INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

PRODUÇÃO DE ISOPRENÓIDES E ESTRATÉGIAS DE ALOCAÇÃO DE RECURSOS EM ESPÉCIES ARBÓREAS DA AMAZÔNIA CENTRAL

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Manaus, Amazonas

Setembro/2020

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

Manaus, Amazonas

Setembro/2020

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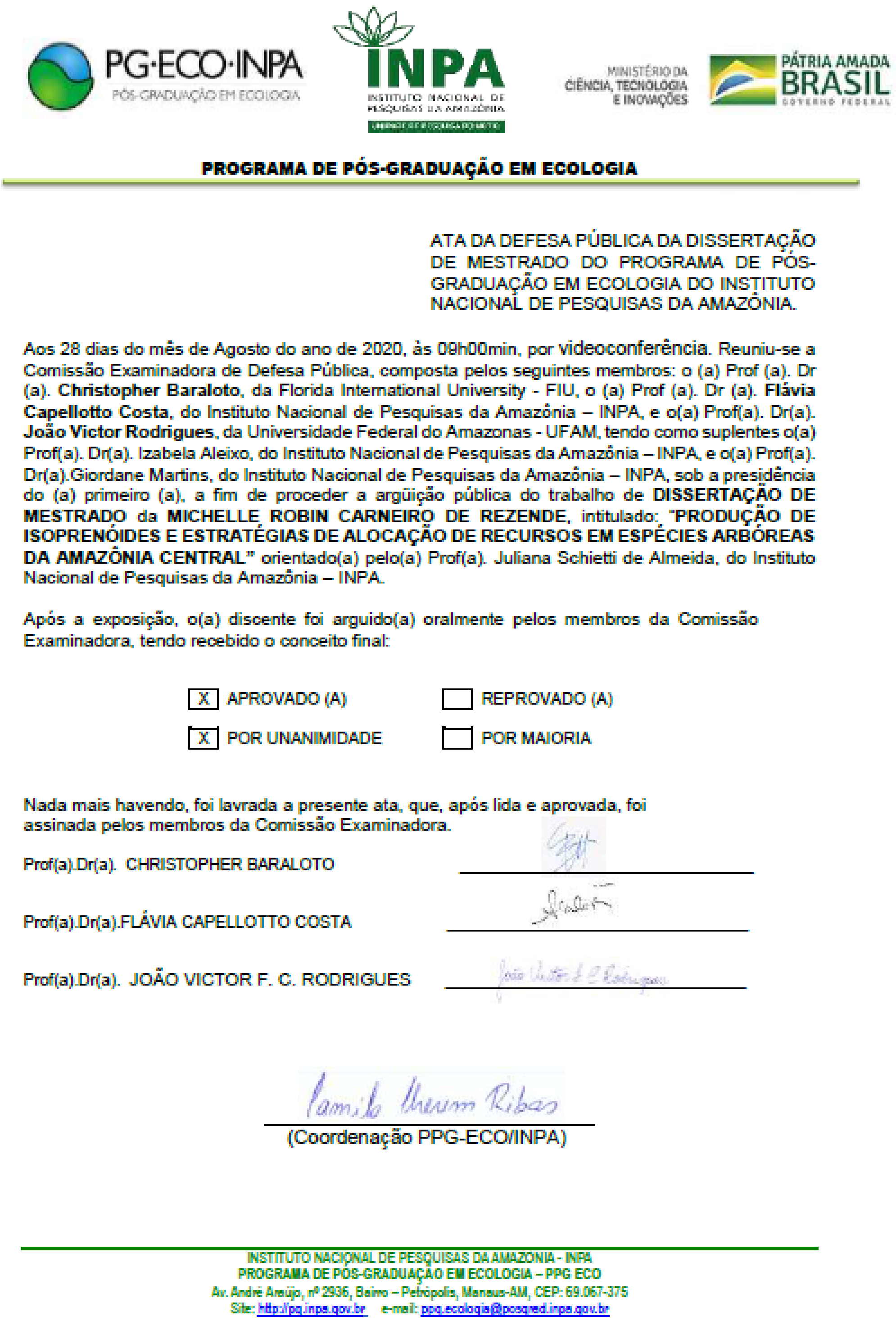

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☒ POR UNANIMIDADE ☐ POR MAIORIA

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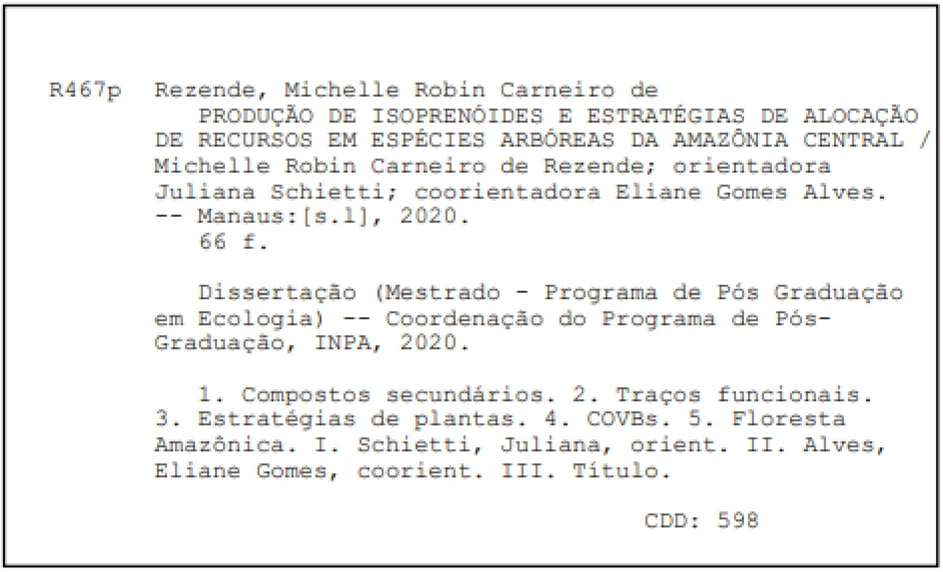

R467p Rezende, Michelle Robin Carneiro de
PRODUÇÃO DE ISOPRENÓIDES E ESTRATÉGIAS DE ALOCAÇÃO DE RECURSOS EM ESPÉCIES ARBÓREAS DA AMAZÔNIA CENTRAL / Michelle Robin Carneiro de Rezende; orientadora Juliana Schietti; coorientadora Eliane Gomes Alves. -- Manaus:[s.l], 2020.
66 f.

Dissertação (Mestrado - Programa de Pós Graduação em Ecologia) -- Coordenação do Programa de Pós-Graduação, INPA, 2020.

1. Compostos secundários. 2. Traços funcionais. 3. Estratégias de plantas. 4. COVBs. 5. Floresta Amazônica. I. Schietti, Juliana, orient. II. Alves, Eliane Gomes, coorient. III. Título.

CDD: 598

SINOPSE

Estudou-se a correlação entre os espectros da economia de carbono - gerados a partir de traços funcionais medidos no nível da folha, da madeira, e da planta-inteira - com a emissão e o estoque de compostos secundários da classe dos isoprenóides, em 27 espécies de árvores da Amazônia Central.

Palavras-chave: compostos secundários, traços funcionais, estratégias de plantas, isopreno, COVBs, floresta Amazônica

AGRADECIMENTOS

A presente dissertação não teria sido possível sem o auxílio e a contribuição de muitas pessoas, às quais sou imensamente grata. Aos meus pais, por todo o carinho e amor, por sempre me apoiarem e me incentivarem na busca de novos sonhos e desafios. Às minhas orientadoras, Juliana Schietti e Eliane Alves, pela orientação e todo o apoio, incentivo, aprendizado e crescimento, tanto profissional quanto pessoal, ao longo desse período de mestrado; pela oportunidade de descobrir, e de me encantar, com a Ecologia Funcional e os Compostos Orgânicos Voláteis Biogênicos, e também de conhecer e trabalhar em lugares incríveis, como o sítio da torre ATTO e o Instituto Max Planck de Biogeoquímica. À Débora Pinheiro Oliveira e à Murielli Garcia Caetano, pela amizade, companheirismo, disposição e auxílio, seja coletando e processando dados em campo, trabalhando no laboratório, ou discutindo artigos. À Elisângela Xavier, pela disponibilidade, bom humor, e ajuda nas preparações e organizações de campo, assuntos de laboratório e demais desafios da vida acadêmica. Aos membros da Família Vegetal, em especial Mirza Bezerra, Laura Martins, Natália Medeiros e Cibelly Honorato, pela amizade, colaboração, e ajuda em coletas de campo e no laboratório. À turma de mestrado 2018, pela companhia, apoio, conversas e risadas, nas disciplinas e nas festas. A todos os membros da equipe logística do ATTO, cujo trabalho e dedicação foram imperativos para o desenvolvimento deste projeto. Ao PELD Mauá pelo inventário de espécies que usamos para selecionar aquelas que avaliamos neste projeto. Ao Dr. Daniel Marra e o Laboratório de Manejo Florestal, pelo empréstimo do equipamento de força de corte. À Juliane Menezes pela ajuda na coleta de fluxo de isoprenóides na campanha de Abril/2019. Ao Instituto Nacional de Pesquisas da Amazônia (INPA) e ao Instituto Max Planck de Biogeoquímica (MPI-BGC) por todo o suporte. Ao projeto ATTO (Ministério Alemão de Educação e Pesquisa, BMBF fundos 01LB1001A; Ministério Brasileiro de Ciência, Tecnologia, Inovação e Comunicação; FINEP/MCTIC contrato 01.11.01248.00). À Andresa de Mello e ao Projeto CENBAM-INCT Centro de Biodiversidade Amazônica (FAPEAM/FDB/INPA#003/2012). À UEA, FAPEAM, LBA/INPA e CEUC/RDS-Uatumã. Por fim, à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa concedida.

RESUMO

Os isoprenóides são compostos orgânicos secundários representados principalmente pelo isopreno e pelos monoterpenos e sesquiterpenos. O isopreno e os monoterpenos constitutivos são compostos que possivelmente mitigam estresse térmico e oxidativo nas folhas, mas a produção de monoterpenos requer mais carbono. Monoterpenos e sesquiterpenos estocáveis podem prover uma proteção induzida contra o ataque de herbívoros e patógenos, contudo sua produção é ainda mais cara em termos de carbono. Essa relação entre os possíveis benefícios e os custos de carbono associados à produção de isoprenóides pode caracterizar um importante compromisso (*trade-off*) do ponto de vista ecológico, e traz a oportunidade de avaliar essa produção através de estratégias econômicas de plantas. No presente estudo, nós investigamos a relação entre emissão e estoque de isoprenóides com traços funcionais dos espectros da economia de carbono da folha, da madeira e da planta inteira, para 27 espécies de Angiosperma na Amazônia Central. De espécies com uma estratégia aquisitiva em nível de folha para espécies com estratégia conservativa, foi vista uma transição da emissão isopreno, de menor custo, para emissão de monoterpenos, de envolve maior custo. No entanto, a capacidade de emitir isopreno parece modular a coordenação entre os espectros econômicos de diferentes partes da planta. Espécies não emissoras de isopreno tenderam a apresentar a mesma estratégia econômica em folhas, madeira e planta inteira, enquanto que espécies emissoras apresentaram estratégias econômicas opostas (e.g. folhas rápidas e madeira e planta-inteira lentas). Os estoques de isoprenóides se mostraram associados a características da madeira e planta-inteira. Espécies com características de madeira e da planta-inteira relacionadas a uma estratégia rápida apresentaram estoques foliares de monoterpenos e sesquiterpenos. Através deste estudo foi possível concluir que os espectros da economia de carbono das plantas coordenam com a emissão e o estoque de isoprenóides. Tais resultados podem contribuir para a integração de compostos secundários às estratégias funcionais de plantas e para o aprofundamento do conhecimento de mecanismos por trás da produção de isoprenóides, podendo também possivelmente contribuir para a otimização das estimativas globais de fluxo desses compostos.

Palavras-chave: compostos secundários, traços funcionais, estratégias de plantas, isopreno, floresta Amazônica, COVBs.

