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EFEITO DA DISPONIBILIDADE DE NUTRIENTES NO SOLO NOS TRAÇOS FÍSICOS FOLIARES EM LINHAGENS DE ÁRVORES TROPICAIS NA AMAZÔNIA CENTRAL

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Sinopse:

Comparei os traços físicos foliares em onze famílias de árvores tropicais em florestas que crescem em solos de argila e florestas que crescem em solos de areia branca. O estudo foi realizado em duas áreas na Amazônia Central: A Reserva Florestal Adolpho Ducke y o Paleocanal do Tarumã. Investiguei a influência dos nutrientes nas estratégias de resistência foliar em ambos ecossistemas.

Palavras-chave: Amazônia Central; tipos de solo; traços físicos foliares; estratégias de resistência foliar; disponibilidade de recursos.

"Comecei com a ideia de descrever o contorno de uma ilha,
e eu vim descobrir as bordas do oceano"
Ludwig Wittgenstein

“A ciência é a disposição de aceitar os fatos, mesmo
quando eles são opostos aos desejos”
Burrhus Frederic Skinner

Este trabajo va dedicado
especialmente a mi madre Sonia,
a Neil, y a mis hermanos Jacob, Rebeca e Isaac.

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RESUMO

A fertilidade do solo e a disponibilidade de água são filtros ambientais importantes que determinam as estratégias de resistência foliar. Massa foliar por área (LMA), espessura foliar (LT), dureza foliar (FP), teor de massa seca foliar (LDMC) e a densidade foliar (LD) são os traços físicos que contribuem à resistência. Portanto, valores altos destes traços refletem menores aquisições de recursos e taxas lentas de crescimento, uma estratégia comum em ambientes menos produtivos associada à eficiência no uso de nutrientes. Pelo contrário, em ambientes mais produtivos, a aquisição de recursos é maior e as taxas de crescimentos são altas, mas o investimento em resistência foliar é menor. O objetivo do presente estudo foi descrever a variação da resistência foliar em termos dos seus traços físicos em florestas sobre solos contrastantes (i.e., florestas sobre solos arenosos pobre em nutrientes e florestas sobre solos argilosos mais férteis) na Amazônia, e verificar se esses traços são consistentemente selecionados em 10 das linhagens de árvores mais abundantes; também testamos se as relações dos traços entre si variam de acordo com tipo de solo e entre sítios. Maior LMA e LT foram observadas em solos arenosos unicamente em um dos sítios amostrais, FP e LDMC só diferiram entre sítios, e LD foi totalmente homogênea entre solos e sítios. As linhagens não apresentaram tendências consistentes em investimento estrutural entre solos e sítios. As correlações entre traços foram consistentes, embora as correlações entre LT com LDMC e LD tenham sido negativas, e algumas não foram significativas em algum dos sítios. Padrões contrastantes na variação dos traços indicam a existência de dois filtros diferentes (água, nutrientes) determinando a resistência foliar em cada sítio amostral. Traços respondem diferentemente a vários filtros ambientais, alterando consequentemente as relações entre eles, levando à falta de consistência no investimento das linhagens refletido nos diferentes padrões de resistência foliar entre habitats e sítios.

Palavras chave: Amazônia Central; tipos de solo; traços físicos foliares; estratégias de resistência foliar; disponibilidade de recursos.

ABSTRACT

Soil fertility and water availability are important environmental filters that determine leaf resistance strategies. Leaf mass per area (LMA), leaf thickness (LT), leaf toughness (FP), leaf dry matter content (LDMC) and leaf density (LD) are the physical traits that contribute to resistance. Therefore, high values of these traits reflect lower resource acquisition and slow growth rates, a common strategy in less productive environments that is associated with nutrient use efficiency by protecting leaves to maximize carbon gain. On the contrary, in more productive environments, resource acquisition is higher and growth rates are high, but the investment in leaf resistance is lower. The objective of the present study was to describe the variation of leaf resistance in terms of its physical traits in contrasting environments (forests in white sand, very poor or clay, slightly more fertile) in the Amazon, and if these traits are consistently selected in 10 of the lineages of trees more abundant; We also tested whether the relationship of traits to each other varies according to soil type and between sites. Higher LMA and LT were observed in sandy soils only at one of the sampling sites, FP and LDMC differed only between sites, and LD was totally homogeneous between soils and sites. Lineages did not present consistent trends in structural investment between soils and sites. The correlations between traits were consistent, although correlations between LT with LDMC and LD were negative, and some were not significant at any of the sites. Contrasting patterns in traits variation indicate the existence of two different filters (water, nutrients) determining leaf resistance at each sampling site. Traits respond differently to various environmental filters, thus altering the relationships between them and leading to lack of consistency in lineage inversion reflected in different patterns of foliar resistance between habitats and sites.

Keywords: Central Amazon; Soil types; Leaf physical traits; Foliar resistance strategies; Availability of resources.

RESUMEN

La fertilidad del suelo y la disponibilidad de agua son filtros ambientales importantes que determinan las estrategias de resistencia foliar. Masa foliar por área (LMA), el grosor foliar (LT), la dureza foliar (FP), el contenido en masa seca foliar (LDMC) y la densidad foliar (LD) son los rasgos físicos que contribuyen a la resistencia. Por lo tanto, valores altos de estos rasgos reflejan menores adquisiciones de recursos y tasas lentas de crecimiento, una estrategia común en ambientes menos productivos que se asocian a la eficiencia en el uso de nutrientes por la protección de hojas para maximizar la ganancia de carbono. Por el contrario, en ambientes más productivos, la adquisición de recursos es mayor y las tasas de crecimiento son altas, pero la inversión en resistencia foliar es menor. El objetivo del presente estudio fue describir la variación de la resistencia foliar en términos de sus rasgos físicos en ambientes contrastantes (bosques en arena blanca, muy pobres o arcilla, un poco más fértil) en la Amazonia, y si esos rasgos son consistentemente seleccionados en 10 linajes de árboles más abundantes; también testamos si las relaciones de los rasgos varían entre sí, de acuerdo al tipo de suelo y entre sitios. Mayor LMA y LT fueron observadas en suelos arenosos, únicamente en uno de los sitios de muestreo, FP y LDMC sólo diferían entre sitios, y LD fue totalmente homogénea entre suelos y sitios. Los linajes no presentaron tendencias consistentes en la inversión estructural entre suelos y sitios. Las correlaciones entre los rasgos fueron consistentes, aunque las correlaciones entre LT con LDMC y LD fueron negativas, y algunas no fueron significativas en alguno de los sitios. Los padrones contrastantes en la variación de los rasgos indican la existencia de dos filtros diferentes (agua, nutrientes) determinando la resistencia foliar en cada sitio de muestreo. Los rasgos responden diferentemente a varios filtros ambientales, alterando consecuentemente las relaciones entre ellos y llevando a la falta de consistencia en la inversión de los linajes, reflejado en los diferentes padrones de resistencia foliar entre hábitats y sitios.

Palabras clave: Amazonia Central; Tipos de suelo; Rasgos físicos foliares; Estrategias de resistencia foliar; Disponibilidad de recursos.

Sumário

INTRODUÇÃO GERAL

Os traços físicos foliares são geralmente associados à eficiência no uso de nutrientes em ambientes com recursos limitados, e à proteção contra herbivoria. Muitos estudos consideram à resistência foliar como defesa contra herbivoria (Coley, 1983; Choong *et al.* 1992; Turner, 1994), mas os traços físicos das folhas podem ser respostas a condições de estresse ambiental oferecendo vantagens como resistência à perda de água ou uso eficiente de nutrientes (Chapin *et al.* 1993; Wright *et al.* 2001, 2002; Andersen *et al.* 2010, 2014). Portanto, a presença dos herbívoros não implica necessariamente que as plantas evoluíram esses traços exclusivamente para resistir aos comedores de folhas (Choong *et al.* 1992; Peeters *et al.* 2007), mas sim às pressões exercidas pela falta de nutrientes, água e luz (Chapin *et al.* 1993; Lamont *et al.* 2002; Onoda *et al.* 2008, 2011). Considerar os traços físicos como defesa, mesmo que a defesa não seja sua função primária (Strauss and Agrawal, 1999), conduz à importância de distinguir entre traços que protegem à planta contra herbívoros e que evoluíram em resposta aos herbívoros, e traços que incidentalmente fazem da planta mais resistente aos herbívoros, mas que evoluíram em resposta a outros fatores, chamados por Edwards (1989) como resistência neutra (Hanley *et al.* 2007). Porém, a significância adaptativa da resistência foliar é ainda controversa (Edwards *et al.* 2000).

Vários trabalhos demonstraram que a fertilidade do solo e a disponibilidade de água são filtros ambientais importantes que determinam as estratégias de resistência foliar (Grime, 1977; Witkowsky and Lamont, 1991; Wright *et al.* 2001, 2002) ao mesmo tempo que controlam a composição das espécies (Swaine, 1996; Quesada *et al.* 2009; Condit *et al.* 2013; Zuquim *et al.* 2014). A Massa Foliar por Área (LMA), espessura foliar (LT), dureza foliar (FP), Teor de Massa Seca Foliar (LDMC) e a densidade foliar (LD) são os traços físicos que contribuem à resistência foliar. Portanto, valores altos destes traços refletem menor aquisição de recursos e taxas lentas de crescimento, uma estratégia comum em ambientes menos produtivos associada à eficiência no uso de nutrientes pela proteção de folhas para maximizar o ganho de carbono e a conservação de água (Salleo and Nardini 2000; Read *et al.* 2000, 2005, 2006). Pelo contrário, em ambientes mais produtivos, a aquisição de recursos é maior e as taxas de crescimentos são altas, mas o investimento em resistência foliar é menor (Coley, 1983; Coley *et al.* 1985; Andersen *et al.* 2010). Portanto, em hábitats que diferem na disponibilidade de recursos, o investimento em resistência foliar pode diferir, como resultado da filtragem ambiental, deste modo o gradiente de fertilidade do solo seleciona traços adequados para o desenvolvimento da planta (Díaz *et al.* 1998; Agrawal and Fishbein 2006).

Na Amazônia central, florestas de campinarana que crescem em solos de areia branca extremamente pobres em nutrientes (Anderson, 1981; Fine *et al*, 2006), e florestas de platôs que crescem em solos argilosos com alta a moderada disponibilidade de nutrientes (Coley *et al.* 1985; Duivenvoorden, 1995; Fine *et al.* 2006) coexistem em um mosaico tanto na escala local y regional (Gentry 1989; 1992), representando os extremos do gradiente de disponibilidade de nutrientes no solo (Nardoto *et al.* 2008; Lamarre *et al.* 2012). Pouco se sabe sobre a variação dos traços físicos foliares entre estes ambientes extremos da Amazônia, e como a disponibilidade de nutrientes determina as estratégias de resistência foliar das linhagens de árvores amazônica, embora alguns poucos estudos tenham avaliado alguns destes traços físicos como parte das suas pesquisas focadas em herbivoria e especialização de hábitats (e.g. Fine *et al.* 2006; Lamarre *et al.* 2012; Endara *et al.* 2015).

