did not fit gamma or Gaussian distributions. We therefore conducted a permutation test for factorial analysis of variance (ANOVA). This permutation test has the disadvantage of not considering species identity as a random effect nested within species origin. We think that the permutation test is more appropriate than GLMM because it would reduce the chance of committing a type I error, as we do not assume a specific distribution of the response variable. For the permutation test for factorial ANOVA, we averaged the values of the response variable of individual species in each treatment. This test was carried out as follows: we first calculated the F value observed for each treatment or interaction between treatments ($F_{observed}$) by carrying out an ordinary factorial ANOVA. Afterwards, we randomised each response variable 5000 times and calculated the F value based on the randomisation ($F_{randomised}$). We finally calculated the P value as the proportion of $F_{randomised}$ exceeding $F_{observed}$. Each response variable was analysed separately. For the permutation test for factorial ANOVA, we adapted the R script presented by Howell (2009). We performed a Levene's test to assess if variances between groups were homogenous using the function leveneTest of the R package Rcmdr.

Functional traits. We arcsine-transformed proportional traits such as LMF, SMF and RMF. The remaining traits were $\log_{10}$-transformed to assure normality. We tested for differences in the functional traits of tree seedlings of white-sand and terra-firme species with a mixed-effect model using the function lme of the R package nlme (Bates et al. 2012). For this, we considered species identity as a random factor. We averaged the values of each response variable (i.e. 14 seedling traits) of individual species. Because we were interested in assessing if habitat-specialist species differed in their functional traits, we included in this analysis only those traits of seedlings growing on their typical soil type without herbivore protection. Finally, we assessed the correlation between the seedling traits with a Pearson correlation analysis by applying the function rcor.test available in the R package ltm (Rizoupolos 2006).

For *Chamaecrista adiantifolia* it was not possible to measure RLAGH, LPS, leaf area and leaf damage due its small leaflets; we therefore only include this species in the analysis of mortality.

Results

Light and soil

Canopy openness was similar between white-sand and terra-firme sites (Table 2). During the course of the experiment, we did not observe gap formation that could have affected the light regime of the experimental plots. Soil texture and soil nutrients differed between white-sand and terra-firme plots (Table 2). We found no block effect on canopy openness, soil texture and soil nutrients (Table 2).

Tree seedling performance

Seedling mortality one month after establishing the experiment (8.6%) might be attributed to damage during transplanting as we found no significant effect of soil type, protection or interaction between soil type and species origin. Considering the deaths recorded between t_0 and t_1, we found that seedlings showed higher probability of mortality when growing in their non-typical soil type (origin × soil; intercept = –2.15, $P < 0.001$; Figure 1). For this period, total seedling mortality reached 13% (67 out of 500). *Monopteryx uaucu* and *Tetragastris panamensis* (terra-firme origin) showed the highest mortality when growing in white-sand forests (44% and 41% respectively). The term 'protection' and its interaction with other terms were excluded from the original model because they did not contribute to explain mortality (protection; intercept ∼0, $P = 0.34$).

We found a generally low and similar RHGR, RLAGR, proportional damage and LPS (Tables 3 and 4). Considering individual seedlings, proportional damage by herbivores ranged from 0 to 0.2 (Table S2). Overall, 41% of the seedlings suffered no herbivore damage during the 13 months of the experiment.
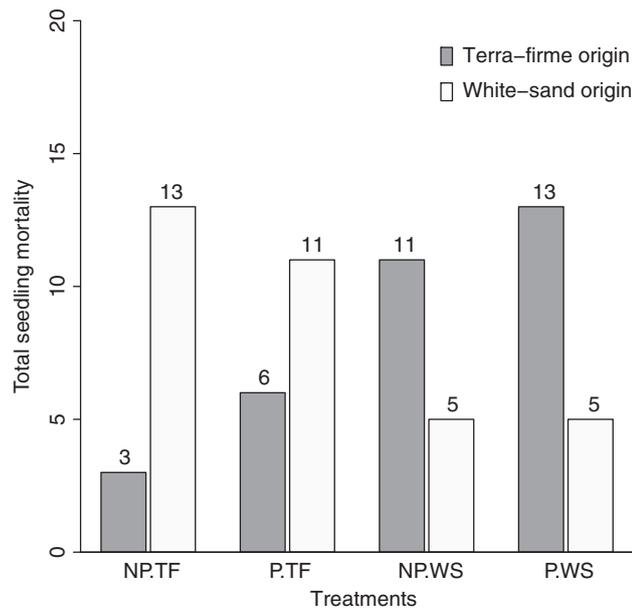
Figure 1. Total seedling mortality of white-sand and terra-firme habitat-specialist species in different treatments after 13 months. Seedlings growing in their non-typical soil type showed a higher probability of mortality than seedlings growing on their typical soil type (species origin × soil; intercept = –2.15, $P < 0.001$). Numbers represent the total seedling mortality observed in each treatment. Labels on the x-axis represent experimental treatments. TF: terra-firme; WS: white-sand; NP: non-protected; P: protected from insect herbivory.

