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ANA LUÍSA FARES BIONDI LIMA

RESISTINDO, APESAR DE TUDO? EFEITO DOS MÚLTIPLOS USOS DO SOLO NAS COMUNIDADES DE MACRÓFITAS EM ECOSSISTEMAS AQUÁTICOS AMAZÔNICOS

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Orientadora: Prof. Dr^{a}. Thaísa Sala Michelan
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Dedico este trabalho aos meus pais,

Almerico Lima e Eliane Fares

“A natureza introduziu uma grande variedade na paisagem, mas o ser humano tem exibido uma tendência a simplificá-la. ”

Rachael Carson

“Pessoas são como plantas: elas crescem em direção à luz. Eu escolhi a ciência, porque a ciência me deu o que eu precisava – uma casa em sua definição mais literal: um lugar seguro de se estar. ”

Hope Jahren

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SUMÁRIO

RESUMO

Os usos do solo são considerados os mais severos mobilizadores de mudança na biodiversidade. Biomas, tais como as florestas tropicais, e ecossistemas, como os ecossistemas aquáticos, estão sendo deteriorados pelos usos do solo, e isso é preocupante, pois são importantes para a biodiversidade global. Macrófitas aquáticas são sensíveis às mudanças que ocorrem no seu hábitat físico, e respondem em diferentes escalas aos efeitos dos usos do solo. O principal objetivo deste trabalho foi avaliar os efeitos dos múltiplos usos do solo na diversidade de macrófitas. Partiu-se das seguintes hipóteses: i) a riqueza de espécies de macrófitas aumenta ao longo de um gradiente de múltiplos usos do solo e ii) a composição de espécies de macrófitas muda ao longo de um gradiente de múltiplos usos do solo. Para isto, foram amostrados, em julho de 2017, 30 ecossistemas aquáticos (riachos, lagos e brejos) localizados no município de Paragominas, Pará, Brasil. A riqueza de espécies foi mensurada pela presença de espécies encontradas em 150 metros dos pontos amostrais. A composição de espécies foi avaliada com um quadrado de $1m^2$, dando uma porcentagem de cobertura para cada espécie que ocorria dentro dele. As variáveis preditoras consistem nas variáveis ambientais locais (parâmetros da água e cobertura de dossel), e nas variáveis de paisagem, que consistem na porcentagem das classes de uso e cobertura do solo presentes em cada ponto amostral, obtidas através de técnicas de geoprocessamento. Para testar a hipótese (i), foram utilizados Modelos aditivos generalizados mistos. Para testar a hipótese (ii) foi usada uma Análise de Redundância baseada em distância. Também foi utilizada Análise de Táxons Indicadores de Limiares para responder a pergunta “Quais espécies são favorecidas em ambientes alterados, podendo ser indicadoras de tal estado?”, utilizando as porcentagens de cobertura os usos do solo. Foram encontradas 49 espécies de macrófitas, dentre elas uma espécie invasora. A riqueza de espécies foi afetada positivamente pelos usos do solo, e negativamente pela cobertura de dossel, corroborando a hipótese (i). Locais alterados podem fornecer mais microhabitats, favorecendo mais espécies, devido ao aumento na incidência de luz, sedimentação, e aumento na quantidade de nutrientes. A composição de espécies foi afetada negativamente pela cobertura de dossel, e positivamente pelo pH e usos do solo, corroborando parcialmente a hipótese (ii). Locais mais alterados podem fornecer maior heterogeneidade de hábitat, aumentando a diversidade de formas de vida. Três espécies foram selecionadas como indicadoras de mudança no uso do solo*: Cabomba aquatica*, *Eleocharis interstincta* e *Utricularia sp*. As comunidades de macrófitas podem estar sofrendo um estágio inicial de sucessão, onde o aparecimento de espécies invasoras é o início da diminuição na diversidade, conforme as consequências das mudanças causadas pelos usos do solo se tornam abrasivas. Estes resultados destacam as macrófitas como indicadoras de ambientes alterados, reforçando o seu potencial uso no monitoramento de ambientes de água doce na Amazônia.

Palavras-chave: plantas aquáticas; mudança de uso do solo; bioindicadores; ecossistemas de água doce neotropicais.

ABSTRACT

Land-use is considered the most severe driver of biodiversity change. Biomes, such as tropical forests, and ecosystems, such as freshwaters, have been damaged by land use, and this is concerning, since they are important to global biodiversity maintenance. Aquatic macrophytes are sensitive to changes that occur on their physical habitat, and they respond at different scales to the effects of land use. This study's main objective was to evaluate the effects of multiple land-use on macrophyte diversity. Our hypotheses were that: i) macrophyte species richness increases in multiple land-use gradients and ii) macrophyte species composition changes along a multiple land-use gradient. For that, we surveyed, in July 2017, 30 aquatic ecosystems (streams, lakes and ponds) located in Paragominas, Pará, Brazil. Species richness was sampled by taking notes of all species that occurred in a 150m transect of each site. We sampled composition data with a 1m2 quadrat, giving a percentage of cover to each species inside it. The predictive variables consisted of the local environmental variables (water parameters and canopy cover), and the landscape variables, which consisted of the percent of land-use and land cover classes present on each sampling site, that were obtained using geoprocessing techniques. To test hypothesis (i), Generalized Additive Mixed Models were used. To test hypothesis (ii), we used a distance-based redundancy analysis. Additionally, a Threshold Indicator Taxa Analysis was performed to identify which species are indicators of the land-use classes used on this study. We recorded 49 macrophyte species, and one of those was considered invasive. Species richness was affected positively by land-use, and negatively by canopy cover, corroborating hypothesis (i). Altered sites could provide more microhabitats, favoring more species, due to increased light incidence, sediment load, and nutrient input. Species composition was affected negatively by canopy cover, and positively related to pH and land-use, partially corroboration hypothesis (ii). More altered sites can provide habitat heterogeneity and increase life-form diversity. Three species were selected as indicators of land-use change: *Cabomba aquatica*, *Eleocharis interstincta* and *Utricularia sp*. Macrophyte communities could be experiencing an early stage of succession, in which the appearing of invasive species could be the start of a decrease in diversity as the consequences of land-use become abrasive. Those results point macrophytes as indicators of altered conditions, reinforcing their potential use to be considered on freshwater assessments on Amazonia.

Keywords: aquatic plants; land-use change; bioindicators; Neotropical freshwaters.