Focamos este estudo nestes traços foliares (LMA, LT, FP, LDMC e LD) para diferentes linhagens de árvores tropicais amazônicas que são abundantes tanto em florestas em areia branca e florestas em argila, com o objetivo de investigar a variação funcional desses traços entre os tipos de solo, e testar se existem diferenças fortes em relação à disponibilidade de nutrientes. Nós postulamos que em solos pobres em nutrientes, as plantas investem em maior resistência foliar para maximizar a eficiência no uso de nutrientes, o que será refletido em maiores valores dos traços físicos como grossura (LT), massa foliar especifica (LMA), conteúdo de matéria seca (LDMC), densidade (LD) e dureza (FP) (Groom & Lamont, 1999). Pelo contrário, em florestas sobre solos argilosos com maior disponibilidade de recursos, prevemos que as plantas investem mais em crescimento, refletido em valores baixos dos seus traços físicos.

Embora exista esta predição simples de alocação em componentes estruturais em função da fertilidade do solo, sabe-se também que outras pressões ambientais podem afetar certos componentes da resistência foliar (e.g., água e luz). A disponibilidade de água é um fator importante que exerce um efeito significante na seleção de espécies com valores maiores de LMA, LT e LD em ambientes secos (de la Riva *et al.* 2016). Por exemplo, LMA é uma variável que depende tanto de LT como LD, e ambas variáveis estão sob o efeito da disponibilidade de água, aumentando os seus valores em sítios secos e consequentemente afetando a LMA, LDMC e FP (Witkowsky and Lamont, 1991; Vile *et al.* 2005; Turner 1994b; de la Riva *et al.* 2016). Portanto, prevemos que a maioria de linhagens filogenéticas serão consistentes nas suas tendências de aumentar o investimento em resistência foliar em solos com baixa disponibilidade de nutrientes, mas também isto poderia depender das relações que os traços físicos têm entre si como resultado das diferentes respostas à disponibilidade de água e à variação desta nas áreas de amostragem.

Neste estudo, avaliamos as diferenças nos traços foliares de resistência entre habitats com alta e baixa disponibilidade de recursos, utilizando uma abordagem comparativa entre 10 linhagens de árvores em dois sítios de amostragem na Amazônia central, e perguntamos: (1) Há maior resistência foliar no ambiente com menor fertilidade, conforme previsto pela hipótese de eficiência no uso de recursos? (2) A variação no investimento em resistência dos grupos evolutivos é consistente entre tipos de solo e sítios de amostragem? (3) As relações entre os traços funcionais são consistentes ou variam de acordo ao tipo de solo e sítios?

OBJETIVOS

Objetivo Geral

Descrever a variação da resistência foliar em termos dos seus componentes funcionais em florestas que crescem em solos de areia branca (solos pobres) e florestas que crescem em solos de argila (relativamente mais ricos em nutrientes) na Amazônia Central.

Objetivos Específicos

1. Determinar se existe consistência na diferenciação dos traços físicos em relação ao tipo de solo de cada hábitat florestal.

2. Determinar se os investimentos em resistência foliar das linhagens de árvores são maiores em solos de areia branca, mantendo o mesmo padrão nos sítios de amostragem.

3. Descrever se as relações dos traços físicos foliares são consistentes entre tipos de solo e sítios de amostragem.

Capítulo 1

Gonzales, C.V & Costa, R. R. C. 2020. Soil and water determine different resistance leaf strategies among abundant tree lineages. Manuscrito submetido para *Forests.*

Abstract: Leaf traits related to resistance, as well as resistance strategies of plants, are expected to be selected under nutrient limitation, to protect plants from loss of tissues to herbivores where building of new tissues is costly. However, at local scales, other environmental stresses could interfere or even supersede the effects of nutrient limitation. To understand together the effects of soil water and nutrient limitation, we analyzed leaf mass per area (LMA), leaf thickness (LT), force to punch (FP), leaf dry matter content (LDMC) and leaf density (LD) of 10 tree lineages across gradients of these two environmental factors in two sites of *terra-firme* forests in central Amazonia. In the site with lower fertility and larger water availability variation, LMA and LT community means increased towards drier but more fertile clay soils, while in the more fertile site these traits increased towards the sand soils which combine both nutrient and water limitation. FP and LDMC increased only towards low fertility, not being affected by water gradients. Leaf resistance strategies differed among sites, with higher investments in LMA and LT in the less fertile white-sand plots of the higher fertility site, but higher investments in LDMC, FP and LD in all plots of the less fertile site. The different tree lineages tended to converge to the same mean response patterns to the environmental gradients, but divergence in some traits was observed, suggesting that allocation in few resistance traits may be enough to protect leaves. In conclusion, both fertility and water availability gradients select the leaf resistance traits in central Amazonian forests, and fertility is only the dominant driver if water is not limited.

Keywords: Resistance leaf; environmental filters; resource use efficiency; fertility gradient; water availability; tropical tree lineages; Central Amazonian.

INTRODUCTION

Understanding the variations of functional traits that contribute to leaf resistance across environmental gradients is a persistent challenge for ecologists [1,2]. Leaf resistance is in general associated with nutrient efficiency in resource-limited environments, and thus to protection against herbivores. Several studies consider leaf physical traits that contributed to leaf resistance as a response against herbivory attack [3–6], although they are also related with water loss resistance and nutrient use efficiency [7–10]. Therefore, leaf resistance will not necessarily be related to herbivory, but also to availability of nutrient and water, and their interaction between them [8,11].

Considering leaf resistance as a defense, even if defense is not its primary function [12], leads to the importance of distinguishing between traits that protect plant against herbivores and thus evolve in response to them, and traits that incidentally make plants more herbivore resistant, but which evolve in response to other factors, called by Edwards (1989) as neutral resistance [13]. However, the adaptive significance of leaf resistance is still much debated [14,15].

Leaf mass per area (LMA), leaf thickness (LT), force to punch (FP), leaf dry matter content (LDMC) and leaf density (LD) are leaf traits that contribute to resistance. Therefore, higher values of these traits reflect lower acquisition and slow growth rates, a common strategy in less productive environments that is associated with nutrient use efficiency and water loss [8,10,15–17]. In contrast, species growing in environments with higher nutrients availability and without water limitation can have short-lived leaves of higher nutrient photosynthetic capacity, which implies less investment in resistance to protection [8,9,11]. Therefore, investment in leaf resistance may vary according to resource availability in different habitats [18,19].

In central Amazonian, *terra-firme* forests vary in structure and composition according to soil texture and nutrient content [20,21]. Forests patches growing on white-sand soils, extremely nutrient poor [22,23] and forests growing on more fertile clay soils [5,24] coexist in a mosaic on both local and regional scales [25], representing the extremes of the soil nutrient availability gradient [26,27]. These forests are also subject to significant topographic variation that determine the depth to the water table and thus the soil water availability, from wet and seasonally waterlogged soils in the valleys to drier soils in the plateaus, which are more susceptible to prolonged dry periods [28–31]. Given that clay soils occur in plateaus and sandy soils in the valleys, water availability and fertility tend to be negatively correlated within local sites, although fertility may vary across site [32,33]. Little is known about the variation of leaf resistance traits among these Amazonian environments, and how both fertility and water gradients determine the leaf resistance strategies across diverse tree lineages.

Based on the prediction of the leaf economic spectrum [34] and previous studies, it can be expected that in forests that grow on nutrient-poor white sand soils, plants invest in greater leaf protection to maximize nutrient's use efficiency at the expense of growth [14,35,36], which will be reflected in higher values of LMA, LT, FP, LDMC and LD. In contrast, in forests that grow on more fertile soils, is expected plants invest more in growth, reflected in low values of these traits [4,23,27]. Besides the variation in the allocation in structural components as a function of soil fertility, water availability can affect certain components of leaf resistance. For example, LMA depends on both leaf thickness and leaf density, and each of these two traits properties can be independently affected by water availability [11,37], consequently affecting LMA, LDMC and FP [35,38,39]. Given the within site negative correlation between soil fertility and water availability in central Amazonia, the association of leaf resistance traits to resource may not be as simple as predicted by the leaf economic spectra. In addition, it is anticipated that most phylogenetic lineages will be consistent in their tendency to increase investment in leaf resistance in low fertility and water availability, but this could also depend on the relationships that resistance traits have among each other as a result of different evolutionary pressures and in response to the interaction between fertility and water availability gradients.

This study evaluated differences in leaf resistance traits along two gradients in central Amazonian forests, using a comparative approach among ten lineages in two sites, to address three main question: (1) How does functional traits that contribute to leaf resistance vary along fertility and water availability gradients? (2)Are there different leaf resistance strategies at community level according to soil fertility and water gradients? (3) How do allocation strategies related to leaf resistance vary among lineages, across these resource gradients?

MATERIALS AND METHODS

Study sites

This study was conducted at two sample sites in Central Brazilian Amazon: Reserva Florestal Ducke (RFD) and the Paleocanal do Tarumã. RFD is located 26 km north of the city of Manaus, between coordinates 02˚44'60"S and 59˚33'36"W, comprising 10,000 ha of tropical rainforests. The structure and floristics of RFD environments are defined mainly by the surface topography: plateaus, slopes and valleys, which affects the soil type. Plateaus are high areas (at 90 – 120 m above sea level), with generally more fertile clay soils, and valleys are lowest areas with sandy soils and generally less fertile soils, with the water table close to the surface (up to 1m deep), getting waterlogged during the rainy season [40–42]. The Paleocanal of Tarumã is located between Tarumã Mirim and Tarumã Açu river basins to the northwest of Manaus, between 02˚44'00"S and 60˚04'00"W coordinates [43]. Most of the Paleocanal of Tarumã vegetation is characterized by dense *terra-firme* forests, with variations in soil types ranging from clayey to sandy soils, but maintaining a flat surface between soil types. The average annual temperature is 26˚C and precipitation 2300 mm, in the studied region [44].

Study design

Data were collected in twelve modified Gentry plots (200×100 m) [45,46], systematically distributed over the area of each site. Three plots per soil type (clay and sand) were installed at each sampling site. In each plot, six saplings (1.5 – 2.4 m height) of each of ten tree lineages (see below) were sampled (one individual per species was preferred). Leaf samples of each individual were collected for functional traits measurements and taxonomic identification. Six to ten soil samples of each plot were collected at regular intervals along the largest axis of the plot.

Environmental measurements

Soil sub-samples were bulked to produce a composite sample for each plot. Before analysis, samples were cleaned of roots, air-dried and sieve through a 2 mm sieve. Fertility was determined as the soil content of exchangeable bases (sum of Ca+2, Mg+, K+ using the *Mehlich 1* method). Analyses were done at the Thematic Laboratory of Soils and Plants at INPA, Manaus.

A proxy of the soil water availability was obtained from the height of the terrain above nearest drainage "HAND" [47]. This metric approximates the water table depth (WTD), and thus the water availability when rains are not refilling the soil. It was extracted from the layer produced by Schietti [48] for Ducke, and C. D. Rennó (unpublished) for Tarumã.