Leaf, wood and whole-plant economic spectra coordinate with isoprenoid emission and storage in central Amazon trees

ABSTRACT

Isoprenoids are secondary organic compounds characterized mainly by isoprene, monoterpenes and sesquiterpenes. Isoprene and constitutive monoterpenes are compounds that possibly mitigate heat and oxidative stress in leaves, but monoterpene production demands more carbon. Storable monoterpenes and sesquiterpenes can provide an induced protection from herbivory attack and pathogens, yet production is even more costly. This relationship between possible benefits and the associated carbon costs of isoprenoid production could characterize an important ecological trade-off, and present the opportunity to assess this production through plant economic strategies. Here we investigate the relationship between isoprenoid emission and storage with functional traits of leaf, wood and whole-plant economic spectra, for 27 tree species in central Amazon. Investments in emissions of isoprene and monoterpenes were more associated to leaf traits. From species with a fast leaf strategy to species with slow leaves, there was a shift from a less costly isoprene production to a more expensive monoterpene one. However, the capacity to emit isoprene seems to modulate the coordination between economic spectra of different plant levels. Species that did not emit isoprene tended to exhibit the same economic strategy for leaf, wood and whole-plant; while isoprene emitters presented opposite strategies (e.g. fast leaves and slow wood/whole-plant traits). The storage of monoterpenes and sesquiterpenes was associated with wood and whole-plant traits. Species with fast wood and whole-plant traits showed leaf storage of monoterpenes and sesquiterpenes. Through this study it was possible to conclude that the carbon economic spectra of plant strategies coordinate with emission and storage of isoprenoids. Such results can contribute to integrating these secondary compounds within plant functional strategy studies, as well as to a deeper ecological understanding of isoprenoid production mechanisms, which could possibly contribute to more accurate global flux estimates.

Key words: secondary compounds, functional traits, plant strategies, isoprene, Amazon forest, functional ecology, BVOCs.

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INTRODUÇÃO GERAL

Isopreno (C_5), monoterpenos (C_{10}) e sesquiterpenos (C_{15}) pertencem à classe abundante e quimicamente diversa de compostos conhecida como isoprenóides (McGarvey & Croteau, 1995; Breitmaier, 2006). Os isoprenóides compreendem o maior grupo entre as principais classes de metabólitos secundários (i.e. isoprenóides, fenóis, alcaloides e compostos sulfúricos) (Guerriero *et al*., 2018) e constituem a maior parte das emissões globais de Compostos Orgânicos Voláteis Biogênicos (COVBs) (Guenther *et al*., 2006, 2012). Esses compostos também exercem impactos significativos em processos de interação biosfera-atmosfera, influenciando a capacidade oxidativa da atmosfera e potencialmente formando aerossóis orgânicos secundários, com provável influência na formação de nuvens (Pöschl *et al*., 2010; Kulmala *et al*., 2013). Já foi demonstrado que florestas tropicais são a principal fonte de emissões (Guenther *et al*., 2012) e a floresta Amazônica representa em torno da metade de todas as florestas tropicais existentes no mundo (Andreae *et al*., 2015; Pölkher *et al*., 2019). Ao longo dos anos foram presenciados consideráveis avanços em relação ao entendimento da produção de isoprenóides, sob perspectivas evolutivas (Dani *et al*., 2014, 2015; Loreto & Fineschi, 2015), bioquímicas (Vickers *et al*., 2009; Jardine *et al*., 2015), sazonais (Alves *et al*., 2016,2018), climáticas (Yáñez-Serrano *et al*., 2020), ecossistêmicas (Gu *et al*., 2017; Sarkar *et al*., 2020) e de composição de espécies (Taylor *et al*., 2018; Jardine *et al*., 2020). Contudo, mecanismos de produção e padrões de emissão de isoprenóides por plantas continuam sendo um tópico de bastante discussão (Sharkey & Singsaas, 1995; Sharkey *et al*., 2008; Monson *et al*., 2013; Sharkey, 2013; Pichersky & Raguso, 2016; Sharkey & Monson, 2017), com poucas informações disponíveis a respeito das interações entre traços funcionais e estratégias ecológicas associadas às emissões, especialmente se tratando de espécies arbóreas da Amazônia.

O isopreno é um composto de emissão constitutiva, que foi revelado como sendo capaz de mitigar o estresse térmico e oxidativo nas folhas (Velikova *et al*., 2012; Taylor *et al*., 2019). Os monoterpenos podem ser de emissão constitutiva e induzida, e monoterpenos constitutivos foram comparados ao isopreno em termos de sua produção e função (Loreto *et al*., 1996; Harrison *et al*., 2013; Jardine *et al*., 2015). Os isoprenóides induzidos, como monoterpenos e sesquiterpenos, são compostos estocáveis, cuja emissão pode ser induzida pelo ataque de herbívoros e patógenos (Gershenzon, 1994; Salazar *et al*., 2018). A habilidade de produzir isoprenóides pode fornecer claros benefícios para a planta, no entanto os processos de síntese e de emissão desses compostos são bioquimicamente caros (Schnitzler *et al.*, 2010) e comprometem um investimento de carbono substancial (Gershenzon, 1994; Pichersky *et al.*, 2006). A produção de monoterpenos constitutivos é mais complexa e requer maiores quantidades de carbono fotossintético quando comparada à de isopreno (Harrison *et al.*, 2013). Os isoprenóides induzidos são ainda mais caros de se produzir, considerando as estruturas de estoque e os substratos consumidos ao longo de reduções bioquímicas (Fahn, 1979; Gershenzon & Croteau, 1993; Goodwin & Mercer, 1983). Tal balanço entre benefícios e custos da produção de isoprenóides pode constituir um importante compromisso (*trade-off*) do ponto de vista ecológico, e deste modo representar uma oportunidade de entender as emissões sob a perspectiva da ecologia funcional, usando a abordagem das estratégias de alocação de recursos e da economia de carbono.

A ecologia funcional permite classificar e identificar espécies de plantas por meio de conjuntos de traços ou características mensuráveis (i.e. traços funcionais), os quais podem afetar a performance do indivíduo (e.g. crescimento, sobrevivência e reprodução) (Violle *et al.*, 2007). A partir de compromissos (*trade-offs*) entre traços funcionais, surgem as chamadas estratégias de plantas, capazes de ordenar e agrupar espécies em espectros contínuos, derivados de similaridades nos mecanismos de resposta ao ambiente (Lavorel *et al.*, 1997; Westoby *et al.*, 2002). Dentre as estratégias propostas (MacArthur & Wilson, 1967; Tilman, 1977; Grime, 1979), as estratégias de alocação de recursos incluem *trade-offs* envolvidos na aquisição, no processamento e na conservação de recursos, o que inclui luz, água, nutrientes e em última análise de carbono; compondo um contínuo "econômico" sob a perspectiva da alocação de recursos (Westoby, 1998; Reich, 2014). Tal contínuo configura espectros distintos para diferentes níveis da planta (e.g. folha, madeira e a planta-inteira), podendo se comportar de maneira coordenada (Reich, 2014; Messier *et al.*, 2017) ou desacoplada (Baraloto *et al.*, 2010; Piston *et al.*, 2019). Com base nos espectros da economia de carbono classificamos as espécies localizadas em cada um dos extremos como aquisitivas (i.e. rápidas) ou conservativas (i.e. lentas) para um determinado nível da planta (Reich, 2014). As espécies aquisitivas possuem valores altos de traços funcionais que proporcionam um aumento da captação de carbono fotossintético, permitindo rápidos retornos por carbono investido e elevando suas taxas de crescimento, porém em detrimento da sua sobrevivência; espécies conservativas são caracterizadas pelo oposto, investindo em traços que podem garantir sua sobrevivência no lugar do seu crescimento, com um retorno mais lento para cada carbono investido (Wright *et al*., 2004; Chave *et al*., 2009; Reich, 2014).

A maioria dessas correlações são relações já testadas e estabelecidas (McGill *et al*., 2006; Osnas *et al*., 2013; Visser *et al*., 2016; Xu *et al*., 2017), contudo poucos estudos até agora incluíram os isoprenóides em análises de comunidades de plantas (Fine *et al*., 2006; Holopainen *et al*., 2013; Salazar *et al*., 2016; Vleminckx *et al*., 2018) e, ao que sabemos, nenhum considerou a importância destes compostos dentro das estratégias econômicas. Enquanto isso, pesquisas recentes com COVBs apontam possíveis associações entre a emissão de isoprenóides e as estratégias ecológicas, porém requerem estudos mais aprofundados (Harrison *et al*., 2013; Dani *et al*., 2014; Fernández-Martínez *et al*., 2017). Entender as emissões de isoprenóides sob a perspectiva da economia de carbono representa não só o aumento do conhecimento a respeito destes compostos dentro das estratégias de plantas, mas também uma maior compreensão das interações ecológicas coordenando as emissões, o que pode contribuir para estimativas de fluxo de COVBs mais acuradas.

No presente estudo, nós investigamos a relação entre a emissão e o estoque de isoprenóides com os espectros econômicos da folha, da madeira e da planta-inteira, para 27 espécies de árvores na Amazônia Central. Nossa hipótese é que, ao longo dos espectros da economia da planta, os investimentos em carbono irão se deslocar da emissão de isopreno, menos custosa, em espécies de estratégia rápida, para a emissão de monoterpenos e o estoque de monoterpenos e sesquiterpenos, ambos mais caros em termos de carbono, em espécies de estratégia lenta.

ARTIGO CIENTÍFICO – **Leaf, wood and whole-plant economic spectra coordinate with isoprenoid emission and storage in central Amazon trees**

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SUMMARY

Isoprene and constitutive monoterpenes are compounds that possibly mitigate heat and oxidative stress in leaves, but monoterpene production demands more carbon. Storable monoterpenes and sesquiterpenes can provide an induced protection from herbivory attack and pathogens, yet production is even more costly.

This relationship between possible benefits and associated carbon costs of isoprenoid production could characterize an ecological trade-off, and present an opportunity to assess production through plant economic strategies. Here we investigate the relationship of isoprenoid emission and storage with functional traits of the leaf, wood and whole-plant economic spectra, for 27 tree species in central Amazon.

As species moved from fast to slow leaf strategy, they shifted from a less costly isoprene production to a more expensive monoterpene production. The capacity to emit isoprene associates with changes in how different parts of the plant spectra coordinate. Storage of monoterpenes and sesquiterpenes emerged as species moved towards fast strategy traits along wood and whole-plant spectra.

The economic spectrum of plant strategies coordinated with emission and storage of isoprenoids. Our findings can contribute to integrating these compounds within plant functional strategies, to provide a deeper ecological understanding of isoprenoid production mechanisms, and possibly to more accurate global flux estimates.

Key words: *isoprenoids, functional traits, plant strategies, isoprene, Amazon forest, functional ecology, BVOCs*.

INTRODUCTION

Isoprene (C_5), monoterpenes (C_{10}) and sesquiterpenes (C_{15}) belong to an abundant and chemically diverse class of secondary compounds known as isoprenoids (McGarvey & Croteau, 1995; Breitmaier, 2006). Isoprenoids make up for the greatest share among the major classes of plant secondary metabolites (i.e. isoprenoids, phenolics, alkaloids and sulphur-containing compounds) (Guerriero *et al*., 2018), and exert significant impacts in biosphere-atmosphere interaction processes, influencing the atmospheric oxidative capacity and potentially forming secondary organic aerosols, probably affecting cloud formation (Pöschl *et al*., 2010; Kulmala *et al*., 2013). They comprehend the largest part of global Biogenic Volatile Organic Compound (BVOCs) emissions (Guenther *et al*., 2006, 2012), with the Amazon forest being responsible for half of the primary source of emissions (Guenther *et al*., 2012; Andreae *et al*., 2015; Pölkher *et al*., 2019). Considerable advances on the understanding of isoprenoid production have been made in the last few years, from evolutionary (Dani *et al*., 2014, 2015; Loreto & Fineschi, 2015), biochemical (Vickers *et al*., 2009; Jardine *et al*., 2015), seasonal (Alves *et al*., 2016,2018), climatic (Yáñez-Serrano *et al*., 2020), ecosystemic (Gu *et al*., 2017; Sarkar *et al*., 2020) and species composition (Taylor *et al*., 2018; Jardine *et al*., 2020) perspectives. Still, production mechanisms and patterns of plant isoprenoid emissions continue to be a topic of great discussion (Sharkey & Singsaas, 1995; Sharkey *et al*., 2008; Monson *et al*., 2013; Sharkey, 2013; Pichersky & Raguso, 2016; Sharkey & Monson, 2017), with scarce information on the associated trait interactions and ecological strategies, especially for Amazonian tree species.