1. CONTEXTUALIZAÇÃO

Há milhares de anos o ser humano altera a paisagem natural a sua volta, com o objetivo de explorar os recursos naturais para sua subsistência (FOLEY et al., 2005; GONZÁLEZ-ABRAHAM et al., 2015). Com o aumento da densidade populacional, o surgimento da industrialização e da agricultura em larga escala, a demanda por matérias primas, e consequentemente a degradação desses ambientes, chegou a níveis elevados (DUNLAP; JORGENSON, 2012; VITOUSEK et al., 1997). Como consequência, a degradação ambiental gera desequilíbrio nos ecossistemas, levando a elevada perda de espécies, a homogeneização das comunidades biológicas, e a subsequente perda de biodiversidade global (MCKINNEY; LOCKWOOD, 1999; VITOUSEK et al., 1997).

Em uma comunidade biológica, cada espécie responde diferentemente a diversos fatores físicos e biológicos, ao longo de uma escala espacial e temporal, que corresponde ao seu nicho ecológico (SHEA; CHESSON, 2002). Proposto primeiramente por Grinnell (1917), o conceito de nicho ecológico é considerado um tema central da ecologia moderna (LEIBOLD, 1995). Ao longo dos anos, suas definições foram alteradas e aperfeiçoadas, entretanto, uma das mais utilizadas é a proposta por Hutchinson (1957), que descreve o nicho como o espaço ecológico definido por todos os fatores, tanto bióticos quanto abióticos, que afetam um determinado organismo, que podem ser inúmeros (um hipervolume *n*-dimensional).

As espécies de uma determinada comunidade podem coexistir ou competir, dependendo da variação das condições ambientais, da variabilidade ambiental ao logo do espaço e do tempo, e das adaptações das espécies (LEWIS, 2009; SHEA; CHESSON, 2002), resultando também nos efeitos que estas espécies terão no ambiente (LEIBOLD, 1995; SHEA; CHESSON, 2002). Espécies aparentemente semelhantes podem coexistir em função das adaptações que as permitem obter recursos de formas diferentes (LEWIS, 2009). Alternativamente, ambientes com recursos e condições ambientais limitados podem favorecer a sobreposição de nicho das espécies, de forma que elas passam a competir (LEIBOLD, 1995; LEWIS, 2009). Neste sentido, a teoria do nicho leva em consideração diversos fatores, dentre eles a competição e coexistência entre espécies, a predação, a estabilidade de uma comunidade e o efeito de distúrbios sobre as mesmas (LEWIS, 2009).

Neste cenário, as ações antrópicas atuam como filtros ambientais, afetando os padrões de disponibilidade de recursos ao alterarem as condições ambientais dos sistemas (SHEA;

CHESSON, 2002; SIQUEIRA; LACERDA; SAITO, 2015), que resultam em diferentes respostas da biota, como perda de táxons que não conseguem se adaptar às novas condições do ambiente e crescimento populacional das espécies resistentes (SHEA; CHESSON, 2002). Estes acontecimentos levam à mudança na composição de espécies e perda de diversidade (SIQUEIRA; LACERDA; SAITO, 2015), com a substituição de espécies especialistas por generalistas altamente adaptadas a um amplo gradiente ambiental e a invasão de espécies exóticas, resultando em uma simplificação dos ecossistemas (MCKINNEY; LOCKWOOD, 1999).

Os problemas ambientais mais discutidos atualmente causados pela ação antrópica são as mudanças climáticas, que são agravadas, dentre outros fatores, pelo desmatamento, a poluição atmosférica, a degradação dos recursos hídricos (DUNLAP; JORGENSON, 2012), e as alterações das paisagens resultantes das mudanças de usos do solo (ALLAN, 2004; SALA et al., 2000). Dentre os ambientes que são mais afetados pelas mudanças dos usos do solo encontram-se os biomas, tais como as florestas tropicais, e ecossistemas, como os ecossistemas aquáticos, que sofrem com os seus efeitos abrasivos, principalmente devido o valor econômico e a importância para a biodiversidade (MALHI et al., 2014; NIETO et al., 2017).

Dentre os ambientes citados, a Amazônia, o bioma que abriga o maior sistema fluvial do planeta, é afetado continuamente por diversas pressões antropogênicas, dentre elas as mudanças causadas pelos usos do solo (MALHI et al., 2014). O desmatamento para fins econômicos, como exploração de madeira, o desenvolvimento agropecuário, a construção de rodovias e a mineração transformaram estas áreas em um verdadeiro mosaico de usos, onde é possível encontrar fragmentos florestais inseridos nas mais diversas paisagens antropogênicas (MALHI et al., 2008, 2014). Todos estes fatores trazem diversas consequências para a diversidade biológica regional, que é afetada pelas mudanças na estrutura, diversidade e funcionamento das florestas. O resultado destas mudanças é a alteração na composição e resiliência da biota, a extinção de táxons e o colapso total de ecossistemas, principalmente de seus ecossistemas aquáticos, o que consequentemente é prejudicial para a biodiversidade global (MALHI et al., 2014).

Os ecossistemas de água doce são importantes para o abastecimento das populações humanas, com valor econômico, social e cultural, e também para a biodiversidade (DUDGEON et al., 2006; NIETO et al., 2017), pois apesar de representarem 0.01% da quantidade de água do mundo, cerca de 6% das espécies descritas habitam estes ambientes

(DUDGEON et al., 2006), e elas podem estar ameaçadas pelas atividades humanas que utilizam ou ocorrem próximas a estes locais (NIETO et al., 2017). A mudança da morfologia dos ambientes, a alta concentração de nutrientes que provocam a proliferação de organismos (ALLAN, 2004; PALMER et al., 2010), a acumulação de substâncias nocivas ao longo dos níveis tróficos (CARDWELL; HAWKER; GREENWAY, 2002), a intoxicação, e a morte dos organismos (POND et al., 2008), são as principais consequências de impactos contínuos aos sistemas aquáticos. Além do mais, a contaminação da água e dos organismos que ali vivem, como peixes, invertebrados e plantas, pode levar a contaminação das pessoas (CEGŁOWSKA et al., 2016; MORAES; QUINZANI JORDÃO, 2002), por vezes de forma irreversível ou debilitante.