Focal lineages

Ten tropical tree lineages were selected among the most abundant and widely distributed in the Amazon basin, containing species associated with both soil types (clay and sand) considered in this study: Lauraceae, Moraceae, Rubiaceae, *Protium* (Burseraceae), *Eschweilera* (Lecythidaceae), Myrtaceae, *Licania* (Chrysobalanaceae), *Bombacoide* (Malvaceae), *Inga* (Fabaceae) and *Micropholis* (Sapotaceae). These lineages are phylogenetically dispersed within the angiosperms, have a variety of physical and chemical strategies to adapt to the natural environment [27], and are among the most abundant in Central Amazonian forests.

Leaf functional traits

Five functional traits associated to leaf resistance were measured in all collected individuals. Three structurally developed and fully expanded leaves (preferably leaves from the middle of branches to avoid old or very young leaves) of each individual were selected [49,50]. Leaves were scanned using a portable scanner (CI-202, CID Bio-Science) to determine their area and then dried at 60˚C for 72 h. Fresh and dry mass was weighed to determine leaf dry mass per unit area (LMA, in g/cm2) and leaf dry mass content (LDMC = Dry Mass/Fresh Mass, in g/g). Force to punch (FP, in N/cm2) was measured as the average of three perforation test with a penetrometer [51]; in the middle of the leaf blade and avoiding major veins; leaf thickness (LT, in mm) was estimated as the average of three measurements with a digital micrometer (Mitutoyo Coolant Proof

IP 65) also in the blade middle and avoiding main veins; leaf density (LD in g/cm3) was calculated as LMA/LT [49,50].

Data analyses

Community means (CM) of traits were calculated as the average of all sampled individuals per plot. The relationships between the plot CM of each functional trait with both soil gradients (sum of bases and WTD) and their interactions were tested using multiple linear models. A principal component analyses (PCA) was used to evaluated the patterns of covariation between traits and to describe leaf resistance strategies of lineages in different environments.

To evaluate whether lineages exhibit similar or dissimilar patterns in their investments to leaf resistance, the average of traits for each lineage over all the individuals sampled was calculated per plot. These lineage's mean values were regressed against the sum of bases, WTD, lineages and their interaction. Then, an ANOVA test was carried out on the fitted models to discriminate which predictors had strongest effects on leaf traits variations. All analyses were conducted in the R statistical environment, version 3.6.1 [52], using the packages, plus "visreg" [53], a*nd figures were produced using the "ggplot2" package [54].*

RESULTS

Environmental differences

There are marked differences in the soil properties between the two study sites. Soil fertility, represented by the sum of bases, was higher in clay soils, independent of sites (clay: 0.26 to 0.34 at Ducke, 0.9 to 1.21 cmol.kg at Tarumã; sand: 0.06 to 0.15 Ducke, 0.67 to 0.79 cmol.kg at Tarumã). However, on average, Tarumã soils were more fertile (0.82 cmol.kg) than those of Ducke (0.15 cmol.kg).

In another hand, the contrast in water table depth (WTD) among clay and sand plots was higher at Ducke, where clayey plateaus had WTD of 37 to 40 m, while in valleys with sandy soils it ranged from 2 to 5 m, very close to surface. In the Tarumã site the differences in WTD were much smaller, from 20 to 24 m in clay soils, and 10 to 20 m in sandy soils.

Leaf traits

Overall, there was moderate variation (CV = 16 to 28 %) of the evaluated functional traits across soil types and sampling sites. LMA, LT and LDMC showed a slightly greater variation in sandy soils at both sites. FP and LD exhibited higher variation in the clay soils of Ducke, however, a contrasting pattern was seen in Tarumã, with higher variation in the sandy soils (Table 1).

Table 1. Range, mean values (± SD) and coefficient of variation for Leaf Mass per Area (LMA), Leaf Thickness (LT), Force to Punch (FP), Leaf Dry Matter Content (LDMC) and Leaf Density (LD) of sand and clay soils at two sites in Central Amazonia, Brazil.

Trait	Abbreviation	Unit	Range	Average ± SD	CV
Leaf Mass per Area	LMA	g/cm^{-2}	35.3 – 148.1	77.54 ± 20.1	25.8
Leaf Thickness	LT	mm	0.12 – 0.68	0.2 ± 0.05	27.6
Force to Punch	FP	N/cm^2	1.35 – 7.06	3.11 ± 0.78	25.3
Leaf Dry Matter Content	LDMC	g/g	0.17 – 0.61	0.43 ± 0.06	15.7
Leaf Density	LD	g/cm^3	0.02 – 0.07	0.04 ± 0.01	22.2

Leaf resistance traits differ along fertility and water availability gradients

The average community means of LMA and LT were conditioned by soil base content (representing soil fertility), water table depth (representing water availability), and an interaction between both environmental gradients (Figure 1 A, C; Table 2). In the site with lower average fertility (Ducke), both leaf traits tended to increase towards the higher clay plateaus, with a deep-water table and higher fertility relative to sands, while in the more fertile site (Tarumã) this relationship exhibited an opposite direction, with LMA and LT decreasing towards clay soils. It should be noted that in Tarumã site, the range of WTD values is smaller than at Ducke, and the lowest WTD values are 10 m, while in Ducke the lowest value is 2 m.

Community means of FP and LDMC were not affected by water availability, but had simple negative relationships with soil fertility, although there was a marginal interaction between fertility and WTD gradients on LDMC variation. It should be noted that in the site with lower average fertility (Ducke), FP and LDMC values are higher than in the site with higher fertility (Figure 1 B, D). LD was the only trait that was not related to the two environmental predictors, nor the interaction between them (Table 2).

Table 2. Results (beta coefficients followed by significance levels) of the linear Model testing the effect of sum of bases, WTD, and their interaction on each community average leaf trait, and the PCA axis that summarizes those traits.

	Sum of Bases	**WTD**	**Sum of Bases: WTD**	***adj. R^2***	***p***
LMA	44.00 ***	0.54 **	-2.14 **	0.71	**< 0.01**
LT	0.12 **	0.001 *	- 0.006 **	0.55	**0.02**
FP	-0.95 *	- 0.001	0.02	0.45	**0.04**
LDMC	-0.08 **	- 0.000	0.003 (.)	0.61	**0.01**
LD	0	0	0	-0.34	0.9
PC1	9.46 **	0.08 (.)	-0.38 **	0.71	**< 0.01**

Significance codes: (***) 0.001; (**) 0.01; (*) 0.05; (.) 0.1.

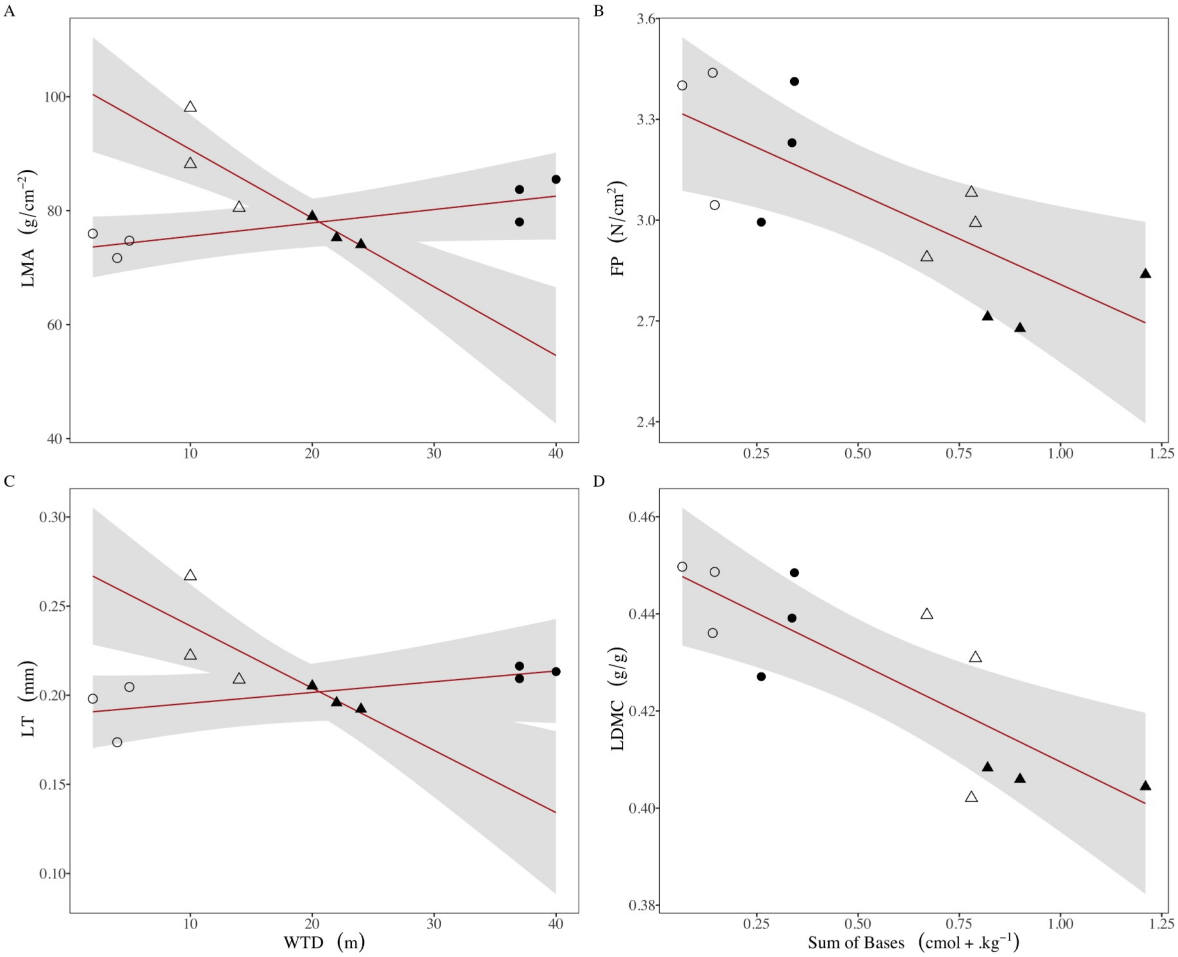

Figure 1. Partial relationships among the average community trait means and the soil gradients of sum of bases and water table depth (WTD). **(A)** Leaf Mass per Area, **(B)** Force to Punch, **(C)** Leaf Thickness, **(D)** Leaf Dry Matter Content. Circles representing Ducke and Triangles the Tarumã plots. Filled symbols representing clay and non-filled the sandy soils.

Resistance leaf strategies

Since leaf traits covary, we summarized their covariation in a PCA to represent the "leaf resistance strategies". The first axis captured 59.8% of all variance, contributed mostly by LDMC, LMA, and LT, while the second axis (24.1% variance) had higher contributions of LD, LMA and FP (Figure 2). The first PCA axis of leaf physical structure is strongly related to soil fertility and WTD, with the same interaction shown before. Scores of the average community means indicate a clear separation between the more fertile (Tarumã) and less fertile (Ducke) sites. Interestingly, the leaf resistance strategies differed among sites, with higher investments in LMA and LT in the less fertile white-sand plots of Tarumã, but higher investments in LDMC, FP and LD in all plots of Ducke, which have lower fertility across both white-sand and clays than Tarumã plots.