Functional traits

The analysis using a mixed-effect model showed that terra-firme species had a slightly higher, and statistically significant, leaf area ratio than white-sand species. All the remaining 13 functional traits were similar between white-sand and terra-firme species (Table 5).

Table 5. Summary of the results of the mixed model with species identity as random factor.

Traits	F	P	Mean (WS)	SD	Mean (TF)	SD
LA	0.80	0.38	74.37	54.10	120.16	95.37
SLA	1.30	0.28	178.75	28.27	200.02	38.29
LAR	**5.74**	**0.03**	43.57	11.74	63.70	16.04
LMF	3.49	0.08	0.25	0.06	0.33	0.08
LPS	0.50	0.49	0.66	0.10	0.62	0.16
LNC	3.99	0.07	15.24	2.04	22.37	8.30
LPC	0.03	0.86	0.83	0.21	0.85	0.35
LKC	0.08	0.78	6.66	2.77	5.76	1.38
RL	0.11	0.73	17.58	7.71	16.30	8.52
RMF	1.36	0.26	0.33	0.11	0.26	0.09
RS	0.15	0.70	0.82	0.30	0.75	0.22
SD	0.35	0.56	0.12	0.03	0.13	0.02
SMF	0.20	0.65	0.36	0.12	0.34	0.06
BIOM	0.03	0.85	0.83	0.21	0.85	0.35

Mean and standard deviation (SD) of absolute values of functional trait of white-sand (WS) and terra-firme (TF) habitat-specialist tree seedlings includes only seedlings growing in their original soil type and without protection from insect herbivory ($n = 47$ and 57, respectively). Significant results are given in bold. For full trait names see Table 1.

Table 3. Mean and standard deviation of relative height growth rate (RHGR), relative leaf area growth rate (RLAGR), proportional damage and leaf punch strength (LPS) of seedlings investigated in a cross-transplant experiment in the upper Rio Negro, Brazil.

Parameter	Species origin	White-sand		Terra-firme	
		Unprotected	Protected	Unprotected	Protected
RHGR (cm cm^{-1} day^{-1})	WS	0.011 ± 0.009	0.014 ± 0.015	0.012 ± 0.010	0.01 ± 0.007
RLAGH (cm^2 cm^{-2} day^{-1})	WS	0.002 ± 0.002	0.002 ± 0.001	0.003 ± 0.005	0.002 ± 0.002
Proportional damage	WS	0.033 ± 0.036	0.022 ± 0.017	0.032 ± 0.028	0.018 ± 0.014
LPS (N mm^{-2})	WS	0.666 ± 0.108	0.674 ± 0.099	0.614 ± 0.093	0.631 ± 0.085
RHGR (cm cm^{-1} day^{-1})	TF	0.01 ± 0.01	0.01 ± 0.01	0.009 ± 0.004	0.014 ± 0.011
RLAGH (cm^2 cm^{-2} day^{-1})	TF	0.002 ± 0.001	0.001 ± 0.001	0.002 ± 0.001	0.002 ± 0.003
Proportional damage	TF	0.027 ± 0.027	0.021 ± 0.029	0.019 ± 0.015	0.022 ± 0.020
LPS (N mm^{-2})	TF	0.635 ± 0.137	0.674 ± 0.167	0.641 ± 0.175	0.617 ± 0.155

WS: white-sand; TF: terra-firme.

Table 4. Results of the permutation test for factorial analysis of variance.