Os usos do solo são formas de exploração de recursos naturais diversos, e o seu estabelecimento e transformações na paisagem são diversos e heterogêneos, resultados de uma mistura de fatores, como a geografia do local e os componentes históricos, culturais e tecnológicos relacionados às singularidades de cada sociedade (GONZÁLEZ-ABRAHAM et al., 2015). Os seus efeitos na integridade física dos sistemas aquáticos, e consequentemente a sua influência na biota, também seguem estes padrões, e suas principais consequências são: alterações na vegetação ripária, o assoreamento do canal, e a mudança da composição química e qualidade da água (SALA et al., 2000), fatores que afetam diretamente a composição da biota aquática local (ALLAN, 2004).

Diversos estudos vêm mostrando que os usos de solo alteram a estrutura da biota aquática amazônica (GARDNER et al., 2013), e do potencial indicador que estes organismos apresentam em resposta à mudança dos usos do solo (BLEICH et al., 2015; SHIMANO; JUEN, 2016). Com a degradação ambiental chegando a estado crítico em diversos espaços amazônicos, torna-se importante aprofundar, atualizar e realizar estudos com novas abordagens que, além de demonstrar os efeitos das mudanças dos usos do solo nos ecossistemas aquáticos amazônicos, contribua para a efetivação de medidas de conservação dos mesmos. Dentre estes organismos, as macrófitas aquáticas são destacadas como grupo de potencial valor indicador das condições ambientais dos ecossistemas aquáticos e das consequências dos usos do solo (BLEICH et al., 2015).

Macrófita aquática é uma denominação ecológica dada ao conjunto de plantas macroscópicas que habitam ambientes aquáticos, que não são algas filamentosas e planctônicas (BORNETTE; PUIJALON, 2011; POMPÊO, 2017). Segundo Cook et al. (1974), macrófitas são vegetais cujas porções fotossintéticas estão permanentemente, ou pelo menos durante vários meses do ano, submersas na água ou flutuando em sua superfície. As macrófitas promovem heterogeneidade e complexidade estrutural ao ambiente, o que é propício para que haja uma alta biodiversidade (LARGE; PRACH, 1999; THOMAZ; CUNHA, 2010). Elas possuem papel importante na ciclagem de nutrientes, com envolvimento nos ciclos do carbono, nitrogênio e fósforo (BORNETTE; PUIJALON, 2011). Também são essenciais na produção primária e de oxigênio nesses sistemas, junto com os fitoplânctons (ESTEVES, 2011). Além disto, são usadas como refúgio, berçário e alimento de vários organismos, como peixes e invertebrados, que se associam a elas (BORNETTE; PUIJALON, 2011; THOMAZ; CUNHA, 2010).

As macrófitas estão distribuídas em várias divisões botânicas, principalmente as divisões Pteridophyta e Spermatomorphyta, que incluem diversas famílias de licófitas, samambaias e angiospermas (CHAMBERS et al., 2008), com a característica comum de terem desenvolvido diversas estratégias adaptativas ao longo de suas histórias evolutivas (relacionadas as suas morfologias e formas de vida) que as tornou capazes de colonizar praticamente todos os tipos de ecossistemas aquáticos: margens de lagos, rios, riachos, reservatórios, regiões costeiras estuarinas e de mares, e também cachoeiras (ESTEVES, 2011; THOMAZ; CUNHA, 2010). Elas também são encontradas em larga escala em ambientes alterados, como em lagoas formadas pela cava de exploração de carvão ou em barragens de rejeito de mineração (POMPÊO, 2017).

Por se tratar de um grupo com diversas origens filogenéticas (CHAMBERS et al., 2008), a classificação ecológica das macrófitas é difícil de ser feita. Entretanto, para fins práticos, elas são classificadas de acordo com suas adaptações morfológicas ao meio aquático, que são representadas pela disposição das folhas na coluna d'água e a ancoragem das raízes, e, portanto, são divididas em formas de vida ou grupos ecológicos (ESTEVES, 2011; POMPÊO, 2017).

Segundo Esteves (2011), existem cinco grupos ecológicos: as emersas, flutuantes livres, submersas enraizadas, submersas livres, e com folhas flutuantes. Macrófitas emersas são plantas enraizadas no substrato que possuem as folhas acima da água. Esta forma de vida fica principalmente localizada em áreas mais rasas, como as margens. As flutuantes livres desenvolvem-se livremente na lâmina d'água, em locais protegidos do vento ou com pouca correnteza, e suas raízes absorvem nutrientes da agua. As submersas enraizadas crescem fixas nos leitos de rios e lagos, têm suas folhas completamente submersas, e somente suas partes reprodutivas se desenvolvem acima da coluna d'água. As submersas livres apresentam raízes pouco desenvolvidas, flutuando abaixo da coluna d’água em locais com pouca correnteza, presas as estruturas de outras plantas. Já as macrófitas com folhas flutuantes possuem raiz e caule submersos, desenvolvendo folhas com pecíolos longos e flexíveis que flutuam na lâmina d’água. Também existem as plantas anfíbias, que habitam ambientes encharcados, conseguindo sobreviver tanto em período de cheia quanto de estiagem, normalmente mudando sua forma anatômica, fisiológica e fenotípica, apresentando, portanto, diferentes morfologias nas fases terrestre e aquática (ESTEVES, 2011; POMPÊO, 2017), e as epífitas, que usam outras plantas aquáticas como substrato (ESTEVES, 2011).

A abundância, composição e riqueza de macrófitas em ambientes aquáticos são influenciadas pelas suas condições físico-químicas (ALEXANDER; WOODFORD; HOTCHKISS, 2008; AOKI et al., 2017; SCHNEIDER et al., 2015). Os principais fatores que determinam a ocorrência de macrófitas em seus ambientes são a incidência de luz, disponibilidade de nutrientes, e a morfologia física dos ambientes, variáveis que influenciam, em conjunto ou isoladamente, as características fotossintéticas do vegetal (BORNETTE; PUIJALON, 2011; CAMARGO; PEZZATO; SILVA, 2003).

Dentre estas variáveis, a incidência de luz está associada à abertura de dossel, fator relacionado à sombra criada pela vegetação ripária, que afeta as macrófitas negativamente, sondo considerada um filtro ambiental para a sua ocorrência (BANDO et al., 2015). As variações de temperatura da água dependem do regime climático natural, e influenciam diretamente o metabolismo de comunidades aquáticas (BORNETTE; PUIJALON, 2011). A temperatura afeta a produção primária, e as macrófitas apresentam tolerância a um amplo gradiente de temperatura (BORNETTE; PUIJALON, 2011). Existem faixas ótimas de temperatura diferentes para cada espécie, havendo variação destas faixas em função da sazonalidade, do ambiente e da localização geográfica (CAMARGO; PEZZATO; SILVA, 2003).