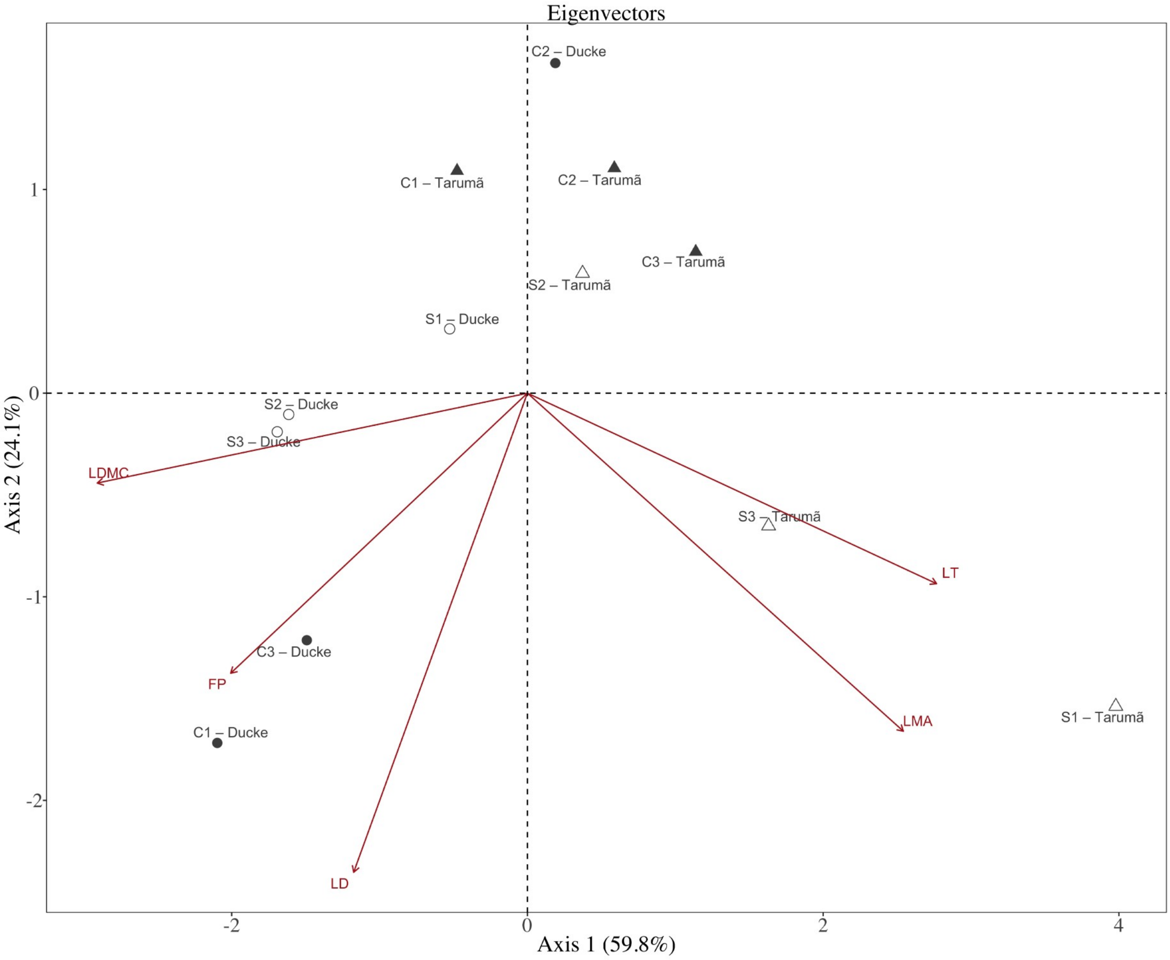

Figure 2. Principal component analysis for twelve plots at two sampling sites arcross sand and clay soils, and eigenvectors of five leaf traits. Traits: LMA, leaf mass per area; LT, leaf thickness; FP, force to punch; LDMC, leaf dry matter content; LD, leaf density. Circles representing Ducke and triangles Tarumã plots. Filled symbols for clay soils and non-filled for sand soils.

Resistance leaf strategies by lineages between soil gradients

The investment in leaf traits across botanical lineages followed the same average patterns shown at the community level (Table 3), although there were significant interactions between WTD, soil fertility and some lineages (Table S1). The five leaf traits increased consistently with water table depth across all lineages in the site with lower soil fertility (Ducke, Figure 3 first column), but had more contrasting patterns of change along WTD in the site with higher soil fertility (Tarumã, Figure 3 second column). Thus, although the average trend was of decreasing LMA and LT and increasing FP and LDMC with WTD in the more fertile Tarumã site, we can see on Figure 3 that some botanical families actually had the opposed trend. For example, Lecythidaceae had higher LMA and LT in the deep-water table clay plots of Tarumã (Figure 3 A, B), and Fabaceae, Rubiaceae and Lauraceae decreased their FP values towards the most fertile plots of Tarumã (Figure 3 C), while other families had the opposite. In the other hand, Sapotaceae and Moraceae decreased their LDMC values as the fertility gradient increased towards the clay plots, contrasting with the mean trend of variation of this trait (Figure 3 C, D). There was no significant effect of fertility, WTD or their interaction on LD, although there were differences in LD among lineages (Table 3).

Table 3. ANOVA results (F values and significance) for the fitted linear model testing the effect of lineages, Sum of Bases, WTD and their interactions for each leaf trait measured.

	LMA	**LT**	**FP**	**LDMC**	**LD**
Lineages	3.74 *	2.24	5.32 *	18.71 ***	20.55 ***
Sum of Bases	2.06	0.56	25.01 ***	8.64 *	0.21
WTD	2.49	2.26	0	1.01	0.56
Lineages: Sum of Bases	0.28	0.09	1.2	0.42	0.48
Lineages: WTD	1.51	0.41	0.72	0.88	1.63
Sum of Bases: WTD	10.77 **	5.27 *	0.4	0.24	0.34

Significance codes: (***) 0.001; (**) 0.01; (*) 0.05; (.) 0.1.

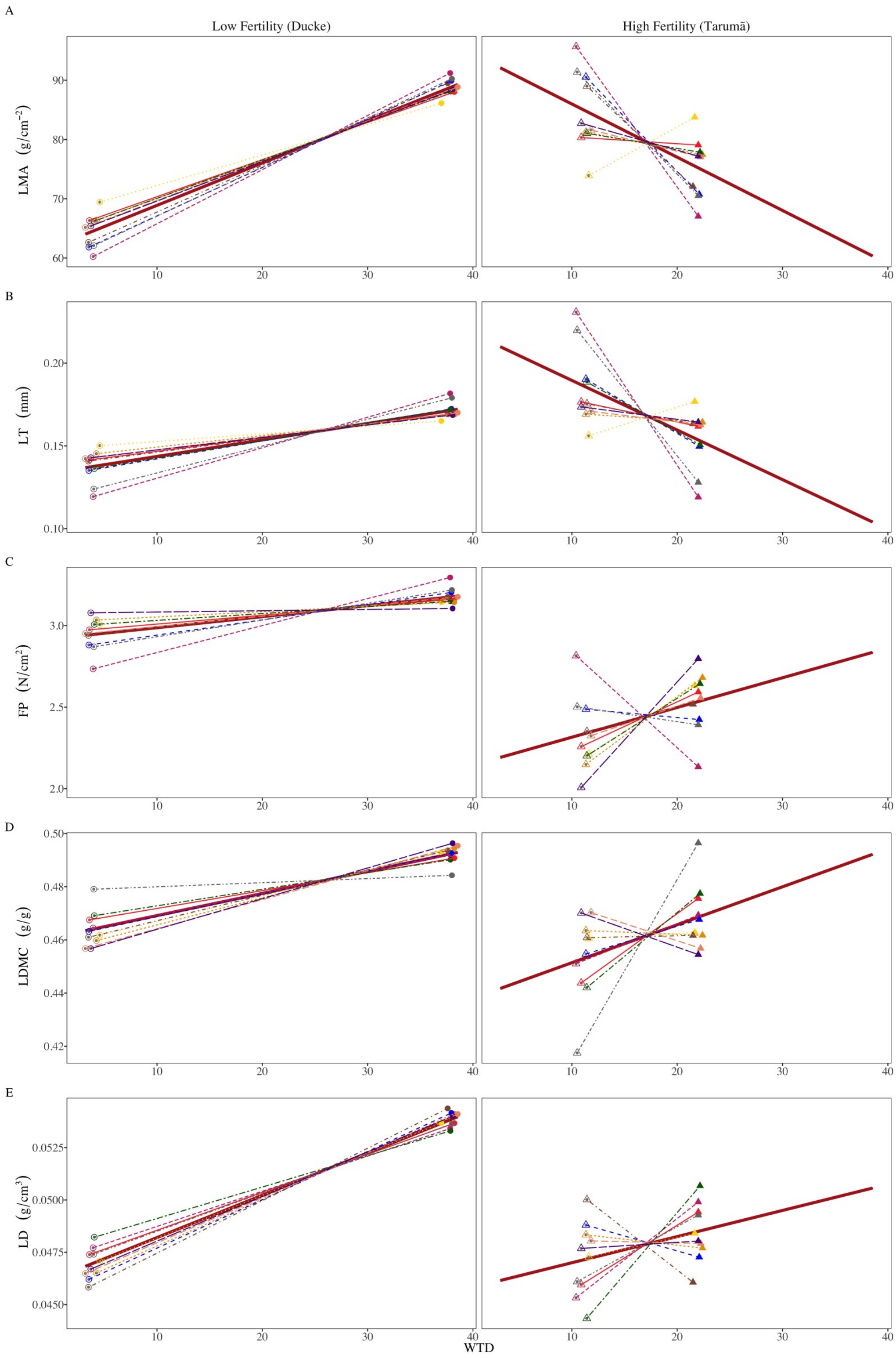
A
Low Fertility (Ducke)
High Fertility (Tarumã)
LMA (g/cm^{-2})
60
70
80
90
B
LT (mm)
0.10
0.15
0.20
C
FP (N/cm^2)
2.0
2.5
3.0
D
LDMC (g/g)
0.42
0.44
0.46
0.48
0.50
E
LD (g/cm^3)
0.0450
0.0475
0.0500
0.0525
10
20
30
40
WTD

Figure 3. Partial relationships among the average community trait means, the soil gradient of sum of bases and water table depth (WTD) and botanical lineages. **(A)** Leaf Mass per Area, **(B)** Force to Punch, **(C)** Leaf Thickness, **(D)** Leaf Dry Matter Content, **(E)** Leaf Density. Filled symbols representing clay and non-filled the sand soils. Burseraceae (red); Chrysobalanaceae (orange); Fabaceae (lilac); Lauraceae (blue); Lecythidaceae (golden); Malvaceae (brown), Moraceae (pink); Myrtaceae (green); Rubiaceae (gray) and Sapotaceae (purple).

DISCUSSION

We investigated whether functional traits related to leaf resistance change along two soil resource gradients (fertility and water availability), which vary both within and across the two studied sites in central Amazonian forests. Our results demonstrate that neither soil fertility or water availability alone drive the selection of leaf resistance strategies, but rather the interaction of them.