Isoprene is a constitutive-emitted compound suggested to mitigate heat and oxidative stress in leaves (Velikova *et al*., 2012; Taylor *et al*., 2019). Monoterpenes may be of constitutive and induced emissions, and constitutive monoterpenes have been compared to isoprene in terms of production and function (Loreto *et al*., 1996; Harrison *et al*., 2013; Jardine *et al*., 2015).

Induced isoprenoids, as monoterpenes and sesquiterpenes, are also storable compounds, whose emissions can be induced by herbivory attack and pathogens (Gershenzon, 1994; Salazar *et al.*, 2018). The ability to produce isoprenoids can provide clear benefits, nonetheless the processes of synthesis and emission of these compounds are biochemically expensive (Schnitzler *et al.*, 2010) and compromise a substantial carbon investment (Gershenzon, 1994; Pichersky *et al.*, 2006). Production of constitutive monoterpenes is more complex and requires higher amounts of photosynthetic carbon when compared to isoprene (Harrison *et al.*, 2013). Induced isoprenoids are even more costly, considering storage structures and substrates consumed throughout biochemical reductions (Fahn, 1979; Gershenzon & Croteau, 1993; Goodwin & Mercer, 1983). Such balance between benefits and costs of isoprenoid production can possibly constitute an important ecological trade-off, and provide an opportunity to understand emissions from the perspective of functional ecology, under a resource allocation, carbon economic approach.

Functional ecology allows the classification and identification of plant species strategies by sets of measurable traits (i.e. functional traits) that can affect individual performance (e.g. growth, survival and reproduction) (Violle *et al.*, 2007). Plant strategies are classifications that emerge from trade-offs between functional traits, ordering and grouping species in continuous spectra, which derive from similarities in environmental response mechanisms (Lavorel *et al.*, 1997; Westoby *et al.*, 2002). Among proposed ecological strategies (MacArthur & Wilson, 1967; Tilman, 1977; Grime, 1979), resource allocation ones cover the trade-offs involved in acquisition, processing and conservation of resources such as light, water, nutrients, and ultimately carbon; composing an “economic” continuum from a resource allocation perspective (Westoby, 1998; Reich, 2014). This continuum configures distinct spectra for different plant levels (e.g. leaf, wood and the whole-plant), which can behave in coordinated (Reich, 2014; Messier *et al.*, 2017) or in decoupled manners (Baraloto *et al.*, 2010; Piston *et al.*, 2019). Based on the carbon economic spectrum we are able to classify species placed towards each end of the spectrum as acquisitive (i.e. fast) or conservative (i.e. slow) for a given plant level (Reich, 2014). Fast species have high values of traits that enhance photosynthetic carbon uptake and faster returns on carbon investment, increasing growth rates though at the expense of survival; slow species are characterized by the opposite, investing on traits that may ensure survival in detriment of growth, with slow returns per carbon investment (Wright *et al.*, 2004; Chave *et al.*, 2009; Reich, 2014).

The majority of such trait correlations are currently tested and established relationships (McGill *et al.*, 2006; Osnas *et al.*, 2013; Visser *et al.*, 2016; Xu *et al.*, 2017), however few studies have so far included isoprenoids in plant community analysis (Fine *et al.*, 2006; Holopainen *et al.*, 2013; Salazar *et al.*, 2016; Vleminckx *et al.*, 2018) and, to our knowledge, none have considered the importance of these compounds within economic strategies. Meanwhile, recent BVOC research points out possible associations between isoprenoid emissions and ecological strategies that require further testing (Harrison *et al.*, 2013; Dani *et al.*, 2014; Fernández-Martínez *et al.*, 2017). Understanding isoprenoid production under a carbon economic perspective means not only increasing the knowledge on these compounds within plant strategies, but also comprehending the ecological interactions coordinating emissions, which could contribute to more accurate BVOC global flux estimates.

Here, we investigate the relationship of emission and storage of isoprenoids with the plant economic spectrum at leaf, wood and whole-plant levels for 27 tree species in central Amazon. We hypothesize that, as species strategies move from fast to slow along plant economic spectra, carbon investments will shift from emissions of isoprene, which are less carbon costly, to monoterpene emissions and storage of monoterpenes and sesquiterpenes, both more carbon expensive.

MATERIAL AND METHODS

Study Site

The study was conducted at the Amazon Tall Tower Observatory (ATTO) and PELD-MAUA (PELD is the acronym in Portuguese for Long Term Ecological Research) experimental plots. Plots are located in the central Amazon, at the Uatumã Sustainable Development Reserve (USDR), about 150 km northeast of the city of Manaus (S 02 08.9° W 059 00.2°) (Supplementary information, Fig. S1). The climate is tropical humid, with mean annual temperature and precipitation of 26.7ºC and 2376 mm, respectively, and is marked by a pronounced rainy season from November to May and a drier season from June to October (Andreae *et al.*, 2015). The reserve covers 424,430 ha with a mosaic of dense non-flooded upland forest vegetation (*terra-firme*), shrubland (*campina*)/closed-canopy (*campinarana*) vegetation on white sands and old non-flooded fluvial terraces (*terraço fluvial*) (Yáñez-Serrano *et al.*, 2015) (Supplementary information, Fig. S2).

Sampling design

We collected functional trait and isoprenoid data for 91 trees across 4 permanent plots covering *terra-firme*, white-sand shrubland/forest (locally called *campina*/*campinarana*) and *fluvial terrace* areas, distributed at least one kilometer from each other along the ATTO access road. Trees represented 30 previously identified (with individual vouchers collected) and confirmed taxonomic species, belonging to 15 families of angiosperm. Species were chosen from a preliminary selection based on their abundance in the PELD MAUA tree species inventory (Andreae *et al*., 2015) and on available functional trait data for wood density, potential height and potential growth rate, obtained from local, regional and global databases (e.g. Zanne *et al*., 2009; Reserva Adolpho Ducke Permanent Plots (PPBio, 2012); TRY Database (Kattge *et al*., 2020)).

This first analysis (not shown) allowed us to select species that were the most representative in terms of abundance, and that could be placed along plant economic spectra, drawn from the multivariate space of functional trait values. In order to maximize variation and enable selection of a broad range of strategies within the spectra, we chose species occurring across the different vegetation types (10 *terra-firme* species; 9 white-sand shrubland species; 3 *white-sand forest* species; and 9 *fluvial terrace* species). In each species we selected and sampled 3-5 trees with similar diameter. Their position along the vertical strata varied with species life history (Table S1). Wood and whole-plant traits were collected from October 2018 - July 2019, while leaf traits and isoprenoid data were collected from November 2018 - April 2019.

We obtained a total of 28 functional traits (19 leaf traits, 4 wood traits and 5 whole-plant traits) and determined average trait values per species (Supplementary information, Table S2). All trait measurements and calculations were performed according to published protocols (Pérez-Harguindeguy *et al.*, 2013) and we describe them in the following sections.

Leaf traits

With the help of a tree climber, we collected branches of at least 2 cm diameter from the most illuminated side of the crown, avoiding visibly unhealthy or damaged leaves, and leaves with epiphylls. After being cut, branches were slowly descended by rope, or grabbed before touching the ground, to prevent stomatal closure due to impact. Collected branches were identified, cut once again under water to eliminate embolism, and placed inside water bottles for transport to the field camp (where they were again cut under water to restore xylem flow before gas exchange measurements described below). We selected one mature and healthy leaf of the branch for isoprenoid flux measurement, another leaf for chlorophyll content measurement and three leaves for stored isoprenoid concentration. For the latter, we used a leaf cutter to get 6-18 discs/leaf (diameter = 1 cm), which were placed inside closed hermetic glass vials and stored in a freezer at -5ºC. After measuring isoprenoid flux on site (section below), we removed the branch from the water, wrapped the terminal piece in moist absorbent paper and placed it in a closed plastic bag for further leaf trait measurements.

We separated three leaves, one of them being the leaf used for isoprenoid flux measurement, to obtain fresh and dry weights, Leaf Thickness (LT) and Leaf Area (LA). For the remaining leaf traits, we gathered a total of eight leaves: three for Force to Punch (FtP), three for Force to Tear (FtT) and two for anatomy (stomata and veins). We weighed the leaves to obtain fresh weight, used a micrometer to measure LT and a table scanner for LA. The leaves were dried in an oven for 72hrs at 60ºC and afterwards weighed to obtain dry weight. We measured FtP using a Pesola® scale (Medio spring scale, item n. 40300) modified with a pressure set (accessory for Medio-scales, item n. 4.004), and FtT using a tearing apparatus (Hendry and Grime, 1993). Leaves set aside for anatomic analyses were cut in the median region and the pieces were placed in plastic containers filled with FAA solution (Formaldehyde 37%, Glacial Acetic Acid and Ethanol 70%) (Johansen, 1940) for 24hrs, which was afterwards replaced by Ethanol 70%. For compound leaves, all measurements were done on leaflets.

We analyzed images of scanned leaves with *ImageJ* software (Schneider *et al.*, 2012) to obtain LA. Specific Leaf Area (SLA) was calculated as the ratio of LA to leaf dry weight. We did not include petioles in the SLA calculation since they can be quite large for rainforest species and are usually more related to leaf positioning rather than biomass efficiency (Poorter *et al.*, 2018). Leaf Mass per Area (LMA) was calculated as 1/SLA. Leaves used for SLA/LMA data were later ground and used for leaf nutrient content analysis. We calculated Leaf Dry Matter Content (LDMC) as the ratio of leaf dry weight to fresh weight. FtP and FtT were quantified in N cm^{-1} and N cm^{-2} respectively (Pérez-Harguindeguy *et al.*, 2013). Chlorophyll content (Chl) was calculated based on SPAD (Minolta SPAD 502 Chlorophyll Meter, Spectrum Technologies Inc., Plainfield, IL, USA) values using an equation for rainforest trees (Coste *et al.*, 2010; Poorter *et al.*, 2018). We processed and analyzed leaf stomatal density (StDens), stomatal guard cell length (StLgth) and vein density (VeinDens) at the Biodiversity and Functional Ecology Lab (National Institute for Amazonian Research – INPA) following adapted protocols (Johansen, 1940). Leaf nutrient content analysis was conducted by the Soil and Plant Thematic Lab (LTSP, INPA), following adapted protocols (EMBRAPA, 1999), and resulted in values of foliar iron (Fe^{+2}), calcium (Ca^{+2}), magnesium (Mg^{+2}), zinc (Zn^{+2}), potassium (K^{+}), phosphorus (P) and nitrogen (N) content.

Wood and whole-plant traits

We measured the total height of the tree (TH) with the help of a tree climber, who placed a metric tape on the highest point of the tree canopy and extended it until it reached the ground. We also took measurements of the two main orthogonal axes of the crown to obtain average crown radius, and with that estimate the crown area (CA) assuming a circular crown shape. With an increment borer (diameter of 5.15 mm) we punctured the tree stem at 1.3 m height and penetrated the wood until the borer reached a depth of about half of the stem diameter (at 1.3 m height), afterwards extracting a wood sample for fresh and dry weight, fresh volume and active xylem depth. We cut and removed the bark of a 5 cm terminal piece of twig to get fresh and dry weights, and fresh volume. We weighed twig and stem wood samples to get fresh weight, then measured fresh volume using water displacement method. Wood samples were dried in an oven for 72hrs at 105°C and weighed to obtain dry weight.