A disponibilidade de nutrientes é descrita como uma das forças mais importantes que governam a sucessão e estruturação de comunidades, afetando a competição entre espécies, e determinando a composição de espécies dentro de uma comunidade (ESPINAR; ROSS; SAH, 2011). Os principais nutrientes que influenciam na produção primária são o fósforo, o nitrogênio e o carbono inorgânico (ESTEVES, 2011). Eles são essenciais para a subsistência das plantas aquáticas (e dos outros organismos fotossintetizantes), e, por isso, algumas adaptaram-se às diversas formas como os nutrientes estão presentes na água, usando diferentes vias para absorvê-los (BORNETTE; PUIJALON, 2011).

Fósforo (P) e nitrogênio (N) estão relacionados com o processo de eutrofização, portanto a sua quantidade é usada para mensurar o estado trófico dos corpos d'água (ESTEVES, 2011; TOIVONEN; HUTTUNEN, 1995). Altas quantidades de P e N em ambientes aquáticos promovem competição e diminuem a heterogeneidade, provocando o crescimento populacional de espécies flutuantes, que em contrapartida matam as espécies submersas, pois a sua cobertura impede a penetração de luz na água (BORNETTE; PUIJALON, 2011). Normalmente, a grande presença de plantas flutuantes indica que o ambiente se encontra eutrofizado, como é comum em lagos de reservatórios (BORNETTE; PUIJALON, 2011; ESTEVES, 2011; POMPÊO, 2017). No entanto, em situações críticas de eutrofização, as macrófitas desaparecem devido competição com fitoplâncton (LARGE; PRACH, 1999; TOIVONEN; HUTTUNEN, 1995). Uma forma de mensurar o estado trófico (e, portanto, inferir na quantidade de P e N) geral de ecossistemas aquáticos é através da condutibilidade (TOIVONEN; HUTTUNEN, 1995).

O metabolismo das macrófitas submersas é influenciado pelo carbono inorgânico. As macrófitas removem carbono por assimilação de matéria orgânica e precipitação de sais carbonados nas folhas (CARPENTER; LODGE, 1986), e possuem a habilidade de assimilar diferentes formas de carbono na água e no ar, dependendo do seu grupo taxonômico e da sua forma de vida (VESTERGAARD; SAND-JENSEN, 2000; ALEXANDER; WOODFORD; HOTCHKISS, 2008; BORNETTE; PUIJALON, 2011) As formas e quantidade de carbono inorgânico presentes na água podem ser expressas através do pH (TOIVONEN; HUTTUNEN, 1995). Além disto, as macrófitas são umas das fontes de oxigênio nos ecossistemas aquáticos (ESTEVES, 2011). Macrófitas submersas oxigenam a água mais eficientemente que macrófitas com folhas flutuantes (BORNETTE; PUIJALON, 2011; CARPENTER; LODGE, 1986). Quando as macrófitas submersas realizam a fotossíntese, o oxigênio liberado se dissolve na água, auxiliando a aeração do ambiente, enquanto as espécies emergentes liberam o oxigênio para fora da água (BORNETTE; PUIJALON, 2011).

Por serem organismos extremamente sensíveis as mudanças ambientais nos ecossistemas aquáticos (LACOUL; FREEDMAN, 2006), e apresentarem respostas diferentes (que podem ser táxon-específicas ou de acordo com sua forma de vida), as macrófitas são consideradas indicadoras da qualidade ecológica e ambiental de seus ecossistemas (KASSAYE et al., 2016; MISHRA et al., 2008; SZOSZKIEWICZ et al., 2016). Por isso, diversos países utilizam índices baseados na diversidade de macrófitas aquáticas para avaliar o status ecológicos de ecossistemas aquáticos de água doce ao redor do mundo

(BARTODZIEJ; LUDLOW, 2009; LYCHE-SOLHEIM et al., 2013; POIKANE et al., 2015, 2018; SZOSZKIEWICZ et al., 2009). Porém, no Brasil, os índices de avaliação de integridade dos corpos d'água propostos pelo Programa Nacional de Avaliação da Qualidade das Águas (PNQA) da Agência Nacional de Águas (ANA) levam em consideração somente os aspectos físicos e químicos dos ambientes, e os organismos aquáticos (dentre eles, as macrófitas) são negligenciados nestas avaliações (UMETSU, 2016).

O presente trabalho teve como objetivo avaliar os efeitos de múltiplos usos do solo na diversidade de macrófitas aquáticas, usando variáveis que explicam o padrão de distribuição das macrófitas nos ambientes aquáticos. Os dados foram coletados em ecossistemas aquáticos localizados na Amazônia Oriental Brasileira, dentro e no entorno de uma área de mineração, em um gradiente de múltiplos usos e coberturas do solo que incluíram vegetação primária, vegetação secundária, pasto e solo exposto. Este estudo visou gerar informações acerca das respostas das macrófitas aquáticas aos múltiplos usos do solo, mostrar o seu valor como indicadoras de mudança ecológica e ambiental, além de produzir informações que contribuam para o manejo e preservação dos ecossistemas aquáticos amazônicos.

Os resultados desta dissertação estão apresentados em formato do artigo intitulado: "Resisting, nevertheless? Effects of land-use on macrophyte communities in Amazonian aquatic ecosystems" (Capítulo 2). Este capítulo foi formatado de acordo com as normas da revista *Ecological Indicators*, a qual será submetido, porém os demais organizações seguem as normas de apresentação de dissertação estabelecidas pela Universidade Federal Rural da Amazônia. As normas da revista podem ser encontradas no Anexo I deste manuscrito.

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2. RESISTING, NEVERTHELESS? EFFECTS OF LAND-USE ON MACROPHYTE COMMUNITIES IN AMAZONIAN AQUATIC ECOSYSTEMS

2.1. Introduction

Most of the world's natural landscapes have suffered with human-induced change (Foley et al., 2005; González-Abraham et al., 2015; Vitousek et al., 1997), because of the vast demand for natural resources (Sala et al., 2000). This modification results in natural environment degradation (Dunlap and Jorgenson, 2012; Vitousek et al., 1997), which consequently causes loss of species, ecosystem's disruption and change in community structure, which affects global biodiversity (McKinney and Lockwood, 1999; Vitousek et al., 1997). Land-use change is considered the major driver of biodiversity change (Sala et al., 2000). Biomes, such as Tropical Forests, and ecosystems, such as Freshwaters, have been damaged by land-use change and are the most threatened by it, because they have economic value, and are important to global biodiversity maintenance (Malhi et al., 2014; Nieto et al., 2017).