The ecological theory posits that leaf resistance traits should emerge as a response to soil nutrient limitation, through selection of investments on though tissues better able to resist herbivores, thus increasing leaf longevity and photosynthetic returns of those hard-won nutrient [9,15,27,55]. However, plants must adjust to multiple environmental pressures at different spatial scales, which may change the patterns expected from the global scale analyses, such as those in the leaf economic spectrum [34]. We observed here that, although lower fertility indeed selected some traits linked to leaf resistance (Force to Punch and Leaf Dry Matter Content), which were consistently higher on low fertility plots irrespective of other factors, other traits (LMA and LT) did not follow that simple expectation and were strongly affected by soil hydrology.

Plateaus with clay soils at Ducke are much drier the during the dry season than the lowland valleys [56], and tree roots probably cannot access the deep (37 – 40 m) water table below plateaus [57]. This suggests that the increase in LMA and LT towards clay soils is a response to the water limitation instead of a response to nutrient levels, since clays have a higher fertility than sands. Therefore, greater investment in LMA and LT do not respond solely to conservation and efficient use of limited nutrients, but rather to conservation and efficient use of water, a more limiting resource in the high plateaus of Ducke. A previous study comparing valley (sand soil) and plateaus (clay soil) canopy trees at Ducke also reported higher LMA for clay species, as well as a number of features associated with water economy, and attributed the selection of these traits to the water gradient [33]. Similarly, other studies reported that species found in water-limited

areas had higher LMA [11,58]. Experiments in greenhouse showed that low water availability in high nutrient fertilized plants led to increased LMA and LD [38]. Thus, greater larger nutrient availability coupled with lower water availability should also generate leaf resistance, as observed in the clay soils of the Ducke plateaus.
In contrast, greater investment in LMA and LT in sand soils with lower fertility in Tarumã, indicate a combined response to conservation and efficient use of soil water and nutrients, since the shorter WTD gradient starting at 10 m means that these sandy soils are subject to stress both due to lack of nutrients and a low water supply during the dry season, when water levels can drop below root access [42,59]. Therefore, the results from our two sites show that differences in the mesoscale (~ 10 km) landscape topography can change the range of variation of soil resources, their correlation and thus the patterns in the selection filters of leaf resistance traits.

The higher values of FP and LDMC in low fertility sand plots of both sites, and also higher on average in the lower fertility site (Ducke) agreed with the classical expectations [60] and empirical studies demonstrating that, at lower fertility environments, plants invest their limited resources in building tough and resistance leaves to avoid loss of nutrients [17,61–63].

Our PCA of the leaf resistance traits suggests that although both fertility and WTD gradients determine the leaf resistance strategies at central Amazonian forests, limitations in nutrient and water can select different strategies. Sandy soils that were both nutrient limited and have water stress (Tarumã) exerted pressure for greater investment in LMA and LT, whereas general nutrient limitation selected for higher investments in FP, LDMC and LD at Ducke [64]. Overall, lineages had convergent trends in the trait variation at site with lower average fertility, suggesting strong filter for higher structural safety against water loss at clay plateaus with lower water availability, besides any phylogenetic constraints.

Overall, lineages had convergent trends in the trait variation at site with lower average fertility, suggesting strong filter for higher structural safety against water loss at clay plateaus with lower water availability, besides any phylogenetic constraints. Nevertheless, some lineages exhibited divergences in their leaf resistance strategies at the site with higher average fertility. To understand this lack of convergence we need to consider (1) the relationships that leaf traits have among each other, and (2) that each lineage could select different leaf resistance strategies, not implying higher investments in all traits evaluated here as a set. First, the components of LMA, the leaf thickness (LT) and leaf density (LD), can be uncorrelated [38,58,65,66], and even totally independent among species in the same environment, indicating that controls on LT and LD can be exerted by different mechanisms [67]. Therefore, changes in either LT or LD may consequently affect LMA, LDMC [11,39] and FP [4,35,68] in different ways across environments with contrasting resource availability [69]. Second, considering how leaf resistance is constituted in terms of those traits, they may differ in response to other environmental gradients not evaluated here, leading to the selection of different leaf resistance strategies in lineages [60,63]. Therefore, each lineage may be investing in at least one resistance trait, but not all resistance traits together [15].

CONCLUSIONS

The results shown here suggest that both fertility and WTD gradients determine leaf resistance strategies in central Amazonian forests. Therefore, nutrients can be only considered as the main determinant of leaf resistance when water is not a limited resource. It is important to consider that functional traits related to leaf resistance may be evolutionary responses to several environmental predictors, including nutrient limitation and water availability. The leaf resistance strategy of a single lineage does not appear to be defined by investing in all resistance traits as a set, the larger investment in one or a few resistance traits seems to be sufficient to ensure tree survival along of studied environmental gradients.

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REFERENCES

1. Violle, C.; Navas, M.-L.; Vile, D.; Kazakou, E.; Fortunel, C.; Hummel, I.; Garnier, E. Let the concept of trait be functional! *Oikos* **2007**, *116*, 882–892.

2. Fortunel, C.; Paine, C.E.T.; Fine, P.V.A.; Kraft, N.J.B.; Baraloto, C. Environmental factors predict community functional composition in Amazonian forests. *J. Ecol.* **2014**, *102*, 145–155.

3. Coley, P.D. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* **1983**, *53*, 209–234.

4. Choong, M.F.; Lucas, P.W.; Ong, J.S.Y.; Pereira, B.; Tan, H.T.W.; Turner, I.M. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytol.* **1992**, *121*, 597–610.

5. Fine, P.V.A.; Miller, Z.J.; Mesones, I.; Irazuzta, S.; Appel, H.M.; Stevens, M.H.H.; Sääksjärvi, I.; Schultz, J.C.; Coley, P.D. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* **2006**, *87*, 150–162.

6. Onoda, Y.; Westoby, M.; Adler, P.B.; Choong, A.M.F.; Clissold, F.J.; Cornelissen, J.H.C.; Díaz, S.; Dominy, N.J.; Elgart, A.; Enrico, L.; et al. Global patterns of leaf mechanical properties. *Ecol. Lett.* **2011**, *14*, 301–312.

7. Chapin, F.S.; Autumn, K.; Pugnaire, F. Evolution of Suites of Traits in Response to Environmental Stress. *Am. Nat.* **1993**, *142*, 78–92.

8. Wright, I.J.; Westoby, M.; Reich, P.B. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *J. Ecol.* **2002**, *90*, 534–543.

9. Andersen, K.M.; Corre, M.D.; Turner, B.L.; Dalling, J.W. Plant-soil associations in a lower montane tropical forest: Physiological acclimation and herbivore-mediated responses to nitrogen addition. *Funct. Ecol.* **2010**, *24*, 1171–1180.

10. Andersen, K.M.; Turner, B.L.; Dalling, J.W. Seedling performance trade-Offs influencing habitat filtering along a soil nutrient gradient in a tropical forest. *Ecology* **2014**, *95*, 3399–3413.

11. De La Riva, E.G.; Olmo, M.; Poorter, H.; Ubera, J.L.; Villar, R. Leaf mass per area (LMA) and its relationship with leaf structure and anatomy in 34 mediterranean woody species along a water availability gradient. *PLoS One* **2016**, *11*, 1–18.

12. Strauss, S.Y.S.; Agrawal, A.A. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.* **1999**, *14*, 179–185.

13. Hanley, M.E.; Lamont, B.B.; Fairbanks, M.M.; Rafferty, C.M. Plant structural traits and their role in anti-herbivore defence. *Perspect. Plant Ecol. Evol. Syst.* **2007**, *8*, 157–178.

14. Edwards, C.; Read, J.; Sanson, G. Characterising sclerophylly: some mechanical properties of leaves from heath and forest. *Oecologia* **2000**, *123*, 158–167.

15. Salleo, S.; Nardini, A. Sclerophylly: Evolutionary advantage or mere epiphenomenon ? *Plant Biosyst.* **2000**, *134*, 247–259.

16. Grime, J.P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **1977**, *111*, 1169–1194.

17. Read, J.; Sanson, G.D.; De Garine-Wichatitsky, M.; Jaffré, T. Sclerophylly in two contrasting tropical environments: Low nutrients vs. low rainfall. *Am. J. Bot.* **2006**, *93*, 1601–1614.

18. Diaz, S.; Cabido, M.; Casanoves, F. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* **1998**, *9*, 113–122.

19. Agrawal, A.A.; Fishbein, M. Plant defense syndromes. *Ecology* **2006**, *87*.

20. Anderson, L.O.; Malhi, Y.; Ladle, R.J.; Aragão, L.E.O.C.; Shimabukuro, Y.; Phillips, O.L.; Baker, T.; Costa, A.C.L.; Espejo, J.S.; Higuchi, N.; et al. Influence of landscape heterogeneity on spatial patterns of wood productivity, wood specific density and above ground biomass in Amazonia. *Biogeosciences* **2009**, *6*, 1883–1902.

21. Quesada, C.A.; Lloyd, J.; Anderson, L.O.; Fyllas, N.M.; Schwarz, M.; Czimczik, C.I. Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences* **2011**, *8*, 1415–1440.

22. Anderson, A.B. White-Sand Vegetation of Brazilian Amazonia. *Biotropica* **1981**, *13*, 199–210.

23. Fine, P.V.A.; Mesones, I.; Coley, P.D. Herbivores promote habitat specialization by trees in Amazonian forests. *Science (80-.).* **2004**, *305*, 663–665.

24. Duivenvoorden, J.F.; Svenning, J.-C.; Wright, S.J. Beta Diversity in Tropical Forests. *Science (80-.).* **2002**, *295*, 636–637.

25. Gentry, A.H. Tropical Forest Biodiversity: Distributional patterns and their conservational significance. *Oikos* **1992**, *63*, 19–28.

26. Nardoto, G.B.; Ometto, J.P.H.B.; Ehleringer, J.R.; Higuchi, N.; Bustamante, M.M.D.C.; Martinelli, L.A. Understanding the influences of spatial patterns on N availability within the Brazilian Amazon forest. *Ecosystems* **2008**, *11*, 1234–1246.

27. Lamarre, G.P.A.; Baraloto, C.; Fortunel, C.; Dávila, N.; Mesones, I.; Rios, J.G.; Ríos, M.; Valderrama, E.; Pilco, M.V.; Fine, P.V.A. Herbivory, growth rates, and habitat specialization in tropical tree lineages: Implications for Amazonian beta-diversity. *Ecology* **2012**, *93*, 195–210.

28. Costa, F.R.C.; Magnusson, W.E.; Luizao, R.C. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *J. Ecol.* **2005**, *93*, 863–878.

29. Jones, M.M.; Tuomisto, H.; Clark, D.B.; Olivas, P. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *J. Ecol.* **2006**, *94*, 181–195.

30. Zuquim, G.; Tuomisto, H.; Jones, M.M.; Prado, J.; Figueiredo, F.O.G.; Moulatlet, G.M.; Costa, F.R.C.; Quesada, C.A.; Emilio, T. Predicting environmental gradients with fern species composition in Brazilian Amazonia. *J. Veg. Sci.* **2014**, *25*, 1195–1207.