Effect	RHGR		RLAGR		Damage		LPS	
	F_{obs}	P	F_{obs}	P	F_{obs}	P	F_{obs}	P
Species origin	1.20	0.28	1.08	0.33	0.08	0.78	0.28	0.59
Soil	0.24	0.69	0.51	0.51	0.10	0.75	1.04	0.30
Protection	0.14	0.71	0.07	0.82	1.71	0.20	0.04	0.83
Species origin × soil	1.33	0.25	0.01	0.97	0.04	0.82	0.10	0.74
Species origin × protection	0.17	0.69	0.53	0.50	0.35	0.55	0.01	0.90
Soil × protection	0.09	0.75	0.01	0.92	0.08	0.78	0.10	0.73
Soil × protection × species origin	0.85	0.35	0.54	0.49	0.31	0.56	0.16	0.69

RHGR: relative height growth rate; RLAGR: relative leaf area growth rate; LPS: leaf punch strength; F_{obs}: observed F-statistic for each effect; P: proportion of permutations giving an F-value equal to or greater than that observed.

We found 11 significant correlations among seedling traits (Table S3). LPS, for instance, was negatively correlated with SLA ($r = -0.87$; $P < 0.01$). Among all species, *Mouriri ficoides* had the highest average LPS (0.96 N mm^{-1}) and the lowest average SLA (143.15 cm^2 g^{-1}). Leaf area and root length were correlated with each other. *Monopteryx uaucu* showed the highest average LA (254.14 cm^2) and highest RL (32.11 cm) (see Tables S3 and S4).

Discussion

Our results provide no evidence that an interaction between herbivory and soil nutrient availability drives habitat association of tree species in white-sand and terra-firme forests of the upper Rio Negro. Although tree seedlings showed higher mortality when growing on their non-typical soil type, growth and herbivore damage were similar regardless of protection from insect herbivores and soil. Additionally, tree seedlings of white-sand and terra-firme species were similar in respect to their functional traits. Albeit with some limitations and uncertainty, as discussed below, our results offer some new insights about mechanisms shaping habitat association of tree species in white-sand and terra-firme forests.

Seedling mortality

The mortality of 8.6% observed one month after setting up the experiment may have been caused by damage to seedlings during transplanting, as we found no effect on mortality of soil type or protection from herbivory. Considering the mortality at the end of the experiment, we found that seedlings had a higher probability of dying when transplanted to their non-typical soil type. It has been shown that low herbivory rates, such as those observed in our system, can cause tree seedling mortality, in spite of their unimportance for seedling growth (Eichorn et al. 2010). After suffering herbivore attack, seedlings may become more vulnerable to pathogene attack and, therefore, are more likely to perish. In this case, pathogen transmission rather than the loss of leaf tissue explains mortality (Eichorn et al. 2010). However, we found no evidence that herbivore damage recorded at the beginning of our experiment could predict future mortality. We therefore argue that herbivory may not be the main factor causing seedling mortality. Instead, our results suggest that soil characteristics may directly prevent seedlings becoming established in their non-typical soil type. Within the scope of this study, we were unable to identify soil-related factors that increased seedling mortality in non-typical soil types. One potential explanation may be related to soil toxicity (H$^+$: high in white-sand and Al^{3+}: high in terra-firme), rather than soil nutrient availability. Luizão et al. (2007) suggested that soil toxicity may limit species distribution between white-sand and terra-firme forests in central Amazonia. This toxicity, however, apparently does not affect the occurrence of climax tree species in Guiana (ter Steege and

Alexander unpublished data, in Banki 2010). This finding questions the role of soil toxicity in limiting the establishment of habitat-specialist species in their non-typical soil type. Another factor that could explain the high mortality of seedlings on their non-typical soil type is soil biota. It has been hypothesised that ectomycorryza (EcM) fungi, such as *Xeromocus amazonicus* Sing. & I. Araujo and EcM trees (*Aldina heterophylla* Spruce ex Benth.) are more abundant in sandy soils than in clayey soils of terra-firme forests (Singer and Araujo 1979). This higher abundance may arise because EcM fungi facilitate nutrient uptake by EcM trees (See and Alexander 1994), giving these species a selective advantage in sandy soils (Kubitz 1989 in Moyersoen et al. 2001). Following this argument, the lack of beneficial EcM fungi could explain the higher mortality of white-sand seedlings in terra-firme forests observed in our experiment. However, the hypothesis that highly abundant white-sand tree species, such as *Eperua* Aubl., have predominately EcM association is not well established. In fact, this genus has been initially reported to form EcM (St. John and Uhl 1983 in Moyersoen et al. 2001), but later on it was documented to form arbuscular mycorrhyza associations (Moyersoen 1993). Taken together, we argue here that a general explanation of the mortality of habitat-specialist species of white-sand and terra-firme in their non-typical soil type is yet to be found. Future research investigating the role of the abiotic factors in microorganism-plant interactions could clarify prevailing mechanisms driving habitat association (e.g. Álvarez-Loayza et al. 2011; Mordecai 2012).