In a biological community, each species responds differently to several physical and biological factors, along a spatial and temporal scale, according to their ecological niche (Shea and Chesson, 2002). In this scenario, human activities, such as land use, affect local environmental variables (Mikulyuk et al., 2011), altering those systems, resulting in different biotic responses, such as loss of taxa that can't adapt to new environmental conditions or population growth of tolerant species (Shea and Chesson, 2002). This causes a decrease in diversity and shifts local community structure (Siqueira et al., 2015), with the substitution of specialist species to generalists highly adapted to an ample environmental gradient, creating simplified ecosystems (McKinney and Lockwood, 1999).

Land-use settlement and changes in the landscape are heterogeneous and continuous, and are a result of a mixture of factors, such as local geography and the historic, cultural and technological components related to the singularity of each society (González-Abraham et al., 2015). Land-use effects on freshwaters follow those patterns, affecting those systems mainly by modifying and causing loss of riparian vegetation, which increases canopy openness on those systems, and also by causing channel siltation, and changing water chemistry and quality (Johnson and Angeler, 2014; Mikulyuk et al., 2011; Sala et al., 2000). Those consequences harm the physical integrity of freshwaters, resulting mainly in habitat loss (Sala et al., 2000), which affect the local aquatic biota's structure directly (Allan, 2004; Johnson and Angeler, 2014). The death of organisms, loss of whole species populations (Pond et al., 2008), and increase of tolerant species (Allan, 2004; Johnson and Angeler, 2014) are the main responses of the biota affected by land-use change.

The high freshwater biodiversity can be explained, in parts, by the presence of aquatic macrophytes, because they increase habitat complexity in different spatial scales (Dibble et al., 2006), which elevates species richness (Lansac-Tôha et al., 2003; Pelicice et al., 2008; Takeda et al., 2003) and functional diversity (Heino, 2008) of other communities. Macrophytes possess a range of life forms, which allows them to colonize several aquatic ecosystems (Esteves, 2011). As such, they have a vast role in ecosystems functions: as food supply for primary consumers, by association with several animals (e.g.: fishes and invertebrates; Bornette and Puijalon, 2011) and microorganisms (eg: periphyton; Esteves, 2011), and as part of nutrient cycles and in the process of sedimentation of particulate matter (Aoki et al., 2017).

Macrophyte species richness and composition are influenced by the physical and chemical conditions of freshwater ecosystems (Alexander et al., 2008; Aoki et al., 2017; Schneider et al., 2015), which can be temporal and spatially structured (Lacoul and Freedman, 2006). Light incidence (Bando et al., 2015), nutrient availability (Aoki et al., 2017) and the physical morphology of freshwaters (Schneider et al., 2015), are examples of limiting factors that can affect macrophytes together or isolated (Bornette and Puijalon, 2011; Schneider et al., 2018, 2015). As such, those factors are considered environmental filters to macrophyte species and life-form occurrence (Schneider et al., 2018).

Furthermore, since macrophytes are sensitive to changes that occur on their physical habitat, land-use is considered a driver of variation in macrophyte communities (Mikulyuk et al., 2011), but they respond at different scales to those effects (Akasaka et al., 2010). The response could be negative, in which land use decreases macrophyte richness (Sass et al., 2010), and causes a dominance of one life-form (Akasaka et al., 2010). But they could be positive as well, with an increase of species richness, due to canopy openness caused by the loss of riparian vegetation, and nutrient availability (Bleich et al., 2015; Elo et al., 2018). On all cases, land-use alters macrophyte community structure (Elo et al., 2018; Sass et al., 2010).

For instance, some species can disappear when impacts cause great changes (such as water turbidity and channel siltation; Allan, 2004), like submerged and free-floating species (Akasaka et al., 2010; Kolada, 2010; Sass et al., 2010). However, those factors (among others, for instance, canopy openness and nutrient input) can also increase growth of tolerant (e.g.:

amphibious and emergent life forms) and opportunistic species (Akasaka et al., 2010; Kolada, 2010; Quinn et al., 2011), and can facilitate invasion by exotic species (Mackay et al., 2010; Quinn et al., 2011). The substitution of submerged and free-floating species to amphibious and emergent-dominated communities indicates succession in macrophyte communities (Gołdyn, 2009). Thus, macrophytes are considered bioindicators of the ecological and environmental quality of freshwater ecosystems (Kassaye et al., 2016; Kolada, 2010; Mishra et al., 2008; Szoszkiewicz et al., 2016). In addition, some can be used to rehabilitate, remediate (Jones et al., 2018; Kassaye et al., 2016), and restore ecosystems degraded by land-use (Alderton et al., 2017), before they get into an unrecoverable state.

This research aims to evaluate the effects of land use in aquatic macrophyte diversity, using variables that can explain macrophyte distributional pattern along those environments. We aimed to answer the following questions: i) does multiple land-use affect aquatic macrophyte richness? Which environmental variables affect species richness?; ii) Is there a difference between macrophyte community composition along a multiple land-use gradient? Which local environmental variables are affecting them?; iii) Which species are favored in altered environments and therefore could be indicators of such state? Thus, our hypotheses are: i) Macrophyte species richness will increase in multiple land-use gradients, due to canopy openness, especially in sites dominated by pasture and bare soil. ii) Macrophyte species composition changes along a land-use gradient. Sites with more percentage of primary and secondary forest (less altered sites) will have more life-form diversity than sites with more percentage of pasture and bare soil, since altered sites will favor amphibious and emergent species dominance, especially the pioneers in ecological succession, due to change in water quality.

2.2. Materials and Methods

2.2.1. Study area

Sampling took place in 30 sites (Figure 1), which comprise streams (20), lakes (6) and ponds (4), located in the municipality of Paragominas, Pará, Brazil (Lat: 02° 59' 45" S; Long: 47° 21' 10" W). The municipality's climate is characterized as wet and hot, with a mean annual temperature of 26 °C, mean air humidity of 81%, and mean annual precipitation of 1.800 millimeters (Pinto et al., 2009). Paragominas vegetation type consists of tropical rainforest, as the municipality is located in the world's largest remaining tropical forest, the

Amazon, and a range of human activities are executed along its territory (e.g.: agriculture, pasture, logging and mining activities; Pinto et al., 2009).