31. Pansonato, M.P.; Costa, F.R.C.; de Castilho, C. V; Carvalho, F.A.; Zuquim, G. Spatial Scale or Amplitude of Predictors as Determinants of the Relative Importance of Environmental Factors to Plant Community Structure. *Biotropica* **2013**, *45*, 299–307.

32. de Castilho, C. V.; Magnusson, W.E.; de Araújo, R.N.O.; Luizão, R.C.C.; Luizão, F.J.; Lima, A.P.; Higuchi, N. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *For. Ecol. Manage.* **2006**, *234*, 85–96.

33. Cosme, L.H.M.; Schietti, J.; Costa, F.R.C.; Oliveira, R.S. The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytol.* **2017**, *215*, 113–125.

34. Wright, I.J.; Reich, P.B.; Westoby, M.; Ackerly, D.D.; Baruch, Z.; Bongers, F.; Cavender-Bares, J.; Chapin, T.; Cornellssen, J.H.C.; Diemer, M.; et al. The worldwide leaf economics spectrum. *Nature* **2004**, *428*, 821–827.

35. Turner, I.M. Sclerophylly: Primarily Protective? *Funct. Ecol.* **1994**, *8*, 669.

36. Brunt, C.; Read, J.; Sanson, G.D. Changes in resource concentration and defence during leaf development in a tough-leaved (Nothofagus moorei) and soft-leaved (Toona ciliata) species. *Oecologia* **2006**, *148*, 583–592.

37. Baraloto, C.; Morneau, F.; Bonal, D.; Blanc, L.; Ferry, B. Seasonal water stress tolerance and habitat associations. *Ecology* **2002**, *88*, 478–489.

38. Witkowski, E.T.F.; Lamont, B.B. Leaf specific mass confounds leaf density and thickness. *Oecologia* **1991**, *88*, 486–493.

39. Vile, D.; Garnier, É.; Shipley, B.; Laurent, G.; Navas, M.L.; Roumet, C.; Lavorel, S.; Díaz, S.; Hodgson, J.G.; Lloret, F.; et al. Specific leaf area and dry matter content estimate thickness in laminar leaves. *Ann. Bot.* **2005**, *96*, 1129–1136.

40. Ribeiro, J.E.L.S.; Hopkins, M.J.G.; Vicentini, A.; Sothers, C.A.; Costa, M.A.S.; Brito, J.; Souza, M.A.D.; Martins, L.H.; Lohmann, L.G.; Assunção, P.A.; et al. *Flora da Reserva Ducke. Guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central*; (INPA);, I.N. de P. da A., (DFID), D. for I.D., Eds.; Midas Printing Ltd. China, 1999;

41. Drucker, D.P.; Costa, F.R.C.; Magnusson, W.E. How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. *J. Trop. Ecol.* **2008**, *24*, 65–74.

42. Tomasella, J.; Hodnett, M.G.; Cuartas, L.A.; Nobre, A.D.; Waterloo, M.J.; Oliveira, S.M. The water balance of an Amazonian micro-cathment: the effect of interannual variability of rainfall on hydrological behaviour. *Hydrol. Process.* **2008**, *1245*, 2133–2147.

43. Pinto, W.H.A.; Carvalho, A. Geoprocessamento aplicado a análise físico-territorial da área do Tarumã - AM. *An. XII Simpósio Bras. Sensoriamento Remoto* **2007**, 3003–3009.

44. Sombroek, W. Spatial and Temporal Patterns of Amazon Rainfall. *AMBIO A J. Hum. Environ.* **2001**, *30*, 388–396.

45. Phillips, O.L.; Martínez, R.V.; Vargas, P.N.; Monteagudo, A.L.; Zans, M.E.C.; Sánchez, W.G.; Cruz, A.P.; Timaná, M.; Yli-Halla, M.; Rose, S. Efficient plot-based floristic assessment of tropical forests. *J. Trop. Ecol.* **2003**, *19*, 629–645.

46. Baraloto, C.; Rabaud, S.; Moltos, Q.; Blancs, L.; Fortunel, C.; Hérault, B.; Dávila, N.; Mesones, I.; Rios, M.; Valderrama, E.; et al. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Glob. Chang. Biol.* **2011**, *17*, 2677–2688.

47. Rennó, C.D.; Nobre, A.D.; Cuartas, L.A.; Soares, J.V.; Hodnett, M.G.; Tomasella, J.; Waterloo, M.J. HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. *Remote Sens. Environ.* **2008**, *112*, 3469–3481.

48. Schietti, J.; Emilio, T.; Rennó, C.D.; Drucker, D.P.; Costa, F.R.C.; Nogueira, A.; Baccaro, F.B.; Figueiredo, F.; Castilho, C. V.; Kinupp, V.; et al. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecol. Divers.* **2014**, *7*, 241–253.

49. Cornelissen, J.H.C.; Lavorel, S.; Garnier, E.; Díaz, S.; Buchmann, N.; Gurvich, D.E.; Reich, P.B.; ter Steege, H.; Morgan, H.D.; Heijden, van der M.G.A.; et al. A handbook of protocols for standardised and easy measurements of plant functional traits worldwide. Aust. J. Bot. 51, 335-380. *Aust. J. Bot.* **2003**, *51*, 335–380.

50. Pérez-Harguindeguy, N.; Díaz, S.; Garnier, E.; Lavorel, S.; Poorter, H.; Jaureguiberry, P.; Bret-Harte, M.S.; Cornwell, W.K.; Craine, J.M.; Gurvich, D.E.; et al. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **2013**, *61*, 167–234.

51. Aranwela, N.; Sanson, G.; Read, J. Methods of assessing leaf-fracture properties. *New Phytol.* **1999**, *144*, 369–393.

52. R Core Team R: A language and environment for statistical computing. *R Found. Stat. Comput. Vienna, Austria* 2019.

53. Breheny, P.; Burchett, W. Package 'visreg': Visualization of Regression Models. *R J.* **2017**, *9*, 56–71.

54. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*; New York, 2016; ISBN 978-3-319-24277-4.

55. Endara, M.J.; Weinhold, A.; Cox, J.E.; Wiggins, N.L.; Coley, P.D.; Kursar, T.A. Divergent evolution in antiherbivore defenses within species complexes at a single Amazonian site. *J. Ecol.* **2015**, *103*, 1107–1118.

56. Hodnett, M.G.; Vendrame, I.; Marques Filho, D.; Oyama, M.D.; Tomasella, J. Soil water storage and groundwater behaviour in a catenary sequence beneath forest in central Amazonia: I. Comparisons between plateau, slope and valley floor. *Hydrol. Earth Syst. Sci.* **1997**, *1*, 265–277.

57. Nepstad, D.C.; De Carvalho, C.R.; Davidson, E.A.; Jipp, P.H.; Lefebvre, P.A.; Negreiros, G.H.; da Silva, E.D.; Stone, T.A.; Trumbore, S.E.; Vieira, S. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **1994**, *372*, 666–669.

58. Cunningham, S.A.; Summerhayes, B.; Westoby, M. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecol. Monogr.* **1999**, *69*, 569–588.

59. Damasco, G.; Vicentini, A.; Castilho, C. V.; Pimentel, T.P.; Nascimento, H.E.M. Disentangling the role of edaphic variability, flooding regime and topography of Amazonian white-sand vegetation. *J. Veg. Sci.* **2013**, *24*, 384–394.

60. Reich, P.B. The world-wide "fast-slow" plant economics spectrum: A traits manifesto. *J. Ecol.* **2014**, *102*, 275–301.

61. Fine, P.V.A.; Daly, D.C.; Muñoz, G.V.; Mesones, I.; Cameron, K.M. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. *Evolution (N. Y).* **2005**, *59*, 1464.

62. Read, J.; Sanson, G.D. Characterizing sclerophylly: The mechanical properties of a diverse range of leaf types. *New Phytol.* **2003**, *160*, 81–99.

63. Read, J.; Sanson, G.D.; Lamont, B.B. Leaf mechanical properties in sclerophyll woodland and shrubland on contrasting soils. *Plant Soil* **2005**, *276*, 95–113.

64. Wright, I.J.; Reich, P.B.; Westoby, M. Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitats. *Funct. Ecol.* **2001**, *15*, 423–434.

65. Niinemets, Ü. Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytol.* **1999**, *144*, 35–47.

66. Niinemets, Ü. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **2001**, *82*, 453–469.

67. Coste, S.; Roggy, J.; Imbert, P.; Born, C.; Bonal, D.; Dreyer, E. Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance Leaf photosynthetic traits of 14 tropical rain forest species in relation. *Tree Physiol.* **2005**, *25*.

68. Onoda, Y.; Schieving, F.; Anten, N.P.R. Effects of light and nutrient availability on leaf mechanical properties of Plantago major: A conceptual approach. *Ann. Bot.* **2008**, *101*, 727–736.

69. Hodgson, J.G.; Montserrat-Martí, G.; Charles, M.; Jones, G.; Wilson, P.; Shipley, B.; Sharafi, M.; Cerabolini, B.E.L.; Cornelissen, J.H.C.; Band, S.R.; et al. Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Ann. Bot.* **2011**, *108*, 1337–1345.

CONCLUSÃO GERAL

Nossos resultados confirmam que há maior estruturação foliar em solos arenosos do Tarumã, sugerindo que o maior investimento em LMA e LT é determinado pelo gradiente de fertilidade do solo. Embora a diferença dos traços estruturais entre tipos de solo na RFAD não tenha sido significativa, observou-se maior investimento estrutural em solos argilosos. Tal padrão contrastante indicaria que os traços estruturais variam mais com a aridez do solo (sujeito ao gradiente hidro-edáfico da área), que com o status de nutrientes.

A fertilidade do solo e a disponibilidade de água estão afetando certos componentes da resistência foliar por diferentes mecanismos, determinando consequentemente as relações que os traços têm entre si. Portanto, os nutrientes podem ser apenas considerados como principal determinante da resistência foliar quando não existe efeito da disponibilidade de água. A resistência foliar de uma linhagem em particular não parece ser definida pelo investimento em todos os traços de resistência como um conjunto, o investimento maior em um ou poucos traços estruturais parece ser suficiente para garantir a sobrevivência em cada um dos ambientes estudados.

REFERÊNCIAS BIBLIOGRÁFICAS

1. Violle, C.; Navas, M.-L.; Vile, D.; Kazakou, E.; Fortunel, C.; Hummel, I.; Garnier, E. Let the concept of trait be functional! *Oikos* **2007**, *116*, 882–892.
2. Fortunel, C.; Paine, C.E.T.; Fine, P.V.A.; Kraft, N.J.B.; Baraloto, C. Environmental factors predict community functional composition in Amazonian forests. *J. Ecol.* **2014**, *102*, 145–155.
3. Coley, P.D. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* **1983**, *53*, 209–234.
4. Choong, M.F.; Lucas, P.W.; Ong, J.S.Y.; Pereira, B.; Tan, H.T.W.; Turner, I.M. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytol.* **1992**, *121*, 597–610.
5. Fine, P.V.A.; Miller, Z.J.; Mesones, I.; Irazuzta, S.; Appel, H.M.; Stevens, M.H.H.; Sääksjärvi, I.; Schultz, J.C.; Coley, P.D. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* **2006**, *87*, 150–162.
6. Onoda, Y.; Westoby, M.; Adler, P.B.; Choong, A.M.F.; Clissold, F.J.; Cornelissen, J.H.C.; Díaz, S.; Dominy, N.J.; Elgart, A.; Enrico, L.; et al. Global patterns of leaf mechanical properties. *Ecol. Lett.* **2011**, *14*, 301–312.
7. Chapin, F.S.; Autumn, K.; Pugnaire, F. Evolution of Suites of Traits in Response to Environmental Stress. *Am. Nat.* **1993**, *142*, 78–92.