Wood density of the twig (WDtw) and of the stem (WDst) were estimated as the ratio of wood dry weight to fresh volume, and wood dry matter content of the twig (WDMCtw) and of the stem (WDMCst) as the ratio of wood dry weight to fresh weight. We obtained active xylem depth using a direct method of light transmission through the wood core sample. We placed the dried stem wood sample above a direct source of light and, with a magnifying glass, we observed and measured with a caliper the extension of open vessels (active xylem vessels) throughout the length of the sample (Cosme *et al*., 2017). This method assumes that active vessels are open and inactive ones have been filled by tylosis. Tree sapwood area (SA) was obtained by subtracting heartwood area (area of extension of inactive vessels) from total basal area (BA), and the ratio of sapwood area to basal area (SABA) was calculated. Finally, we calculated the proportions of crown area to basal area (CABA) and total height to basal area (THBA).

Isoprenoid flux measurements

The flux of emitted isoprenoids was measured on site using a commercial gas exchange portable system IRGA - LI6400XT (LiCor, USA). A hydrocarbon filter (Restek Pure Chromatography, Restek Corporations, USA) was installed at the air inlet of the IRGA to remove isoprenoids from incoming ambient air. All tubing in contact with the sampling air was PTFE. Before each measurement, a chamber blank sample was obtained from the empty leaf chamber. The leaf, or leaflet when compound leaf, was separately enclosed in the leaf chamber with standard conditions until net assimilation (A_n), stomatal conductance (g_s) and internal CO_2 concentration (C_i) were stable. The stability criteria for measurements was assigned to up to one standard deviation of the mean A_n. The flow rate of air going into the leaf chamber was 400 μmol s^{-1}, CO_2 and H_2O concentrations were 400 μmol mol^{-1} and 21 mmol mol^{-1} (relative humidity of ~60%), respectively. Photosynthetic photon flux density (PPFD) was set to 1000 μmol m^{-2} s^{-1} and leaf temperature to 30ºC. Air exiting the IRGA leaf chamber was routed to fill adsorbent cartridges (stainless steel tubes filled with Tenax TA and Carbograph 5 TD adsorbents) at a rate of 200 sccm during 10 min, which resulted in 2 L air samples for isoprenoid chemical analysis.

Emitted isoprenoid identification and quantification

Isoprenoids accumulated in the adsorbent cartridges were determined by laboratory analysis at the Chemical Analysis Lab (State University of Amazonas - UEA). The cartridges were analyzed with a thermal desorption system (TD; Markes International, UK) interfaced with gas chromatograph-mass spectrometer and flame ionization detectors (GC-MS-FID; 7890B-GC and 5977A-MSD series, Agilent Technologies, USA). We loaded the cartridges in the TD automatic sampler (TD-100, Markes International, UK), which connects to the thermal desorption system. Then, the collected samples were dried by purging for 5 min with 50 sccm of ultrahigh-purity helium (all flow vented out of the split vent) before being transferred (300ºC for 10 min with 50 sccm of ultrapure nitrogen) to the thermal desorption cold trap held at -10ºC (Unity Series 1, Markes International, UK). During GC injection, the trap was heated to 300ºC for 3 min while backflushing with carrier gas (helium) at a flow rate of 6.0 sccm directed into the column (Agilent HP-5, 5% phenyl methyl siloxane capillary, 30.0 m x 320 μm x 0.25 μm). The oven ramp temperature was programmed with an initial hold of 6 min at 27ºC, followed by an increase to 85ºC at 6ºC min^{-1}, followed by a hold at 200 ºC for 6 min.

We confirmed the identification of emitted isoprenoids from samples by comparison of retention time with a solution of authentic liquid standards in methanol (Sigma-Aldrich, USA) and comparison to the library of the National Institute of Standards and Technology (NIST). The GC-MS-FID was calibrated by injecting different amounts of gas standards into separate cartridges. The gas standard composition is shown on Supplementary information (Table S3) (Apel & Riemer Environmental Inc., USA). Calibration curves were carried out at least thrice before the analysis of the sample cartridges, in order to get a mean correlation coefficient >= 0.98. In addition, two standard cartridges were analyzed at every 20 samples to check system sensitivity. Isoprenoid concentration was determined using the sample volume that was passed through each cartridge. This volume is the integration of the mass flow rate measured and controlled by the pump used to suck the air coming out from the IRGA leaf chamber. Once the volume mixing ratio of isoprenoids (ppbv) was obtained, leaf emission flux was determined using the equation ($F = R\text{ppbv} \times Q/A$), where F (nmol m^{-2} s^{-1}) is leaf flux of isoprenoid emission; $Rppbv$ (nmol mol^{-1}) is isoprenoid concentration of the sample; Q is flow rate of air into the leaf chamber (400×10^{-6} mol s^{-1}); and A is the area of leaf within the chamber (0.02 m^2 and 0.06 m^2). Compounds were identified using Agilent Enhanced ChemStation (MSD ChemStation F.01.01.2317, Agilent Technologies Inc., USA) and quantified using OriginPro (OriginPro 8 SR0 v8.0724, OriginLab Corporation, USA).

Stored isoprenoid identification and quantification

Stored isoprenoid concentration in the leaf discs was determined from laboratory analysis at the Chemical Analysis Lab (State University of Amazonas - UEA). Qualitative and quantitative data for isoprenoid concentration were obtained using a combination of the static headspace gas chromatography (HS-GC) system (Jorge & Trugo, 2003) and manual injections in the GC-MS-FID system. We combined these methods because the HS-GC system allows only for compound quantification, whereas the GC-MS-FID system provides compound identification as well. For each species at least three samples were analysed by GC-MS-FID and 3-5 samples were analysed via HS-GC.

For the HS-GC system, each vial was placed separately inside the headspace oven (AOC-5000 Plus AutoSampler, Shimadzu) and heated to volatilize the isoprenoids stored inside the leaf. The oven temperature program started at 50°C for 10 min, increasing to 80°C at 2°C min^{-1} and to 200°C at 4°C min^{-1}, then held at 200ºC for 10 min previous to the injection of 1 mL of the gas imprisoned inside the vial into the GC column (Agilent HP-5, 5% phenyl methyl siloxane capillary, 30.0 m x 320 µm x 0.25 µm). The injector and detector temperatures were set to 150°C and 250°C, respectively. The carrier gas was helium, at a flow rate of 1.6 mL min^{-1} and the split ratio was 1:50. During GC injection, the trap was heated to 300ºC for 3 min while backflushing with carrier gas (helium) at a flow rate of 6.0 sccm directed into the column (Agilent HP-5, 5% phenyl methyl siloxane capillary, 30.0 m x 320 µm x 0.25 µm).

For manual injections in the GC-MS-FID system, we first heated the vials in an oven for 60 min at 60ºC to volatilize the isoprenoids stored inside the leaf, and using a glass syringe we sampled 1 mL of the air inside the vial and injected it directly into the column. During GC injection, the trap was heated to 300ºC for 3 min while backflushing with carrier gas (helium) at a flow rate of 6.0 sccm directed into the column (Agilent HP-5, 5% phenyl methyl siloxane capillary, 30.0 m x 320 µm x 0.25 µm).

We confirmed the identification of stored isoprenoids from samples by comparison of retention time with liquid standards (Sigma-Aldrich, USA) and comparison to the library of the National Institute of Standards and Technology (NIST). We calibrated the GC-MS-FID for stored isoprenoids by injecting a solution of known concentrations of liquid monoterpene standards (α-Pinene, β-Pinene, Limonene, 3-Carene) and injecting solutions of different concentrations of liquid β-Caryophyllene standard into the column (Supplementary information, Table S4). We quantified stored monoterpene concentration by comparing the peak area of the standards with the peak area of the compounds found in our samples. We quantified sesquiterpene concentration using a six point calibration curve. For samples analyzed in the HS-GC system, compound identification was done by comparison of HS-GC with GC-MS-FID chromatograms, assuming that compound profile is conserved within species. Compounds were identified using Agilent Enhanced ChemStation (MSD ChemStation F.01.01.2317, Agilent Technologies Inc., USA) and quantified using OriginPro (OriginPro 8 SR0 v8.0724, OriginLab Corporation, USA).

Statistical Analysis

We performed a principal component analysis (PCA) to ordinate species according to their functional traits and to extract, from the multivariate space of trait correlations, the first two axes capturing most variation on species traits (PC1 and PC2). With the aim of improving the total percentage of variation covered by the first two PCA axes, only functional traits with a minimum 18% correlation with any of the first two axes were retained and included in the analysis (Table 1). The resulting PCA (Fig. 1) comprised 18 functional traits (11 leaf traits, two wood traits and five whole-plant traits).

For carbon investment analyses, isoprenoid emissions were standardized to units of µg(C) g^{-1}(leaf) h^{-1}, and isoprenoid storage to µg(C) g^{-1}(leaf). Due to large differences in magnitudes of fluxes for different compounds, the monoterpene emission data were log transformed. Since only six species stored monoterpenes and the magnitude of stored monoterpene concentration was much small compared to sesquiterpene storage, we added the two variables and analysed them as total isoprenoid storage (monoterpenes + sesquiterpenes). Because about half our dataset comprised species that did not emit isoprene (14), or store compounds (15), we treated both (isoprene emission and isoprenoid storage) as binary variables (presence/absence).

To test how monoterpene emission was associated with the plant economic spectra we performed additive linear multiple regression models of monoterpene emission rates (dependent variable) as a function of PC1 and PC2 axes (independent variables). To assess the relationship between plant economic spectra and the capacity to emit isoprene we conducted an ANCOVA between PC1 and PC2 by the presence/absence of isoprene emission. To evaluate how isoprenoid storage capacity was related to the plant economic spectra, we performed logistic multiple regression models of presence/absence of total isoprenoid (monoterpene+sesquiterpene) storage as a function of PC1 and PC2 axes. Given the potential phylogenetic autocorrelation between species, all analyses were performed comparing models described above with models including phylogenetic information (time-scaled branch length according Neves *et al*. 2020). We reconstructed phylogenetic relationships among the 27 species using PhyloMatic v.3 (Webb & Donoghue, 2005), based on the Neves *et al* (2020) genus-level phylogeny of Amazonian angiosperms (Fig. 2). The mode of evolution lambda was selected by the comparison with Brownian motion and Orntein-Uhleck models, and selection was based on the lowest Akaike Information Criterion (AIC) value using the *fitContinuous* function of the GEIGER R package (Pennell *et al*., 2014). Models were performed via the *phylolm* function of the PHYLOLM R package (Ho & Ane, 2014), the results of phylogenetic models are presented as plots from the VISREG R package (Breheny & Burchett, 2017) and correlation coefficients were obtained using the *r2* function of the RR2

R package (Ives, 2018). All statistical analyses were performed using the platform R x64 3.6.1 (R Core Team, 2019).

RESULTS

Our PCA analysis shows the coordination of functional traits reflecting carbon economic spectra for different plant levels (Fig. 1). A leaf spectrum is represented by the first axis (PC1), and wood and whole-plant spectra are being reflected in the second axis (PC2). Towards their positive end, the values of fast strategy traits increase (and slow trait values decrease), whereas in the direction of their negative end, slow strategy trait values increase (and fast trait values decrease). The first two axes of PCA explained 50.4% of trait data variation. Traits correlated with PC1 and PC2 are indicated in Figure 1 and the percentage correlation values (loadings) are presented in Supplementary information (Table S5).

Of the 30 Amazon tree species we analyzed, almost all emitted isoprenoids (27) although only a few were capable of storage (12). Thus we divided the species into two major groups: one of strict emitters (15 species; Em), and one that both emits and stores isoprenoids (12 species; EmS); with no clear distinction between groups in terms of their combination of leaf, wood and whole-plant traits (Fig. 1). We excluded three species from the analysis, one species that only stored (*Trichilia schomburgkiana*) and two that neither emitted nor stored isoprenoids (*Geissospermum sericeum* and *Ecclinusa guianensis*).

Of the species we analyzed for leaf isoprenoid emissions, 13 emitted isoprene and 23 emitted monoterpenes. Nine species emitted both isoprene and monoterpenes (33%), four species were strict isoprene emitters (15%) and 14 (52%) only emitted monoterpenes. Six species were able to store monoterpenes, while 11 stored sesquiterpenes. Five species stored both monoterpenes and sesquiterpenes (42%), one species stored only monoterpenes (8%), and six species stored only sesquiterpenes (50%).