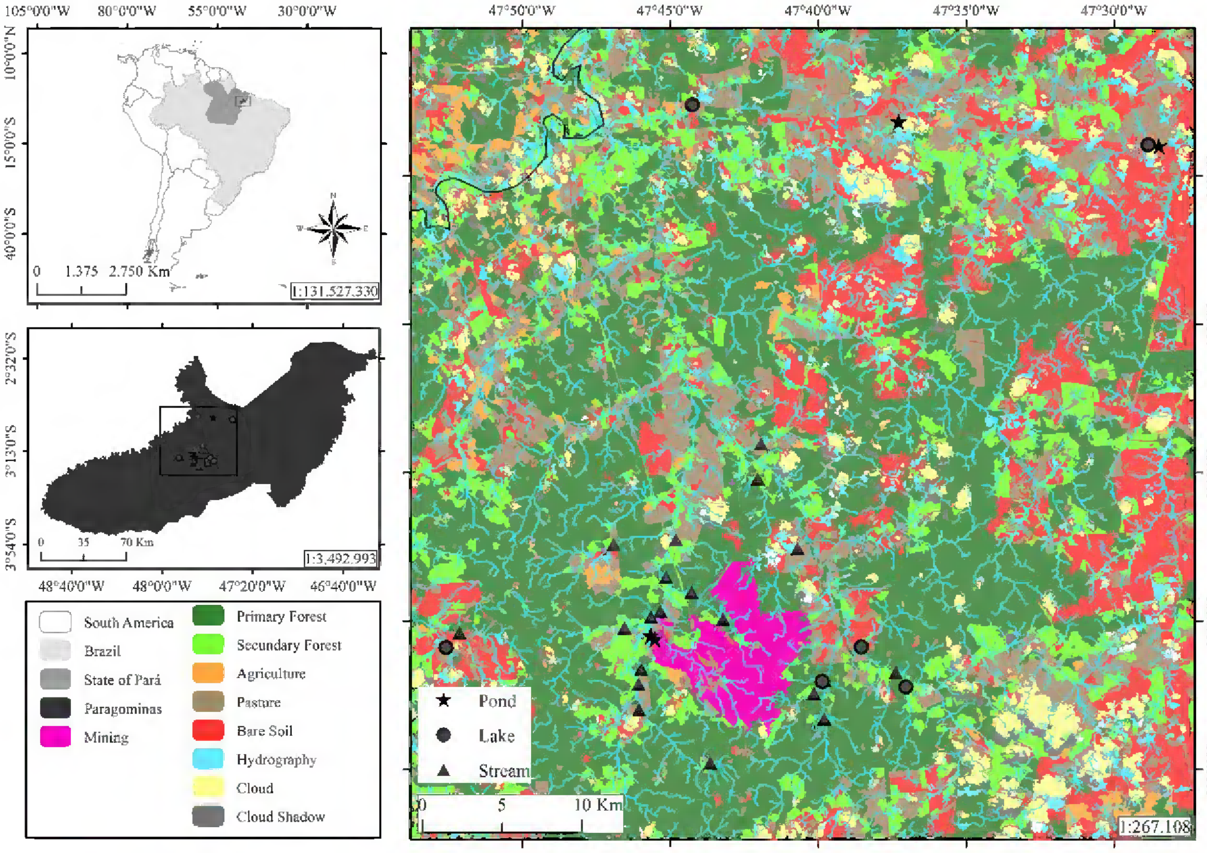


Figure 1: Map of the sampling sites (Paragominas municipality, PA, Brazil). The shape of the sites represents the type of ecosystem. Star: pond; Circle: lake; Triangle: Stream.

2.2.2. *Sampling design*

Fieldwork took place in July 2017. We sampled macrophyte abundance-based composition data with a 1m2 (1m x 1m) quadrat, putting it in one place of each sampling site. A percentage of cover was given to each species inside the quadrat, and we considered that macrophyte composition. Species richness data were sampled by taking notes of all macrophyte species that occurred in a 150m transect of each aquatic ecosystem. All sampling sites were at least 1 km apart.

Macrophytes were collected manually or using pruning shears. We identified the species in the field, when it was possible, and the non-identified material herborized following Herbarium techniques. After that, they were identified to the smallest possible taxonomic group. For that, we used specialized literature (Amaral et al., 2008; Lorenzi, 2008; Pott and Pott, 2000), consulted specialists, and comparison with material deposited in the João Murça Pires (MG) Herbarium, located in the Museu Paraense Emílio Goeldi, where all fertile plants of this study were deposited. Botanical nomenclature followed APG IV (Angiosperm Phylogeny Group; Byng et al., 2016) for vascular plants, and PPG I (Pteridophyte Phylogeny Group; Schuettpelz et al., 2016) for ferns and lycophytes, and we used the *Tropicos* website of the Missouri Botanical Garden as well as the *Brazil Flora Group* to confirm species and authors names.

Life-forms were classified according to Esteves (2011), which divides macrophytes in amphibious, emergent, epiphyte, floating-leafed, free-floating, free-submerged and rooted-submerged. They were also determined according to specialized literature (Amaral et al., 2008; Pott and Pott, 2000), and macrophyte checklists for the country containing life-form information (Abe et al., 2015; Moura-júnior et al., 2015, 2013; Pivari et al., 2013).

Local environmental variables, which corresponded to Limnological data, were measured using a multiparameters probe (Horiba U-50), consisting of: pH, temperature (ºC), water turbidity (ntu), conductivity (µS/cm), dissolved oxygen (mg/L) and total dissolved solids (ppm). We also measured canopy cover above the quadrats using a densiometer, which we later converted to percentage, according to the index proposed by Peck et al. (2006).

2.2.3. Acquisition of remote sensors data to land-use and cover characterization

Landscape variables consisted of Land-use and Land cover classes present on the 30 sampling sites, which were characterized using different geoprocessing softwares: ArcGIS 10.1 (ESRI, 2014), PCI Geomatica V10.1 (Hill, 2007) and Ecognition 9 (Definiens, 2009). We identified Land-use and Land cover classes using Image Digital Processing (PDI) from the RapidEye Earth Imaging System (REIS) optic sensor. The REIS Images are of commercial use, but we acquired data for research purposes on the Brazilian Ministry of Environment website (http://geocatalogo.mma.gov.br/). The selected images were from the year of 2015, the last year that the databank provided. REIS images were acquired and orthorectified in a geographic coordinates system projected in the geodesic DATUM WGS 84.