8. Wright, I.J.; Westoby, M.; Reich, P.B. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *J. Ecol.* **2002**, *90*, 534–543.

9. Andersen, K.M.; Corre, M.D.; Turner, B.L.; Dalling, J.W. Plant-soil associations in a lower montane tropical forest: Physiological acclimation and herbivore-mediated responses to nitrogen addition. *Funct. Ecol.* **2010**, *24*, 1171–1180.

10. Andersen, K.M.; Turner, B.L.; Dalling, J.W. Seedling performance trade-Offs influencing habitat filtering along a soil nutrient gradient in a tropical forest. *Ecology* **2014**, *95*, 3399–3413.

11. De La Riva, E.G.; Olmo, M.; Poorter, H.; Ubera, J.L.; Villar, R. Leaf mass per area (LMA) and its relationship with leaf structure and anatomy in 34 mediterranean woody species along a water availability gradient. *PLoS One* **2016**, *11*, 1–18.

12. Strauss, S.Y.S.; Agrawal, A.A. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.* **1999**, *14*, 179–185.

13. Hanley, M.E.; Lamont, B.B.; Fairbanks, M.M.; Rafferty, C.M. Plant structural traits and their role in anti-herbivore defence. *Perspect. Plant Ecol. Evol. Syst.* **2007**, *8*, 157–178.

14. Edwards, C.; Read, J.; Sanson, G. Characterising sclerophylly: some mechanical properties of leaves from heath and forest. *Oecologia* **2000**, *123*, 158–167.

15. Salleo, S.; Nardini, A. Sclerophylly: Evolutionary advantage or mere epiphenomenon ? *Plant Biosyst.* **2000**, *134*, 247–259.

16. Grime, J.P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **1977**, *111*, 1169–1194.

17. Read, J.; Sanson, G.D.; De Garine-Wichatitsky, M.; Jaffré, T. Sclerophylly in two contrasting tropical environments: Low nutrients vs. low rainfall. *Am. J. Bot.* **2006**, *93*, 1601–1614.

18. Diaz, S.; Cabido, M.; Casanoves, F. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* **1998**, *9*, 113–122.

19. Agrawal, A.A.; Fishbein, M. Plant defense syndromes. *Ecology* **2006**, *87*.

20. Anderson, L.O.; Malhi, Y.; Ladle, R.J.; Aragão, L.E.O.C.; Shimabukuro, Y.; Phillips, O.L.; Baker, T.; Costa, A.C.L.; Espejo, J.S.; Higuchi, N.; et al. Influence of landscape heterogeneity on spatial patterns of wood productivity, wood specific density and above ground biomass in Amazonia. *Biogeosciences* **2009**, *6*, 1883–1902.

21. Quesada, C.A.; Lloyd, J.; Anderson, L.O.; Fyllas, N.M.; Schwarz, M.; Czimczik, C.I. Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences* **2011**, *8*, 1415–1440.

22. Anderson, A.B. White-Sand Vegetation of Brazilian Amazonia. *Biotropica* **1981**, *13*, 199–210.

23. Fine, P.V.A.; Mesones, I.; Coley, P.D. Herbivores promote habitat specialization by trees in Amazonian forests. *Science (80-.).* **2004**, *305*, 663–665.

24. Duivenvoorden, J.F.; Svenning, J.-C.; Wright, S.J. Beta Diversity in Tropical Forests. *Science (80-.).* **2002**, *295*, 636–637.

25. Gentry, A.H. Tropical Forest Biodiversity: Distributional patterns and their conservational significance. *Oikos* **1992**, *63*, 19–28.

26. Nardoto, G.B.; Ometto, J.P.H.B.; Ehleringer, J.R.; Higuchi, N.; Bustamante, M.M.D.C.; Martinelli, L.A. Understanding the influences of spatial patterns on N availability within the Brazilian Amazon forest. *Ecosystems* **2008**, *11*, 1234–1246.

27. Lamarre, G.P.A.; Baraloto, C.; Fortunel, C.; Dávila, N.; Mesones, I.; Rios, J.G.; Ríos, M.; Valderrama, E.; Pilco, M.V.; Fine, P.V.A. Herbivory, growth rates, and habitat specialization in tropical tree lineages: Implications for Amazonian beta-diversity. *Ecology* **2012**, *93*, 195–210.

28. Costa, F.R.C.; Magnusson, W.E.; Luizao, R.C. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *J. Ecol.* **2005**, *93*, 863–878.

29. Jones, M.M.; Tuomisto, H.; Clark, D.B.; Olivas, P. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *J. Ecol.* **2006**, *94*, 181–195.

30. Zuquim, G.; Tuomisto, H.; Jones, M.M.; Prado, J.; Figueiredo, F.O.G.; Moulatlet, G.M.; Costa, F.R.C.; Quesada, C.A.; Emilio, T. Predicting environmental gradients with fern species composition in Brazilian Amazonia. *J. Veg. Sci.* **2014**, *25*, 1195–1207.

31. Pansonato, M.P.; Costa, F.R.C.; de Castilho, C. V; Carvalho, F.A.; Zuquim, G. Spatial Scale or Amplitude of Predictors as Determinants of the Relative Importance of Environmental Factors to Plant Community Structure. *Biotropica* **2013**, *45*, 299–307.

32. de Castilho, C. V.; Magnusson, W.E.; de Araújo, R.N.O.; Luizão, R.C.C.; Luizão, F.J.; Lima, A.P.; Higuchi, N. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *For. Ecol. Manage.* **2006**, *234*, 85–96.

33. Cosme, L.H.M.; Schietti, J.; Costa, F.R.C.; Oliveira, R.S. The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytol.* **2017**, *215*, 113–125.

34. Wright, I.J.; Reich, P.B.; Westoby, M.; Ackerly, D.D.; Baruch, Z.; Bongers, F.; Cavender-Bares, J.; Chapin, T.; Cornellssen, J.H.C.; Diemer, M.; et al. The worldwide leaf economics spectrum. *Nature* **2004**, *428*, 821–827.

35. Turner, I.M. Sclerophylly: Primarily Protective? *Funct. Ecol.* **1994**, *8*, 669.

36. Brunt, C.; Read, J.; Sanson, G.D. Changes in resource concentration and defence during leaf development in a tough-leaved (Nothofagus moorei) and soft-leaved (Toona ciliata) species. *Oecologia* **2006**, *148*, 583–592.

37. Baraloto, C.; Morneau, F.; Bonal, D.; Blanc, L.; Ferry, B. Seasonal water stress tolerance and habitat associations. *Ecology* **2002**, *88*, 478–489.

38. Witkowski, E.T.F.; Lamont, B.B. Leaf specific mass confounds leaf density and thickness. *Oecologia* **1991**, *88*, 486–493.

39. Vile, D.; Garnier, É.; Shipley, B.; Laurent, G.; Navas, M.L.; Roumet, C.; Lavorel, S.; Díaz, S.; Hodgson, J.G.; Lloret, F.; et al. Specific leaf area and dry matter content estimate thickness in laminar leaves. *Ann. Bot.* **2005**, *96*, 1129–1136.

40. Ribeiro, J.E.L.S.; Hopkins, M.J.G.; Vicentini, A.; Sothers, C.A.; Costa, M.A.S.; Brito, J.; Souza, M.A.D.; Martins, L.H.; Lohmann, L.G.; Assunção, P.A.; et al. *Flora da Reserva Ducke. Guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central*; (INPA);, I.N. de P. da A., (DFID), D. for I.D., Eds.; Midas Printing Ltd. China, 1999;

41. Drucker, D.P.; Costa, F.R.C.; Magnusson, W.E. How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. *J. Trop. Ecol.* **2008**, *24*, 65–74.

42. Tomasella, J.; Hodnett, M.G.; Cuartas, L.A.; Nobre, A.D.; Waterloo, M.J.; Oliveira, S.M. The water balance of an Amazonian micro-cathment: the effect of interannual variability of rainfall on hydrological behaviour. *Hydrol. Process.* **2008**, *1245*, 2133–2147.

43. Pinto, W.H.A.; Carvalho, A. Geoprocessamento aplicado a análise físico-territorial da área do Tarumã - AM. *An. XII Simpósio Bras. Sensoriamento Remoto* **2007**, 3003–3009.

44. Sombroek, W. Spatial and Temporal Patterns of Amazon Rainfall. *AMBIO A J. Hum. Environ.* **2001**, *30*, 388–396.

45. Phillips, O.L.; Martínez, R.V.; Vargas, P.N.; Monteagudo, A.L.; Zans, M.E.C.; Sánchez, W.G.; Cruz, A.P.; Timaná, M.; Yli-Halla, M.; Rose, S. Efficient plot-based floristic assessment of tropical forests. *J. Trop. Ecol.* **2003**, *19*, 629–645.

46. Baraloto, C.; Rabaud, S.; Moltos, Q.; Blancs, L.; Fortunel, C.; Hérault, B.; Dávila, N.; Mesones, I.; Rios, M.; Valderrama, E.; et al. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Glob. Chang. Biol.* **2011**, *17*, 2677–2688.

47. Rennó, C.D.; Nobre, A.D.; Cuartas, L.A.; Soares, J.V.; Hodnett, M.G.; Tomasella, J.; Waterloo, M.J. HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. *Remote Sens. Environ.* **2008**, *112*, 3469–3481.

48. Schietti, J.; Emilio, T.; Rennó, C.D.; Drucker, D.P.; Costa, F.R.C.; Nogueira, A.; Baccaro, F.B.; Figueiredo, F.; Castilho, C. V.; Kinupp, V.; et al. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecol. Divers.* **2014**, *7*, 241–253.

49. Cornelissen, J.H.C.; Lavorel, S.; Garnier, E.; Díaz, S.; Buchmann, N.; Gurvich, D.E.; Reich, P.B.; ter Steege, H.; Morgan, H.D.; Heijden, van der M.G.A.; et al. A handbook of protocols for standardised and easy measurements of plant functional traits worldwide. Aust. J. Bot. 51, 335-380. *Aust. J. Bot.* **2003**, *51*, 335–380.

50. Pérez-Harguindeguy, N.; Díaz, S.; Garnier, E.; Lavorel, S.; Poorter, H.; Jaureguiberry, P.; Bret-Harte, M.S.; Cornwell, W.K.; Craine, J.M.; Gurvich, D.E.; et al. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **2013**, *61*, 167–234.

51. Aranwela, N.; Sanson, G.; Read, J. Methods of assessing leaf-fracture properties. *New Phytol.* **1999**, *144*, 369–393.