Table 1. Functional traits of leaf, wood and whole-plant obtained for 27 Amazonian tree species and abbreviations (Abv) used in this study.

Level	Trait	Abv	Units
Leaf	Leaf Mass per Area	LMA	g cm^{-2}
	Leaf Thickness	LT	mm
	Force to Punch	FtP	N cm^{-1}
	Stomatal Density	StDens	stomata mm^{-2}
	Stomatal Length	StLgth	mm
	Chlorophyll Content	Chl	µg cm^{-2}
	Foliar Calcium Content	Ca	g kg^{-1}
	Foliar Magnesium Content	Mg	g kg^{-1}
	Foliar Nitrogen Content	N	g kg^{-1}
	Foliar Phosphorus Content	P	g kg^{-1}
	Foliar Zinc Content	Zn	mg kg^{-1}
Wood	Wood Density of the stem	WDst	g cm^{-3}
	Wood Dry Matter Content of the stem	WDMCst	mg g^{-1}
Whole-plant	Basal Area	BA	m^2
	Total Height	TH	m
	Sapwood Area per Basal Area	SABA	m^2 m^{-2}
	Crown Area per Basal Area	CABA	m^2 m^{-2}
	Total Height per Basal Area	THBA	m m^{-2}

Our phylogeny of measured species represents diverse coverage of two major clades - the Rosids (e.g., Fabaceae) and the Asterids (e.g., Lecythidaceae) - and one representative of the Magnoliids (Annonaceae). We observed monoterpene storage across the Rosids clade, but none in the Asterids or Magnoliids (Fig. 2). Isoprene emission showed some apparent genus- and family-level conservatism, but as with sesquiterpene storage, there was no clear pattern at deeper levels in the phylogeny (Fig. 2).

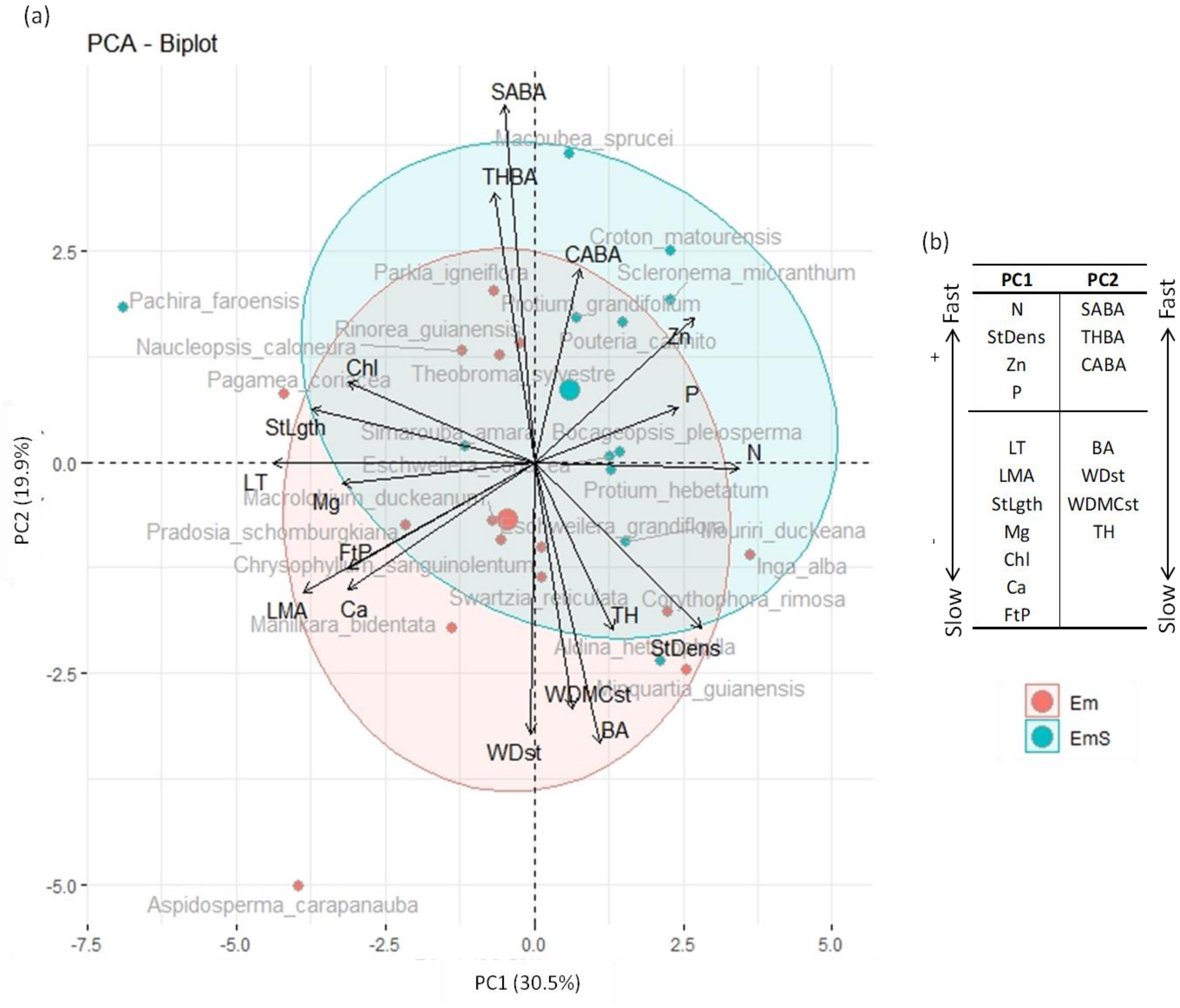

Figure 1. (a) Principal component analysis (PCA) of functional trait data obtained for 27 species of trees in central Amazonia. PC axes form two independent economic spectra, of leaf (PC1) and wood/whole-plant (PC2). Positive and negative score values refer to fast and slow strategy for both axes. Species are colored according to emission and storage capacities: strict emitters (Em) and species that emit and also store (EmS). Big circles represent the average PCA score of the group. (b) Traits correlated with PC1 and PC2, arrows indicate the direction of the relationship: positive correlation values mean increase in fast strategy trait values for PC1 (N, StDens, Zn, P) and slow strategy trait values for PC2 (BA, WDst, WDMCst, TH), negative correlation values mean an increase in slow strategy trait values for PC1 (Ca, FtP, Mg, Chl, StLgth, LMA, LT) and fast trait values for PC2 (CABA, THBA, E, gs, A, SABA); complete trait names are presented in Table 1 and percentage correlation values are presented in Supplementary information (Table S4).

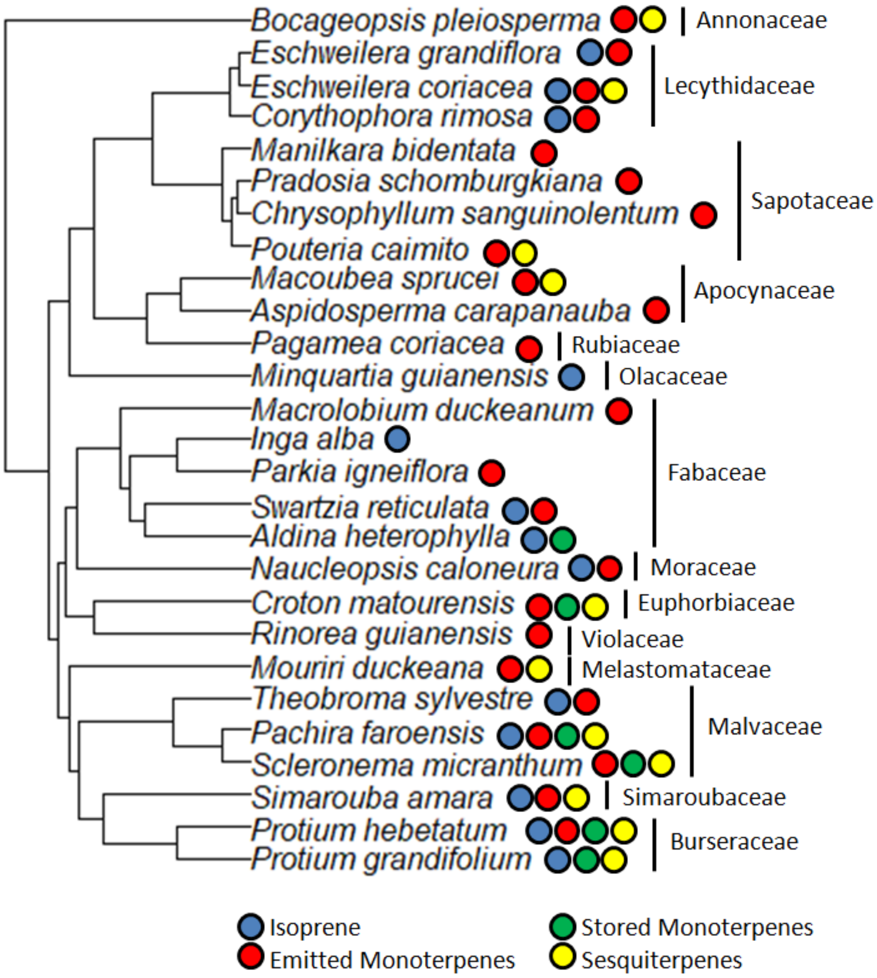

Figure 2. Reconstruction of phylogenetic relationships among 27 tree species in 14 families, based on Neves *et al*. (2020) genus phylogeny of Amazonian angiosperms. Species are labelled according to the capacity to emit or store a given type of compound.

Statistical models with and without phylogenetic information had equal statistical support, with similar AIC values and correlation coefficients. Monoterpene emissions from leaves varied along the leaf economic spectrum, with emission rates increasing toward slower leaf strategies (decreasing PC1, Fig. 3). Monoterpene emissions showed a significant negative relationship with foliar phosphorus (P) content ($r^2 = 0.32$, $p<0.01$; Supplementary information, Fig. S3). The pattern of greater monoterpene emissions in slower leaves was stronger among strict emitters (emitters that do not store; $r^2=0.47$, $p<0.01$; Fig. 3b), and the pattern was absent for the subset of species that also stored monoterpenes or sesquiterpenes ($r^2=0.0017$, $p=0.68$; Fig. 3c).

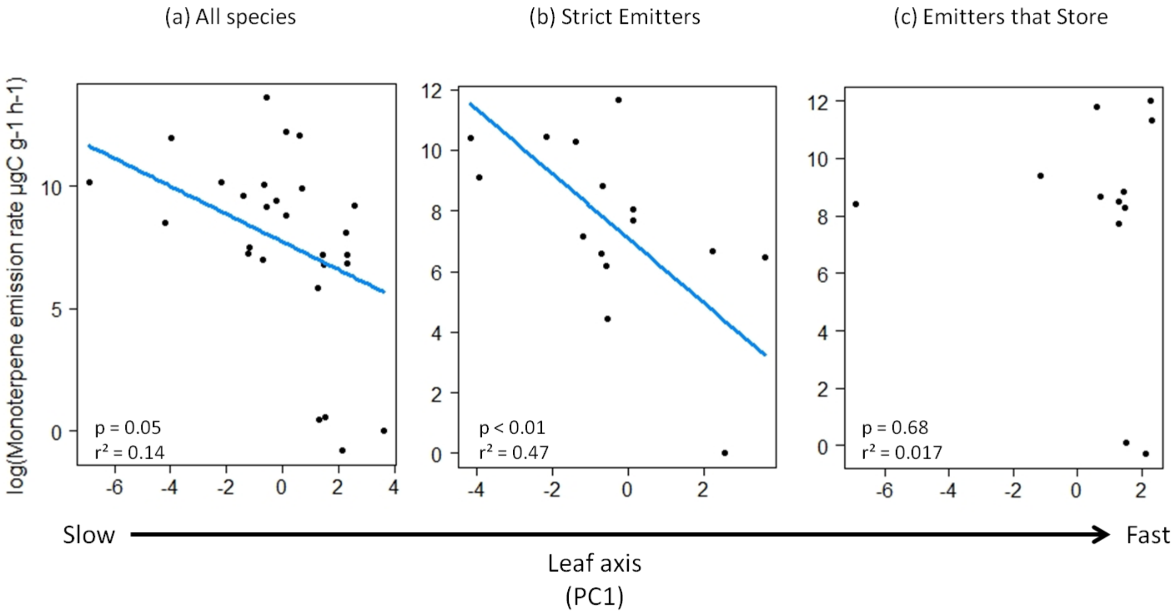

Figure 3. Relationship between log of monoterpene emission rates and the leaf economic spectrum (PC1, see Fig.1) for all 27 species (a), and subsets of species that only emit (b) and that also store (c). Analyses include phylogenetic relationships between genera.