The images were submitted to atmospheric correction, a process that attenuates the effects of the atmosphere in the target's spectral response in the images and convert pixel values from digital numbers to reflectance values, on PCI Geomatics 2015 software, using the ATCOR Ground Reflectance module. After atmospheric correction, we made the mosaic in PCI Geomatics' OrtoEngine module. The REIS mosaic was submitted to a guided object classification using Ecognition 9. We validated the classes using TerraClass 2014 images provided by the Brazilian National Institute for Space Research – INPE (Almeida et al., 2016). After that, we calculated the Kappa Index (0.72), which reflects the supervised classification quality, and classified it according to Landis and Koch (1977) and Piroli (2010), being considered acceptable for the results obtained.

The identified land-use/land cover classes on the sites were: (a) Primary vegetation, which comprises areas occupied by tropical rainforest; (b) Secondary vegetation, a vegetation that resulted from natural succession processes after total or partial primary vegetation suppression caused naturally; (c) Pasturelands, areas occupied by intensive and/or extensive livestock, and (d) bare soil, areas of unprotected soil, especially those containing road systems such as dirt roads, highways, and mining areas. Each land-use/land cover class dimension was quantified in km^2 with a 300m circular buffer on each sampling site using the software ArcGIS 10.1, and they were later converted to cover percentage (%).

2.2.4. Data Analysis

First, we tested for multicollinearity between local environmental predictors using Spearman Correlation Matrices, in which we excluded variables that had values >0.6. Since most land-use variables were correlated among themselves, but still needed to teste our hypotheses, we chose to summarize them, using a Principal Component Analysis (PCA) axis. As a model of axis selection, we used the Broken-Stick criterion (Jackson, 1993), and the axes retained represent land-use contribution in one dimension, that were used as the land-use variables in the models to test our hypotheses.

Prior visual analysis revealed that the relationship between species richness and local environmental and landscape variables was non-linear. Because of this, we used a Generalized Additive Mixed Model (GAMM; Wood, 2004) to test our hypothesis (i). GAMMs are suited for data with non-linear relationships and they can incorporate random effects to account to spatially nested observations (Zuur et al., 2009). On this particular study, we chose to include the type of ecosystem (stream, pond and lake) as the random effect that was spatially structuring our other variables on the models.

Since we wanted to test the effect of land-use on species richness, and identify which local environmental variables affect them, we built two models: one that only has land-use as the predictive variable, and another that has local environmental variables as predictors. All environmental variables were standardized, aside from the land-use variable, which corresponds to the PCA axis. We also tested for overdispersion on the response variable, which was significant for both models. Therefore, the family that best suits the data used in this study is the quasipoisson (Zuur et al., 2009).

To test our hypothesis (ii), and see which environmental variables affected species composition, we used a distance-based redundancy analysis (dbRDA), a more flexible model that accepts different types of matrixes (Legendre and Anderson, 1999), and supports us to control the influence of one or more variables in the analysis using the "Condition" function. Therefore, it allowed us to use a Bray-Curtis matrix for abundance-based composition data, a set of environmental predictors, and to control the effects of the type of ecosystems. The species matrix was log-transformed, while the environmental matrix was standardized, save from the land-use variable (PCA axis). A permutation test at 999 permutations validated this model.

To answer question (iii) which life forms are favored in altered environments and therefore could be indicators of such state? and identify which species are indicators of the land-use classes used on this study, we performed a Threshold Indicator Taxa Analysis (TITAN) for each one of the landscape variables, following Baker and King, (2010). TITAN combines and extends Change-point Analysis (King and Richardson, 2003; Qian et al., 2003) and Indicator Species Analysis (IndVal; Dufrêne and Legendre, 1997), aiming to identify taxon-specific responses to anthropogenic changes in order to assess in which point the community as a whole exhibits a tipping point in response to continuous environmental gradients (Baker and King, 2010). It is a method that reveals declines in community data that are either linear or nonlinear and can otherwise be masked or lost by aggregate community metrics and identifies which value of the environmental gradient maximizes association of a taxon's frequency and abundance, which could be positive or negative (King et al., 2016).

TITAN uses bootstrapping to identify reliable indicator taxa, and relies on two criteria to select them: purity and reliability (Baker and King, 2010). Purity is when the taxon's change in frequency and abundance occurs in the same direction for ≥95% of the bootstrapped runs, be it a positive (z+) or negative (z-) response. Reliability consists in the proportion of bootstrap change points in which IndVal scores consistently result in P-values considered statistically significant (in this case $P \leq 0.05$; (Baker and King, 2010). On this study, we ran the analysis using 500 bootstraps. For our community matrix, we followed Baker and King's (2010) recommendation, and excluded all taxa that had less than 3 occurrences.

We performed all the analyses in software R 3.5.1 (R Core Team, 2018). We Performed PCA using the function 'prcomp' in R core package. For the GAMM, we used the 'gamm' function of the package mgcv version 1.8-24 (Wood, 2004). For dbRDA, we used the function 'capscale' on the package vegan version 2.5-3 (Oksanen et al., 2018). We ran TITAN in the package TITAN2 version 2.1 (Baker et al., 2015).

2.3. Results

2.3.1. Community structure and environmental variables

We recorded 49 species, divided in 23 families of vascular plants, ferns and lycophytes (Table 1). Cyperaceae and Poaceae had the largest number of species: 15 and seven species, respectively. *Eleocharis* R.Br. (Cyperaceae) was the richest genus, with four species recorded, followed by *Rhynchospora* Vahl (Cyperaceae) and *Ludwigia* L. (Onagraceae), with three species each. *Calyptrocarya glomerulata* (Brongn.) Urb. (Cyperaceae), the most frequent species, was recorded in 17 sites, followed by *Cabomba aquatica* Aubl. (Cabombaceae, found in 15 sites), *Utricularia* sp L. (Lentibulariaceae, 14 sites) and *Fuirena umbellata* Rottb. (Cyperaceae, 14 sites). We also recorded an invasive species, *Urochloa arrecta* (Hack. ex T.Durand & Schinz) Morrone & Zuloaga (Poaceae), in six sites. The richness per site varied from one to sixteen species and 38.77% of species were recorded only one or two times.