Seedling growth and herbivory

The low RHGR and RLAGR observed may be linked to the duration of the experiment (13 months), which may be insufficient to allow for seedling growth in low-dynamic environments, such as white-sand and terra-firme forests. Additionally, light availability was potentially reduced in our experiment by the mosquito net placed on top of the cages, which may have further contributed to the low RHGR and RLAGR.

The low growth rates of seedlings reported here are, however, comparable with values reported elsewhere under the closed canopy of tropical rainforests (Darrigo 2011). In the understory of terra-firme forests, light typically limits seedling growth (Clark and Clark 1992; Poorter 1999). In the more open white-sand forests (Anderson 1981), soil characteristics, such as soil nutrient concentration (Coomes and Grubb 1996) and soil toxicity (Luizão et al. 2007, see also discussion above) are reported to limit seedling growth. Regarding soil nutrient, Baraloto et al. (2006), by conducting a fertilising experiment, have shown that P addition did not promote the growth of *Eperua grandiflora* (Aubl.) seedlings, which is a typical white-sand species. It is possible that other soil nutrients (see Lawrence 2003) or a combination of factors related to soil characteristics, including soil biota, limit seedling growth in white-sand forests.

In resource-limited environments, seedling growth can be negatively affected already by low herbivory rates (Zangerl et al. 2002), but similarly to Eichorn et al. (2010), we found no evidence for such a relationship. Thus, our findings provide no indication that herbivory limits seedling growth in the upper Rio Negro. According to the resource-availability hypothesis, we expected seedlings of white-sand species to show a lower growth rate than seedlings of terra-firme species on both soil types. Additionally, we expected terra-firme species to show a higher growth rate than white-sand species on both soil types when protected from herbivores. We found, however, no effect of soil type or herbivory on growth rates of tree seedlings of habitat-specialist species. The number of seedlings included in our experiment may be insufficient to allow detection of differences between treatments (see Table S2). Our findings should therefore be interpreted with caution. The similar RLAGR and RHGH in the two soil types may be linked to low overall seedling growth in our experiment. By contrast, Fine et al. (2004, 2006) in a much greater difference in soil nutrients than the one present in our system reported, for a similar transplanting experiment, a strong effect of soil and herbivory protection on seedling growth. If, as in our case, species in both white-sand and terra-firme forests are adapted to low soil nutrient availability (see Table 6), herbivore protection becomes unimportant in affecting seedling growth. Transplanting experiments applying fertilisers conducted in forests similar to those analysed by us have failed to show a positive influence of soil nutrient availability on seedling growth (Baraloto et al. 2005; Luizão et al. 2007). In fact, seedling growth, just as seedling mortality, may be subject to interactions between several factors (e.g. Baraloto and Couteron 2010). Identifying the main

factors that influence seedling growth in white-sand and terra-firme forest may thus require longer-term monitoring under a more complex experimental design than the one presented here.

We found that leaf damage was low in the unprotected plots. Low herbivory could be the result of the low number of leaves produced, as herbivory affects new leaves more than it affects old ones (Coley and Barone 1996). In our experiment, new leaves constituted a minority of those present on the seedlings; therefore our results represent herbivory rates occurring mostly on mature leaves. During the period of one year, 34% of the seedlings growing in unprotected plots had no leaf damage and 92% of all seedlings had damage to less than 10% of leaf area. Of all seedlings growing in the unprotected plots, only three individuals had more than 20% leaf damage (*Scleronema* cf. *micranthum*, *Eperua purpurea* and *Virola calophylla* growing in white-sand plots). Comparable herbivory rates have been previously reported for tree seedlings elsewhere (Eichorn et al. 2010), and can be explained by the high values of leaf punch strength (see discussion below).