52. R Core Team R: A language and environment for statistical computing. *R Found. Stat. Comput. Vienna, Austria* 2019.

53. Breheny, P.; Burchett, W. Package 'visreg': Visualization of Regression Models. *R J.* **2017**, *9*, 56–71.

54. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*; New York, 2016; ISBN 978-3-319-24277-4.

55. Endara, M.J.; Weinhold, A.; Cox, J.E.; Wiggins, N.L.; Coley, P.D.; Kursar, T.A. Divergent evolution in antiherbivore defenses within species complexes at a single Amazonian site. *J. Ecol.* **2015**, *103*, 1107–1118.

56. Hodnett, M.G.; Vendrame, I.; Marques Filho, D.; Oyama, M.D.; Tomasella, J. Soil water storage and groundwater behaviour in a catenary sequence beneath forest in central Amazonia: I. Comparisons between plateau, slope and valley floor. *Hydrol. Earth Syst. Sci.* **1997**, *1*, 265–277.

57. Nepstad, D.C.; De Carvalho, C.R.; Davidson, E.A.; Jipp, P.H.; Lefebvre, P.A.; Negreiros, G.H.; da Silva, E.D.; Stone, T.A.; Trumbore, S.E.; Vieira, S. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **1994**, *372*, 666–669.

58. Cunningham, S.A.; Summerhayes, B.; Westoby, M. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecol. Monogr.* **1999**, *69*, 569–588.

59. Damasco, G.; Vicentini, A.; Castilho, C. V.; Pimentel, T.P.; Nascimento, H.E.M. Disentangling the role of edaphic variability, flooding regime and topography of Amazonian white-sand vegetation. *J. Veg. Sci.* **2013**, *24*, 384–394.

60. Reich, P.B. The world-wide "fast-slow" plant economics spectrum: A traits manifesto. *J. Ecol.* **2014**, *102*, 275–301.

61. Fine, P.V.A.; Daly, D.C.; Muñoz, G.V.; Mesones, I.; Cameron, K.M. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. *Evolution (N. Y).* **2005**, *59*, 1464.

62. Read, J.; Sanson, G.D. Characterizing sclerophylly: The mechanical properties of a diverse range of leaf types. *New Phytol.* **2003**, *160*, 81–99.

63. Read, J.; Sanson, G.D.; Lamont, B.B. Leaf mechanical properties in sclerophyll woodland and shrubland on contrasting soils. *Plant Soil* **2005**, *276*, 95–113.

64. Wright, I.J.; Reich, P.B.; Westoby, M. Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitats. *Funct. Ecol.* **2001**, *15*, 423–434.

65. Niinemets, Ü. Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytol.* **1999**, *144*, 35–47.

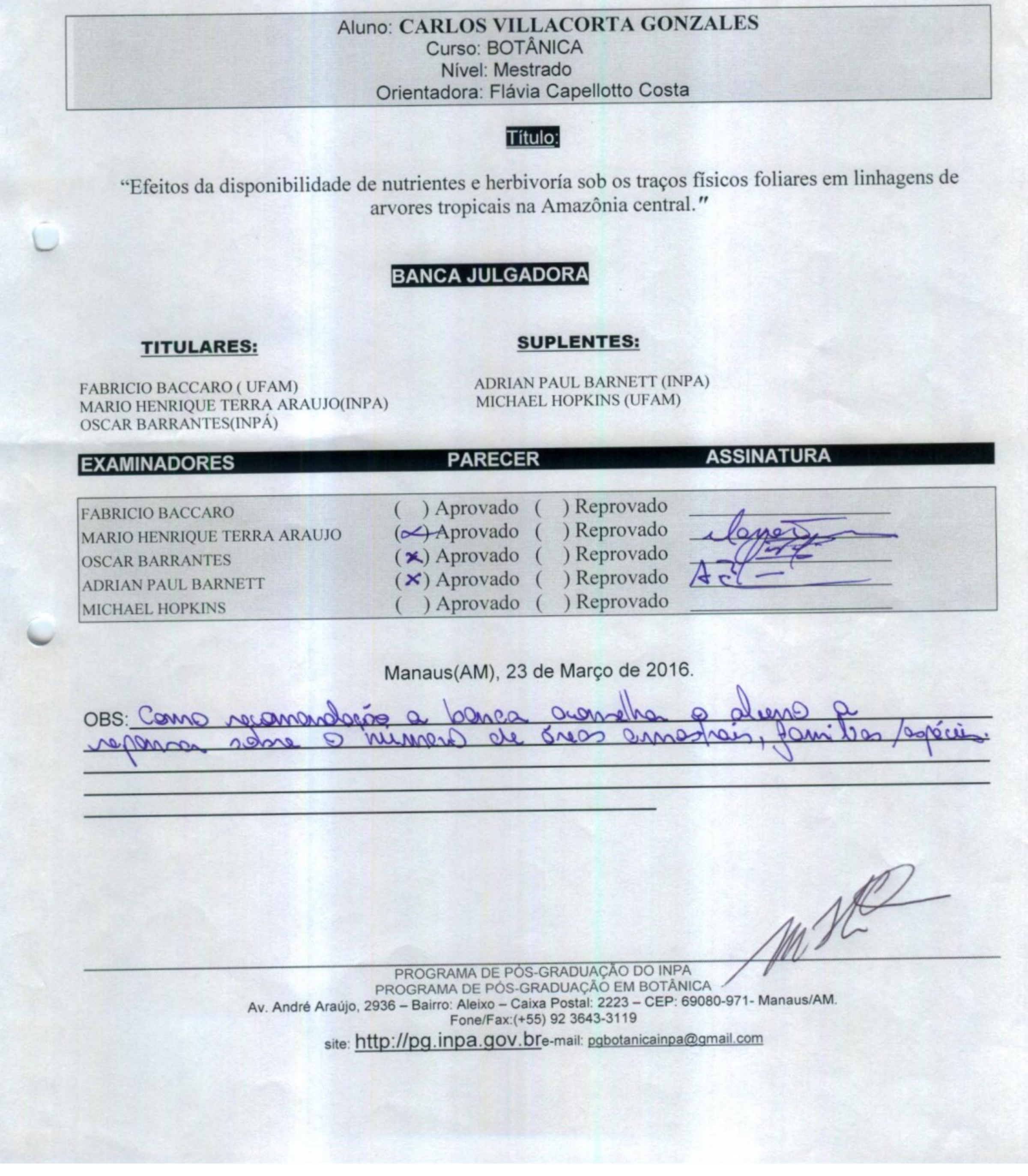
66. Niinemets, Ü. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **2001**, *82*, 453–469.

67. Coste, S.; Roggy, J.; Imbert, P.; Born, C.; Bonal, D.; Dreyer, E. Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance Leaf photosynthetic traits of 14 tropical rain forest species in relation. *Tree Physiol.* **2005**, *25*.

68. Onoda, Y.; Schieving, F.; Anten, N.P.R. Effects of light and nutrient availability on leaf mechanical properties of Plantago major: A conceptual approach. *Ann. Bot.* **2008**, *101*, 727–736.

69. Hodgson, J.G.; Montserrat-Martí, G.; Charles, M.; Jones, G.; Wilson, P.; Shipley, B.; Sharafi, M.; Cerabolini, B.E.L.; Cornelissen, J.H.C.; Band, S.R.; et al. Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Ann. Bot.* **2011**, *108*, 1337–1345.

APÊNDICE A – ATA DA AULA DE QUALIFICAÇÃO



INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
DIVISÃO DOS CURSOS DE PÓS-GRADUAÇÃO

AULA DE QUALIFICAÇÃO

PARECER

Aluno: **CARLOS VILLACORTA GONZALES**
Curso: BOTÂNICA
Nível: Mestrado
Orientadora: Flávia Capellotto Costa

Título:

"Efeitos da disponibilidade de nutrientes e herbivoría sob os traços físicos foliares em linhagens de arvores tropicais na Amazônia central."

BANCA JULGADORA

TITULARES:	**SUPLENTES:**
FABRICIO BACCARO (UFAM)	ADRIAN PAUL BARNETT (INPA)
MARIO HENRIQUE TERRA ARAUJO(INPA)	MICHAEL HOPKINS (UFAM)
OSCAR BARRANTES(INPÁ)	

EXAMINADORES	PARECER		ASSINATURA
FABRICIO BACCARO	( ) Aprovado	( ) Reprovado	
MARIO HENRIQUE TERRA ARAUJO	[✓ Aprovado]	( ) Reprovado	
OSCAR BARRANTES	[✓ Aprovado]	( ) Reprovado	
ADRIAN PAUL BARNETT	[✓ Aprovado]	( ) Reprovado	
MICHAEL HOPKINS	( ) Aprovado	( ) Reprovado	

Manaus(AM), 23 de Março de 2016.

OBS: Como recomendação a banca aconselha o aluno a repensar sobre o número de áreas amostrais, famílias/espécies.

PROGRAMA DE PÓS-GRADUAÇÃO DO INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA
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APÊNDICE B – ATA DA DEFESA ORAL PÚBLICA

ATA DEFESA PÚBLICA DE DISSERTAÇÃO DE MESTRADO DISCENTE DO PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos vinte sete dias do mês de junho de 2017 às 09:00h, na sala de seminários da Biblioteca INPA-Campus I, reuniu-se a Comissão Examinadora da Defesa Pública, composta pelos seguintes membros: Dr. Eduardo Magalhães Borges Prata, do Instituto Nacional de Pesquisas da Amazônia (INPA), Dr. Rafael Leandro de Assis, Instituto Nacional de Pesquisas da Amazônia (INPA/PDBFF) e Dr. Fabrício Beggiato Baccaro, da Universidade Federal do Amazonas (UFAM), tendo como suplentes: Dr. Alberto Vicentini, do Instituto Nacional de Pesquisas da Amazônia (INPA), e Dr. Mário Henrique Terra Araújo, Universidade Estácio de Sá, sob a presidência do primeiro, a fim de proceder a arguição pública da **DISSERTAÇÃO DE MESTRADO**, intitulada: **"Efeito da disponibilidade de nutrientes no solo nos traços físicos foliares em linhagens de árvores tropicais na Amazônia Central"** discente: **Carlos Villacorta Gonzales**, sob orientação da Doutora Flávia Regina Capellotto Costa. Após a exposição, dentro do tempo regulamentar, a discente foi arguida oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

EXAMINADORES	PARECER		ASSINATURA
EDUARDO MAGALHAES BORGES PRATA	(X) APROVADO	( ) REPROVADO	
RAFAEL LEANDRO DE ASSSIS	(x) APROVADO	( ) REPROVADO	
FABRICIO BEGGIATO BACCARO	(X) APROVADO	( ) REPROVADO	
ALBERTO VICENTINI	( ) APROVADO	( ) REPROVADO	
MARIO HENRIQUE T. ARAÚJO	( ) APROVADO	( ) REPROVADO	

Manaus (AM), 27 de junho de 2017.

OBS:____

Dr. Michael John Gilbert Hopkins
Coordenador do Programa de
Pós Graduação em Botânica
PO. 258/ 2014 - DCRO/ INPA

Nada mais havendo, foi lavrado a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.