The emission of isoprene varied as a function of both leaf spectrum (PC1) and wood and whole-plant spectra (PC2) (Fig. 4). Plants that emitted isoprene showed fast leaf traits with slow wood and whole-plant traits, or vice verse (e.g. slow leaf traits with fast wood and whole-plant traits). In contrast, non-emitting plants fell on an axis where leaf and wood/whole-plant traits were positively correlated (r^2=0.42, $p<0.001$; Fig. 4).

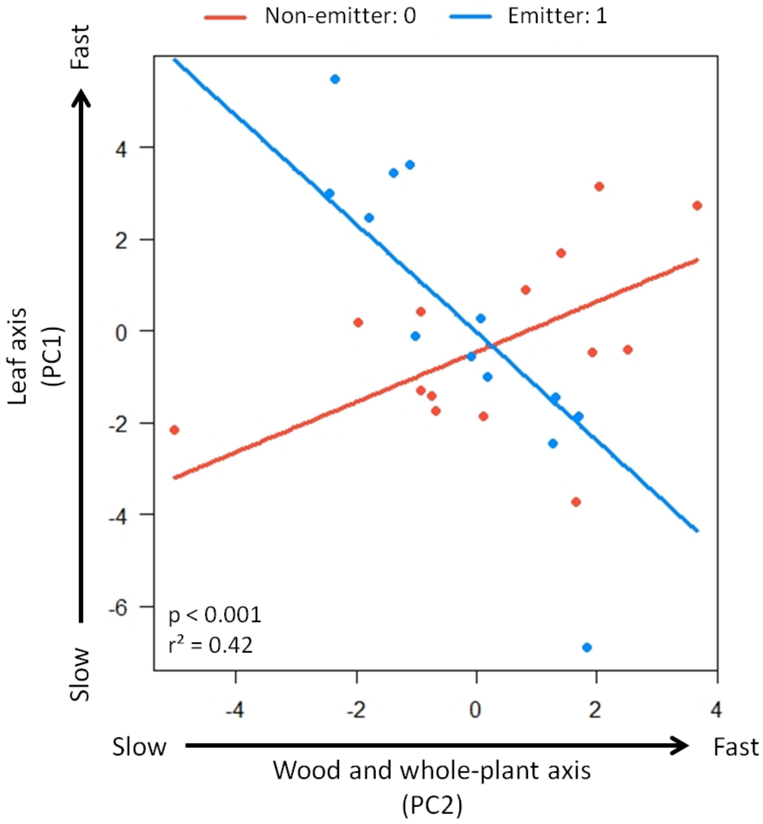

Figure 4. Relationship between the leaf (PC1) and wood/whole-plant (PC2) economic spectra in isoprene emitter (1) and non-emitter (0) tree species. Analyses include phylogenetic relationships between genera.

The capacity to store isoprenoids coordinated with wood and whole-plant spectra, and contrary to our hypothesis, we saw a shift to investment in storage as species moved towards fast strategies for these plant levels (r^2=0.17, p<0.05; Fig. 5). Regression models to assess the relationship of PC1/PC2 with the presence/absence of monoterpene and sesquiterpene storage, stored compound concentration and isoprene emission rates were non-significant.

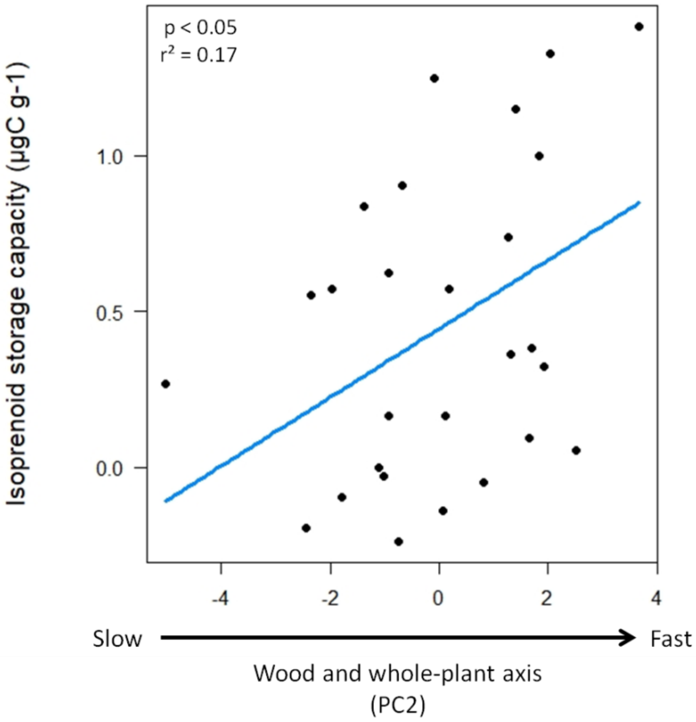

Figure 5. Partial residuals of the relationship between isoprenoid (monoterpene+sesquiterpene) storage capacity (absence/presence) and the wood/whole-plant economic spectra (PC2) for all tree species. Analyses include phylogenetic relationships between genera.

DISCUSSION

The first two axis of the PCA analysis (Fig. 1) revealed patterns of correlation between functional traits that reflected mainly a leaf spectrum (PC1), and wood and whole-plant spectra (PC2). Species placed towards the positive end of PC1 have nutrient-rich, large and thin leaves, with high density of small stomata - traits that can promote a more efficient carbon uptake (Wright *et al*., 2004; Reich, 2014). On the other hand, species placed towards the negative end of this leaf spectrum show the opposite; i.e. leaves with a low foliar nutrient content, that are small, thick, hard to puncture, with large, low density stomata - traits that may favour carbon conservation instead of uptake (Wright *et al*., 2004; Reich, 2014). Meanwhile, species with positive values of PC2 have a softer, lighter wood, and are taller, with larger crowns and larger active xylem vessel area relative to basal area, indicating a higher investment in carbon acquisition at the wood and whole-plant levels (Chave *et al*., 2009; Reich, 2014). Finally, species with negative values of PC2 show dense, heavy wood, and are shorter in stature with smaller crowns and smaller active xylem vessel area relative to basal area - traits that would reflect a strategy of carbon conservation for wood and whole-plant levels (Chave *et al*., 2009; Reich, 2014).

The observed pattern of slow leaf monoterpene emissions is consistent with our first hypothesis. In the tropics, constitutive monoterpene emission have been demonstrated as light-dependent, produced via plastidic 2-*C*-methyl-D-erythritol 4-phosphate (MEP) pathway (Zhao *et al*., 2016; Jardine *et al*., 2017) like isoprene (Loreto *et al.*, 1996; Harrison *et al*., 2013), perhaps having a similar protective role against heat and oxidative stress (Jardine *et al*., 2011; Velikova *et al*., 2012). Knowing that the synthesis of monoterpenes probably competes for precursors and reducing power also involved in the production of isoprene (Harrison *et al*., 2013), it would be expected that leaves with slow carbon turnover rates would be able to benefit from not only this abiotic stress protection, but also from the chemical signalling properties provided by the production of more costly compounds like monoterpenes. Furthermore, emission of monoterpenes was negatively related with foliar P content (Supplementary information, Fig. S3), consistent with previous findings on the relationship of this nutrient with monoterpene emissions (Fernández-Martínez *et al*., 2017).

Isoprene emitters showed combinations of fast and slow strategies, either having fast leaves with slow wood and whole-plant traits, or slow leaves with fast wood and whole-plant traits. We did not find any studies that could help to understand why isoprene emissions would promote this inverse correlation of strategies, or why some emitters presented a combination of slow leaves with fast wood and whole-plant traits. We expected that the production of isoprene would be favored in leaves with faster carbon turnover rates since the compound allows leaves to maintain high photosynthetic rates even when facing elevated temperatures (Velikova *et al*., 2012; Taylor *et al*., 2019), and costs little to be produced, which would reflect in high growth rates for the tree. Yet, isoprene emitters with fast leaf traits also showed slow wood and whole-plant traits. A possible explanation for this kind of strategy combination could be the position which these trees occupy within the forest strata, with crowns that remain mostly below the forest canopy, where they would be more susceptible to the occurrence of sunflecks (Way & Pearcy, 2012). It is an environment of perhaps mild, prolonged diffuse light exposure, but one that is temporally more variable and punctuated by moments of direct sunlight. These moments could cause a rapid increase in leaf temperature, and trigger the emission of isoprene as a short-term stress response (Singsaas & Sharkey, 1998; Singsaas *et al*., 1999; Niinemets *et al*., 2011; Way & Pearcy, 2012; Harrison *et al*., 2013; Taylor, 2017).

Storable compounds can be quite expensive to manufacture, since they require extensive chemical reduction, complex storage secretory structures and have a large investment of carbon associated (Fahn, 1979; Gershenzon & Croteau, 1993; Goodwin & Mercer, 1983). However, contrary to our hypothesis, we observed that isoprenoid storage was actually a quality of species with fast traits for wood and whole-plant spectra. In fact, although storable isoprenoids have a high gross production cost, slow metabolic turnover rates of isoprenoid pools (Gershenzon, 1994), combined with the employment of individual compounds in multiple biological functions (Pichersky & Raguso, 2016) and a possible enhanced nutrient uptake promoted by arbuscular mycorrhiza (Sharma *et al*., 2017) are mechanisms that can significantly reduce the net cost of storable isoprenoid production. This could also indicate a wood/whole-plant level trade-off, in which trees with fast strategy would invest and benefit from chemical defenses and other biological advantages (e.g., attraction of pollinators) provided by these storable isoprenoids, whereas slow trees would favor a structural, mechanical defense. Further studies are needed to test this hypothesis.

The observation that isoprenoid storage was better explained by wood and whole-plant spectra without a significant relationship with the leaf spectrum possibly indicates different carbon budgets inside each plant level. Production of constitutive emitted isoprenoids depends on the available substrate on the short time-scales associated with transcriptional regulation at the beginning of the MEP pathway (Harrison *et al*., 2013; de Souza *et al*., 2018), whereas production of induced storable isoprenoids is regulated by longer time scales required for gene activation involving other metabolic pathways (e.g. phytohormones, chloroplastic pigments and electron carriers) (Owen & Peñuelas, 2005; de Souza *et al*., 2018) with demands that are downstream of the MEP pathway and compromise photoassimilates, energy supply and reducing power for the tree as whole (Loreto & Sharkey, 1993; Li & Sharkey, 2013). The production of storable isoprenoid pools would hence represent a higher level, wood and whole-plant carbon balance; while monoterpene emissions would consist on a more specific leaf-level budget, associated with a short-term constant loss of recently assimilated carbon

(Delwich & Sharkey, 1993; Affek & Yakir, 2002; Karl *et al*., 2002), with isoprene emissions being determined by combinations of traits throughout the tree (leaf, wood and whole-plant).