Seedling traits

White-sand and terra-firme species were expected to differ in certain functional traits (Table 1). Our results, however, show similar average values for the functional traits of white-sand and terra-firme species, although with a large variation among species in the average values of traits (Table 5). These results are in line with our findings related to similar RHGR, RLAGR and proportional herbivore damage. The results thus indicate similar growth and defence strategies of both white-sand and terra-firme

Table 6.   Soil nutrient concentration and leaf punch strength (LPS) of white-sand and terra-firme forest in the upper Rio Negro and in western Amazonia.

Site	Soil/difference between soils	Total P (mg kg^{-1})	N (mg g^{-1})	C (mg g^{-1})	LPS	Region	Reference (soil; LPS)
San Carlos de Río Negro, Venezuela	Clayey	58.08	0.83	15.64	0.4−1.0	URN	RAINFOR plot SCR-01; Reich 1991; Reich 1995
	Sandy	22.54	0.70	13.38	*	URN	RAINFOR plot SCR-05
	Difference	**35.53**	**0.13**	**2.26**	*	URN	
Middle Içana River, Brazil	Clayey	54.40	1.07	16.22	0.46−0.95	URN	This study
	Sandy	7.52	0.39	6.61	0.54−0.85	URN	This study
	Difference	**46.88**	**0.68**	**9.61**		URN	
Allpahuayo, Peru	Clayey	90.13	0.71	7.62	*	WA	RAINFOR plot ALP-12
	Sandy	7.59	0.15	1.80	*	WA	RAINFOR plot ALP-03
	Difference	**82.55**	**0.56**	**5.82**		WA	
Allpahuayo, Peru	Clayey	80.17	1.02	10.75	*	WA	RAINFOR plot ALP-22
	Sandy	11.39	0.34	4.65	*	WA	RAINFOR plot ALP-21
	Difference	**68.78**	**0.68**	**6.10**		WA	
Allpahuayo, Mishana, Peru	Clayey	*	*	*	0.06−0.12	WA	Fine et al. (2006)
	Sandy	*	*	*	0.06−0.23	WA	Fine et al. (2006)

URN: upper Rio Negro; WA: western Amazonia. Values of soil nutrient content for RAINFOR plots is average of five soil samples collected at 30-cm depth; a detailed description of soil sampling and determination methods is given in Quesada et al. (2010). Differences in soil nutrient content between clayey and sandy soils are given in bold. Soil nutrient values for the middle Içana River represents averages of sites presented in this study, LPS represents the range (minimum−maximum), * represents no available information.

species, which may be explained by the generally low soil nutrient availability in both forest types.

The low herbivory rates observed in our study are consistent with our results for LPS, which ranged from $0.3-1.2$ N mm^{-2}. These values are comparable to the data from San Carlos de Río Negro, which ranged from $0.4-1$ N mm^{-2} (Reich et al. 1991, 1995). Compared to the LPS registered in western Amazonia ($0.06-0.2$ N mm^{-2} (Fine et al. 2006)), the species in the upper Rio Negro have up to 12 times tougher leaves. Fine et al. (2006) found that seedlings, on average, had 17% higher leaf strength when growing on white-sand soils, whereas we found an increase of only 3%. This suggests that in the upper Rio Negro, leaf strength, which is influenced by soil nutrient and water availability during leaf formation and growth, is rather similar in both white-sand and terra-firme forests.

Why are herbivores of minor importance for habitat association of tree species in the upper Rio Negro?

Herms and Mattson (1992) suggested expressing herbivory as a sigmoid function of resource availability (Figure 2). Typically, herbivory remains low and relatively constant in habitats where resource availability is low, but gradually increases and eventually approaches its maximum as resource availability increases. We propose that herbivory may only affect habitat specificity, if habitats sufficiently differ from each other along the sigmoid 'resource availability-herbivory' curve. Accordingly, we suggest that resource availability and herbivory of both white-sand and terra-firme forests in the upper Rio Negro may be located in close proximity of each other before the lower inflexion
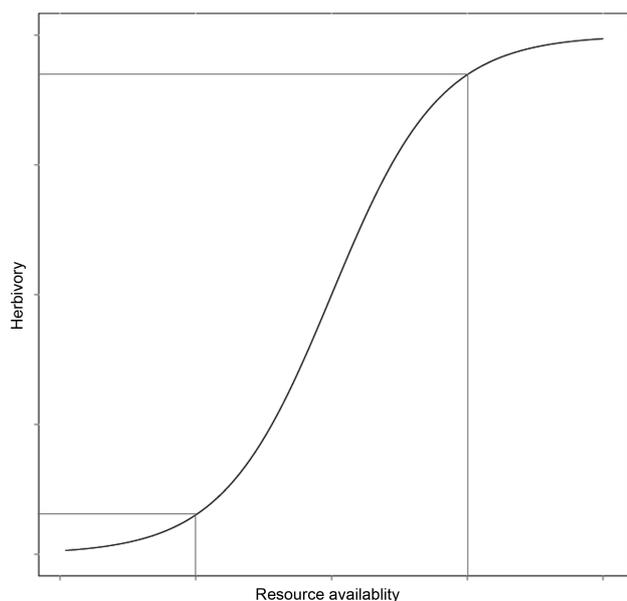

Figure 2. Theoretical function describing the relationship between resource availability and herbivory. The interaction between resource availability and herbivory may influence habitat association only if habitats are located sufficiently far from each other between the two inflexion points on the curve.

point of the sigmoid curve. We may thus argue that for tree seedlings, herbivores appear to be of minor importance for habitat association in the upper Rio Negro.

The resource availability in white-sand and terra-firme forests of the upper Rio Negro may be similar, as the relatively small differences in soil nutrient availability as well as soil texture suggests. Specifically, the soils in terra-firme forests have a relatively high sand content (Table 2), which could contribute to the low soil nutrient availability in this soil type. We suggest that plant growth, herbivory and traits might vary between habitats only if differences in soil nutrient availability, or other relevant resources, are large enough to trigger differences in plants growth and herbivore defence strategy. Soil nutrient differences between white-sand and terra-firme forests vary across Amazonia. For instance, soils of terra-firme forests vary in their nutrient availability across Amazonia due to large-scale differences in geology and geomorphology (Quesada et al. 2010). In western Amazonia, terra-firme forests grow on clay soils originating from Andean sediments (ca. 66 Ma and more recently). In the upper Rio Negro, however, terra-firme forests occur in soils originating from the Guiana shield formation (ca. 2500 Ma) and for this reason are much less fertile than soils of terra-firme forest in western Amazonia. However, soils of white-sand forests of western Amazonia and of the upper Rio Negro might have a similar origin. Additionally, both forest types in western Amazonia may have continuous volcanic input (Jan Sevink, pers. comm.), keeping fertility of white-sand and terra-firme forests relatively high. Therefore, differences in soil fertility between white-sand forests and the adjacent terra-firme forests may vary in a predictable way depending on the geological and geomorphological history. This variation may influence the mechanisms shaping habitat association of tree species across Amazonia.

Conclusions

We found no evidence that an interaction between herbivory and soil nutrient availability contributes to habitat association of tree species in white-sand and terra-firme forests of the upper Rio Negro. This finding may have been influenced by the overall low soil nutrient availability of both habitats in combination with the short duration of our transplantation experiment. In addition, habitat-specialist tree species seem to show similar traits indicating that similar growth and defence strategies are acting in both forest types. This may suggest that the overall low soil-nutrient availability does not allow for a sufficient difference along the continuum of the resource availability-herbivory curve (see Figure 2). If mechanisms driving habitat association of tree species are tightly connected to soil nutrient availability, their importance varies in a predictable manner across Amazonia. Such mechanisms might be affected by the geological and geomorphological history. In order to better predict to what extent resource availability and herbivory drive habitat association, future research should aim at identifying the inflexion points of the resource

availability-herbivory curve. Our research suggests that when analysing tropical forests with extremely low soil nutrient availability, reciprocal transplanting field experiments should be carried out for longer time periods, and consider a larger number of seedlings as well as additional biotic and abiotic factors (e.g. herbivore and pathogen attacks, below ground species interaction, as well as light and soil nutrient) than those considered here. An approach that follows plant development from seed to sapling may help identifying the life stage that is critical for maintaining habitat association of tree species in white-sand and terra-firme forests.

Notes on contributors

Juliana Stropp's research focuses on the ecology of tropical tree communities and biogeography.

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