While previous studies assumed that about 20-38% tropical species emitted isoprene (Harley *et al*., 2004; Loreto & Fineschi, 2015), more recent studies have revealed that this percentage can be even higher, up to 62% (Jardine *et al*., 2020). Similarly, almost half the trees we studied (48%) emitted isoprene, and divided into emitters of isoprene only (15%) and emitters of both isoprene and monoterpenes (33%). With the exception of four species that only emitted isoprene, all species were able to emit monoterpenes (85%) and more than half of them (52%) only emitted monoterpenes. Such a high number of monoterpene emitters could be a reflection of the great species richness and complexity of ecological interactions (e.g. plant-herbivore, plan-plant, plant-pollinators) found in Amazonian tree communities, factors that were shown to be associated with increases in monoterpene emissions rates (Kigathi *et al*., 2019). The considerably higher proportion of monoterpene emitters to isoprene emitters corroborates with recent observations for a site in eastern Amazonia (Sarkar *et al*., 2020), which found that the magnitude of monoterpene emissions could be higher than previously suggested as great as ~10% that of isoprene emissions (Fineschi *et al*., 2013; Guenther *et al*., 2012; Sindelarova *et al*., 2014). However, recent studies in Amazonian late successional forests have shown higher numbers of isoprene emitters compared to monoterpene emitters (Jardine *et al*., 2020) as well as great ecosystem-level isoprene emission rates (Yáñez-Serrano *et al*., 2020).

Even though the capacity to emit monoterpenes appeared almost in all species (except for *Aldina heterophylla*, *Inga alba*, *Minquartia guianensis* and *Protium grandifolium*), emission of isoprene seems to be spread across different phylogenetic tree groups without a clear pattern, perhaps suggesting that isoprene emission capacity was gained and lost multiple times during evolution (Loreto *et al*., 2009; Monson *et al*., 2013; Sharkey *et al*., 2013) or is conserved only when plant genera undergo extensive speciation (Dani *et al*., 2014). Also, the capacity to emit isoprene may have been conserved only in narrow ranges of environmental conditions where emissions had clear advantages for the plant (Monson *et al*., 2013), as indicated by the unique functional niches (Taylor, 2017) of leaf, wood and whole-plant trait interactions that we found for isoprene emitters. Additionally, the high number of strict monoterpene emitters and emitters of both compounds observed corroborates with current hypothesis that isoprene synthase (ISPS) evolved from a large class of monoterpene synthases (TPS-b) (Sharkey *et al*., 2013; Li *et al*., 2017; Jardine *et al*., 2020).

Our results indicated that the spectra of plant economy were generally more efficient in explaining the presence and absence of emission or storage rather than the rates of emission or the concentration of stored compounds. This lack of strong patterns may reflect a methodological artefact. We calculated the emission rates based on leaf emission capacity (Ec) under standard light and temperature conditions (Guenther *et al*., 1995) and some studies indicate that Ec acclimates seasonally and over environmental gradients (Niinemets *et al*., 2010). Also, we quantified isoprenoid storage using a novel approach that consisted of shutting down leaf metabolism by freezing the samples, and afterwards using heat to volatilize stored compounds, then injecting the imprisoned gas in a GC-MS system. An eventual compound loss as a consequence of volatilization or leaching during transportation could result in underestimation of stored compounds, especially considering possible low system sensitivity and high detection limits.

Our finding that isoprene emission changes the direction in which different plant spectra coordinate was surprising, and revealed the importance of working with traits (e.g., whole-plant traits) that are usually uncommon in functional ecology studies. We demonstrated that plant carbon economic strategies can be used to explain isoprenoid production capacity (Guenther *et al*., 2006; Pacifico *et al*., 2011), and such finding may represent opportunities to further explore different functional trait interactions and plant ecological strategies in the soil-plant-atmosphere continuum. In view of a possible global climate change scenario, that may have effects on species turnover and composition of Amazonian tree communities (Zhang *et al*., 2018; Esquivel-Muelbert *et al*., 2019; Gomes *et al*., 2019), together with the increasing evidence of an isoprenoid production dependency on species diversity and ecological strategies (Fernández-Martínez *et al*., 2017; Taylor *et al*., 2018; Jardine *et al*., 2020), using a carbon economic approach to assess isoprenoid emissions might help elucidate future patterns of BVOC fluxes as well as the consequent impacts in ecosystem-atmosphere dynamics (Arneth *et al*., 2007, 2010; Heald *et al*., 2009; Hantson *et al*., 2017; Yáñez-Serrano *et al*., 2020).

ACKNOWLEDGEMENTS

We thank the National Institute for Amazonian Research (INPA) and the Max Planck Institute for Biogeochemistry (MPI-BGC) for the continuous support. We acknowledge the support by the ATTO project (German Federal Ministry of Education and Research, BMBF funds 01LB1001A; Brazilian Ministry of Science, Technology, Innovation and Communication; FINEP/MCTIC contract 01.11.01248.00); UEA, FAPEAM, LBA/INPA and SDS/CEUC/RDS-Uatumã; and Project CENBAM-INCT Centro de Biodiversidade Amazônica (FAPEAM/FDB/INPA/#003/2012). We also truly thank PELD Mauá for providing the species inventory dataset for initial selection of species; Dr. Daniel Marra and the Forest Management Lab for the tearing apparatus; and Juliane Menezes for her help in the April/2019 field campaign. We especially thank the field assistants and all the people involved in the logistic support of the ATTO project, who were all imperative for the development of this study. MR was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

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SUPPLEMENTARY INFORMATION

Figure S1. Location of the ATTO site, adapted from Botía *et al* (2020). Background topography is based on the Shuttle Radar Topography Mission (NASA-JPL, 2013) elevation model. Red polygon highlights the limits of the Uatumã Sustainable Development Reserve (USDR), and major rivers are labeled. Background layer of the insert map: ©OpenStreetMap contributors 2020. Distributed under a Creative Commons BY-SA License.

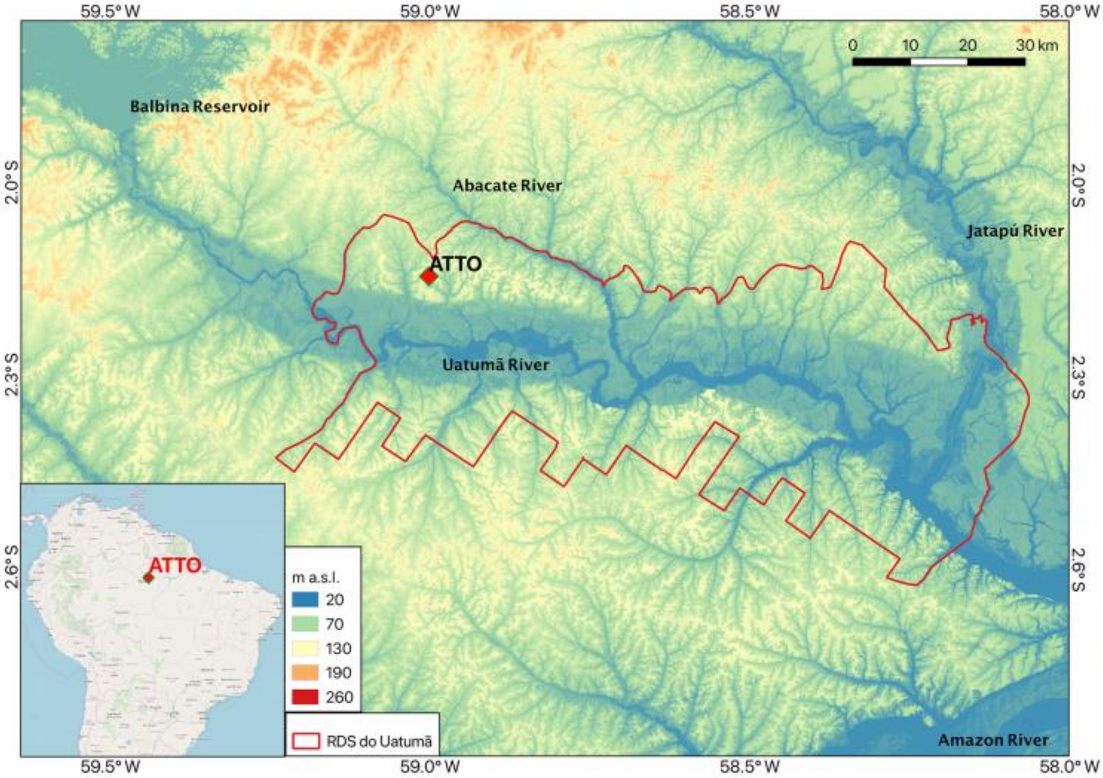


Figure S2. Types of vegetation found in the ATTO site: (a) dense, non-flooded upland forest vegetation (*terra-firme*); (b) closed-canopy vegetation on white sands (*campinarana*); (c) shrubland vegetation on white sands (*campina*); and (d) old non-flooded alluvial terraces (*terraço fluvial*). Photos: Débora Pinheiro Oliveira (a,d) and Francine Faia Fernandes (b,c).

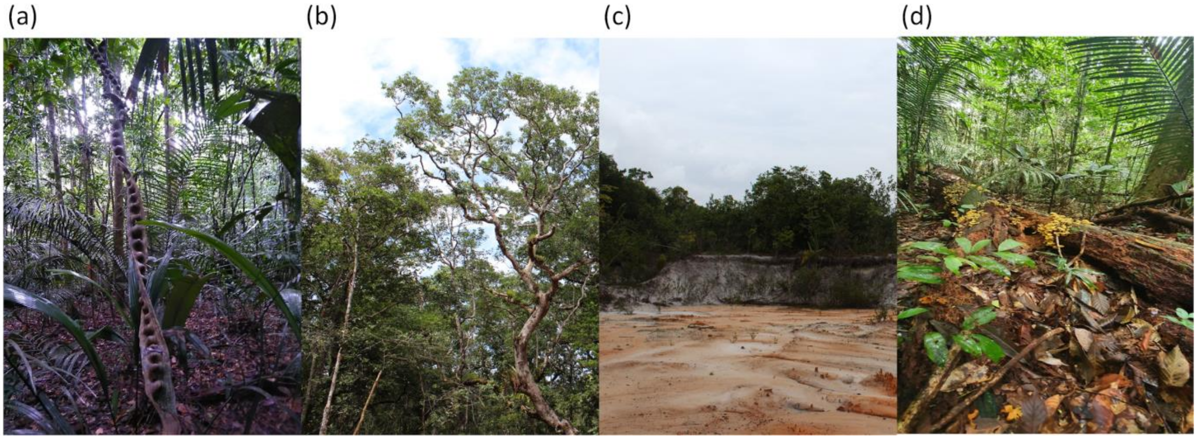


Figure S3. Relationship between log of monoterpene emission rates and foliar phosphorus content. Analyses include phylogenetic relationships between genera.

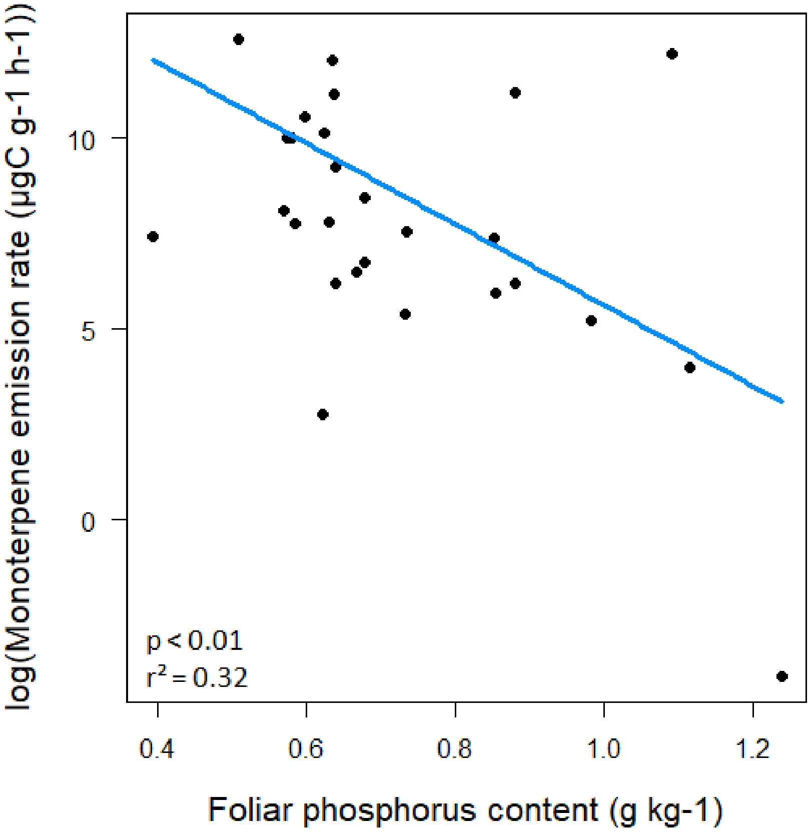


Table S1. Species, family, vegetation type, position in the vertical strata and range of diameter at 1.3 m height (DBH; cm) values (minimum and maximum) for 30 Amazonian tree species evaluated in this study.

Species	Family	Vegetation type	Vertical Strata	DBH (min-max)
Bocageopsis pleiosperma	Annonaceae	Fluvial Terrace	Canopy	16.2 - 28.7
Aspidosperma carapanauba	Apocynaceae	Terra Firme	Canopy	42.7 - 51.7
Geissospermum sericeum	Apocynaceae	Terra Firme	Sub-canopy	17.2 - 51.0
Macoubea sprucei	Apocynaceae	WS Shrubland	Sub-canopy	14.2 - 21.3
Protium grandifolium	Burseraceae	Terra Firme	Sub-canopy	13.9 - 19.0
Protium hebetatum	Burseraceae	WS Forest	Sub-canopy	13.5 - 22.2
Croton matourensis	Euphorbiaceae	Fluvial Terrace	Canopy	17.3 - 22.0
Aldina heterophylla	Fabaceae	WS Shrubland	Sub-canopy	29.4 - 51.5
Inga alba	Fabaceae	Fluvial Terrace	Canopy	38.5 - 60.5
Macrolobium duckeanum	Fabaceae	WS Shrubland	Sub-canopy	10.4 - 12.8
Parkia igneiflora	Fabaceae	WS Shrubland	Sub-canopy	12.3 - 19.0
Swartzia reticulata	Fabaceae	Terra Firme	Sub-canopy	37.4 - 38.8
Corythophora rimosa	Lecythidaceae	Terra Firme	Sub-canopy	32.3 - 40.5
Eschweilera coriacea	Lecythidaceae	WS Forest	Sub-canopy	12.8 - 21.4
Eschweilera grandiflora	Lecythidaceae	Terra Firme	Sub-canopy	11.0 - 39.3
Pachira faroensis	Malvaceae	WS Shrubland	Canopy	12.7 - 17.2
Scleronema micranthum	Malvaceae	Terra Firme	Sub-canopy	15.0 - 20.2
Theobroma sylvestre	Malvaceae	Fluvial Terrace	Sub-canopy	10.1 - 12.0
Mouriri duckeana	Melastomataceae	Fluvial Terrace	Canopy	11.5 - 47.0
Trichilia schomburgkiana	Meliaceae	Fluvial Terrace	Sub-canopy	16.0 - 17.3
Naucleopsis caloneura	Moraceae	Terra Firme	Sub-canopy	14.5 - 17.0
Minquartia guianensis	Olacaceae	Fluvial Terrace	Sub-canopy	34.5 - 41.0
Pagamea coriacea	Rubiaceae	WS Shrubland	Sub-canopy	14.0 - 16.1
Chrysophyllum sanguinolentum	Sapotaceae	WS Forest	Sub-canopy	22.0 - 35.7
Ecclinusa guianensis	Sapotaceae	Terra Firme	Sub-canopy	14.5 - 29.7
Manilkara bidentata	Sapotaceae	WS Shrubland	Sub-canopy	14.5 - 20.2
Pouteria caimito	Sapotaceae	Fluvial Terrace	Sub-canopy	11.1 - 16.2
Pradosia schomburgkiana	Sapotaceae	WS Shrubland	Sub-canopy	14.6 - 16.2
Simarouba amara	Simaroubaceae	Fluvial Terrace	Canopy	37.0 - 44.2
Rinorea guianensis	Violaceae	Terra Firme	Sub-canopy	16.0 - 17.9

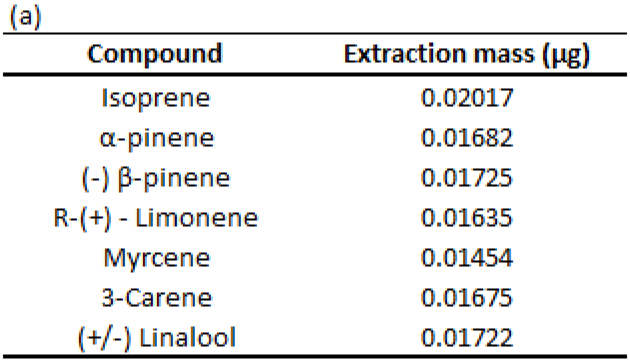
Table S2. Functional traits of leaf, wood and whole-plant measured and calculated for 27 Amazonian tree species and abbreviations (Abv) used in this study.

Level	Trait	Abv	Units
Leaf	Leaf Area	LA	cm^2
	Specific Leaf Area	SLA	cm^2 g
	Leaf Mass per Area	LMA	g cm^{-2}
	Leaf Dry Matter Content	LDMC	mg g^{-1}
	Leaf Thickness	LT	mm
	Force to Tear	FtT	N cm^{-2}
	Force to Punch	FtP	N cm^{-1}
	Vein Density	VeinDens	veins mm^{-2}
	Stomatal Density	StDens	stomata mm^{-2}
	Stomatal Length	StLgth	mm
	Chlorophyll Content	Chl	µg cm^{-2}
	Foliar Calcium Content	Ca	g kg^{-1}
	Foliar Iron Content	Fe	mg kg^{-1}
	Foliar Magnesium Content	Mg	g kg^{-1}
	Foliar Manganese Content	Mn	mg kg^{-1}
	Foliar Nitrogen Content	N	g kg^{-1}
	Foliar Phosphorus Content	P	g kg^{-1}
	Foliar Potassium Content	K	g kg^{-1}
	Foliar Zinc Content	Zn	mg kg^{-1}
Wood	Wood Density of the stem	WDst	g cm^{-3}
	Wood Density of the twig	WDtw	g cm^{-3}
	Wood Dry Matter Content of the stem	WDMCst	mg g^{-1}
	Wood Dry Matter Content of the twig	WDMCtw	mg g^{-1}
Whole-plant	Basal Area	BA	m^2
	Total Height	TH	m
	Sapwood Area per Basal Area	SABA	m^2 m^{-2}
	Crown Area per Basal Area	CABA	m^2 m^{-2}
	Total Height per Basal Area	THBA	m m^{-2}

Table S3. Composition and concentration (ppbv) of standard gases used for quantification and identification of isoprene and emitted monoterpenes.

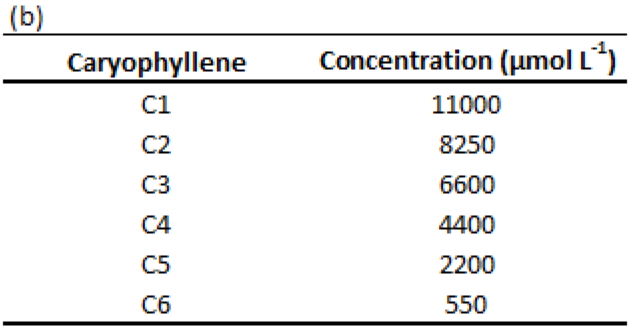
Compound	**Concentration (ppbv)**
Isoprene	500.7 ±5%
Methacrolein	517.3 ±5%
Methyl Vinyl Ketone	458.1 ±5%
Butanal	497.3 ±5%
Methyl Ethyl Ketone	478.9 ±5%
Benzene	493.8 ±5%
Toluene	484.2 ±5%
Ethylbenzene	489.0 ±5%
m -Xylene	494.6 ±5%
p -Xylene	481.6 ±5%
o -Xylene	502.2 ±5%
α-Pinene	477.7 ±5%
Camphene	474.6 ±5%
1-Octene-3-ol	495.9 ±5%
Sabinene	396.1 ±5%
β-Pinene	500.6 ±5%
Myrcene	353.1 ±5%
p -Cymene	481.3 ±5%
β-Phellandrene	380.6 ±5%
3-Carene	450.1 ±5%
γ-Terpinene	522.2 ±5%
Limonene	488.7 ±5%
cis -β-Ocimene	148.3 ±5%
o -Cymene	463.7 ±5%
trans -β-Ocimene	315.8 ±5%
Terpinolene	440.8 ±5%

Table S4. (a) Extraction mass (μg) of different liquid monoterpene standards for identification and quantification of stored monoterpenes; (b) Concentrations (μmol L^{-1}) of liquid caryophyllene standard six-point calibration curve for quantification of stored sesquiterpenes.



(a)

Compound	Extraction mass (μg)
Isoprene	0.02017
α-pinene	0.01682
(-) β-pinene	0.01725
R-(+) - Limonene	0.01635
Myrcene	0.01454
3-Carene	0.01675
(+/-) Linalool	0.01722



(b)

Caryophyllene	Concentration (μmol L^{-1})
C1	11000
C2	8250
C3	6600
C4	4400
C5	2200
C6	550

Table S5. Functional traits and percentage correlation values (loadings) of leaf, wood and whole-plant extracted from Principal Component Analysis (PCA; Figure 1). Trait names are in Table 1.

PC1		PC2	
Trait	**%Correlation**	**Trait**	**%Correlation**
N	30.70	BA	30.15
StDens	24.08	WDst	29.25
Zn	23.60	WDMCst	22.48
P	21.53	TH	19.70
Ca	-24.86	CABA	-19.80
FtP	-26.34	THBA	-27.71
Mg	-26.53	E	-31.32
Chl	-27.84	gs	-31.84
StLgth	-32.09	A	-35.17
LMA	-34.00	SABA	-36.62
LT	-38.33		

SÍNTESE

Os resultados indicaram que os espectros da economia de carbono das plantas parecem se correlacionar com a emissão e o estoque de isoprenóides. Observamos que a emissão de monoterpenos e o estoque de isoprenóides coordenam separadamente com os níveis de espectro econômico capturados na análise de componentes principais (PCA) - o espectro da folha e o da madeira e da planta-inteira. As taxas de emissão de monoterpenos variaram em relação ao espectro foliar, e as espécies com maiores taxas de emissão de monoterpenos tiveram tendência a ter traços de folha lentos. Surpreendentemente, a capacidade de emitir isopreno mudou a maneira com a qual os espectros coordenavam, indicando que espécies emissoras de isopreno podem exibir tanto folhas rápidas e traços lentos de madeira/planta-inteira, como folhas lentas e traços de madeira/planta-inteira rápidos. E, contrário à nossa hipótese, a capacidade de estocar isoprenóides surgiu conforme as espécies começaram a apresentar traços rápidos para os níveis de madeira e planta-inteira.

Nossos resultados mostraram que a emissão de isopreno muda a maneira com a qual os diferentes espectros da planta coordenam, e revelaram a importância de se trabalhar com traços (e.g. traços da planta-inteira) pouco comuns em estudos de ecologia funcional. Demonstramos que estratégias da economia de carbono podem ser utilizadas para explicar a capacidade de produção de isoprenóides (Guenther *et al*., 2006; Pacifico *et al*., 2011), e tal descoberta pode representar oportunidades para, no futuro, explorar diferentes interações entre traços funcionais e estratégias ecológicas de plantas. Tendo em vista um possível cenário de mudanças climáticas globais, o qual poderá ter efeitos sobre o *turnover* de espécies e a composição de comunidades arbóreas da Amazônia (Zhang *et al*., 2018; Esquivel-Muelbert *et al*., 2019; Gomes *et al*., 2019), além das evidências cada vez maiores da dependência da produção de isoprenóides em função da diversidade de espécies e das estratégias ecológicas (Fernández-Martínez *et al*., 2017; Taylor *et al*., 2018; Jardine *et al*., 2020), o uso de uma abordagem de economia de carbono para avaliar emissões de isoprenóides pode ajudar a elucidar futuros padrões de fluxo de COVBs, assim como os consequentes impactos na dinâmica ecossistema-atmosfera (Arneth *et al*., 2007, 2010; Heald *et al*., 2009; Hantson *et al*., 2017; Yáñez-Serrano *et al*., 2020).

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