Family	**Species**	**Life-form**
Alismataceae	*Sagittaria guyanensis* Kunth	Floating-leaved
Asteraceae	*Eclipta alba* (L.) Hassk.	Emergent
	Rolandra argentea Rottb.	Emergent
Blechnaceae	*Blechnum serrulatum* Rich.	Amphibious
Cabombaceae	*Cabomba aquatica* Aubl.	Rooted-submerged
Convolvulaceae	*Ipomoea asarifolia* (Desr.) Roem. & Schult.	Amphibious
Cyperaceae	*Calyptrocarya glomerulata* (Brongn.) Urb.	Emergent
	Cyperus haspan L.	Amphibious
	C. odoratus L.	Amphibious
	Diplacrum capitatum (Willd.) Boeckeler	Amphibious
	Eleocharis confervoides (Poir.) Steud.	Rooted-submerged
	E. interstincta (Vahl) Roem. & Schult.	Emergent
	E. flavescens (Poir.) Urb.	Emergent
	E. plicarhachis (Griseb.) Svenson	Emergent
	Fuirena umbellata Rottb.	Emergent
	Oxycaryum cubense (Poepp. & Kunth) Lye	Emergent
	Rhynchospora ciliata (Vahl) Kük.	Emergent
	R. corymbosa (L.) Britton	Emergent
	R. holoschoenoides (Rich.) Herter	Amphibious
	Scleria cf gaertneri Raddi	Amphibious
	S. microcarpa Nees ex Kunth	Amphibious
Eriocaulaceae	*Tonina fluviatilis* Aubl.	Rooted-submerged
Hymenophyllaceae	*Trichomanes hostmannianum* (Klotzsch) Kunze	Amphibious
Hydrocharitaceae	*Apalanthe granatensis* (Bonpl.) Planch.	Rooted-submersed
Lentibulariaceae	*Utricularia sp*	Free-submerged
Lindsaeaceae	*Lindsaea lancea* (L.) Bedd.	Amphibious
Lycopodiaceae	*Palhinhaea cernua* (L.) Franco & Vasc.	Amphibious
Nymphaeaceae	*Nymphaea rudgeana* G.Mey.	Floating-leaved
Ochnaceae	*Sauvagesia erecta* L.	Amphibious
Onagraceae	*Ludwigia cf hyssopifolia* (G.Don) Exell	Amphibious
	L. leptocarpa (Nutt.) H.Hara	Emergent
	L. cf nervosa (Poir.) H.Hara	Amphibious
Plantaginaceae	*Bacopa sp*	Emergent
Poaceae	*Homolepis aturensis* (Kunth) Chase	Amphibious
	Hymenachne amplexicaulis (Rudge) Nees	Amphibious
	Leersia hexandra Sw.	Amphibious
	Orthoclada laxa (Rich.) P.Beauv.	Amphibious
	Rugoloa pilosa (Sw.) Zuloaga	Emergent
	Trichanthecium parvifolium (Lam.) Zuloaga & Morrone	Emergent
	Urochloa arrecta (Hack. ex T.Durand & Schinz) Morrone & Zuloaga	Emergent
Pteridaceae	*Adiantum cf humile* Kunze	Amphibious
	Adiantum tomentosum Klotzsch	Amphibious
	Ceratopteris sp	Emergent

Rubiaceae	*Borreria verticillata* (L.) G.Mey	Amphibious
	Borreria latifolia (Aubl.) K.Schum.	Amphibious
Saccolomataceae	*Saccoloma cf inaequale* (Kunze) Mett.	Amphibious
Tectariaceae	*Triplophyllum sp*	Amphibious
Thelypteridaceae	*Thelypteris interrupta* (Willd.) K.Iwats	Amphibious
Xyridaceae	*Xyris jupicai* Rich.	Amphibious

Table1: List of macrophyte species found in the 30 sampling sites in Paragominas, Pará, Brazil.

On this study, we recorded five macrophyte life forms. The amphibious life form had the largest number of species (26) that comprises 53% of total species richness, followed by emergents, who accounted for 33% of species (16). The other life forms included floating leaved, with 4% (2 species), rooted-submerged, with 8% (4), and free submerged species, with 2% (1) of total species richness.

Related to the local environmental variables, we observed that canopy cover varied greatly among the ecosystems, from 0% to 100% of cover, and had the biggest standard deviation (Table 2). Turbidity also varied greatly among the sampling sites, with a variation of 0.600 ntu to 32.167 ntu. Water temperature varied mildly among sites, from 22.870 °C to 31.110 °C, where higher temperatures occurred in sites that had less canopy cover, and was correlated to it. Conductivity, dissolved oxygen and total dissolved solids also varied mildly among sampling sites.

Variable	Unit	Min	Max	Mean±SD
Canopy Cover	%	0.000	100.000	43.021±39.615
Temperature	°C	22.870	31.110	25.773±1.883
pH		3.927	6.157	4.934±0.428
Conductivity	mS/cm	0.021	0.160	0.036±0.010
Turbidity	ntu	0.600	32.167	6.781±6.344
Dissolved Oxygen	mg/L	3.420	9.590	7.018±1.275
Total Dissolved Solids	ppm	0.014	0.104	0.024±0.007

Table 2: Local environmental variables investigated in the 30 sampling sites in Paragominas, Pará, Brazil, with their minimum, maximum, mean values and standard deviations.

The landscape variables also varied among sites (Figure 2). Primary forest had the highest cover in a site (89.013%), and the highest standard deviation (27.851). Followed by bare soil (maximum: 79.676%, standard deviation: 17.605), pasture (max: 74.568; SD: 16.152), and secondary forest (Max: 72.360; SD: 15.740). All land-use classes didn't occur on at least one site. Most of the time, in sites where there was a strong primary forest cover, there was less cover of bare soil and pasture (Figure 2).

For the summarization of the landscape variables, the Broken-stick criterion retained the first axis of the PCA, which represented 61.24% of the total variance (Table 3). Primary vegetation was the variable that mostly contributed to the formation of this axis, and was negatively correlated to it, along with bare soil and pasture activities, who were also highly correlated with the first axis, but positively (Table 3).

	Loadings		Correlation	
Variable	PCA1	PCA2	PCA1	PCA2
Primary Vegetation	**-0.760**	0.291	**-0.965**	0.234
Secondary Vegetation	-0.044	**-0.841**	-0.080	**-0.959**
Pasture	**0.455**	-0.057	**0.782**	-0.062
Bare Soil	**0.463**	0.453	**0.763**	0.472
Eigenvalue	886.764	354.796	-	-
Broken-stick	754.120	392.142	-	-
% Explained	61.240	24.500	-	-

Table 3: Loadings of the first two axes of the Principal Component Analysis (PCA) performed with the landscape variables. Variables in bold correspond to the ones that contributed the most to the axis formation, and that correlated with the axes.

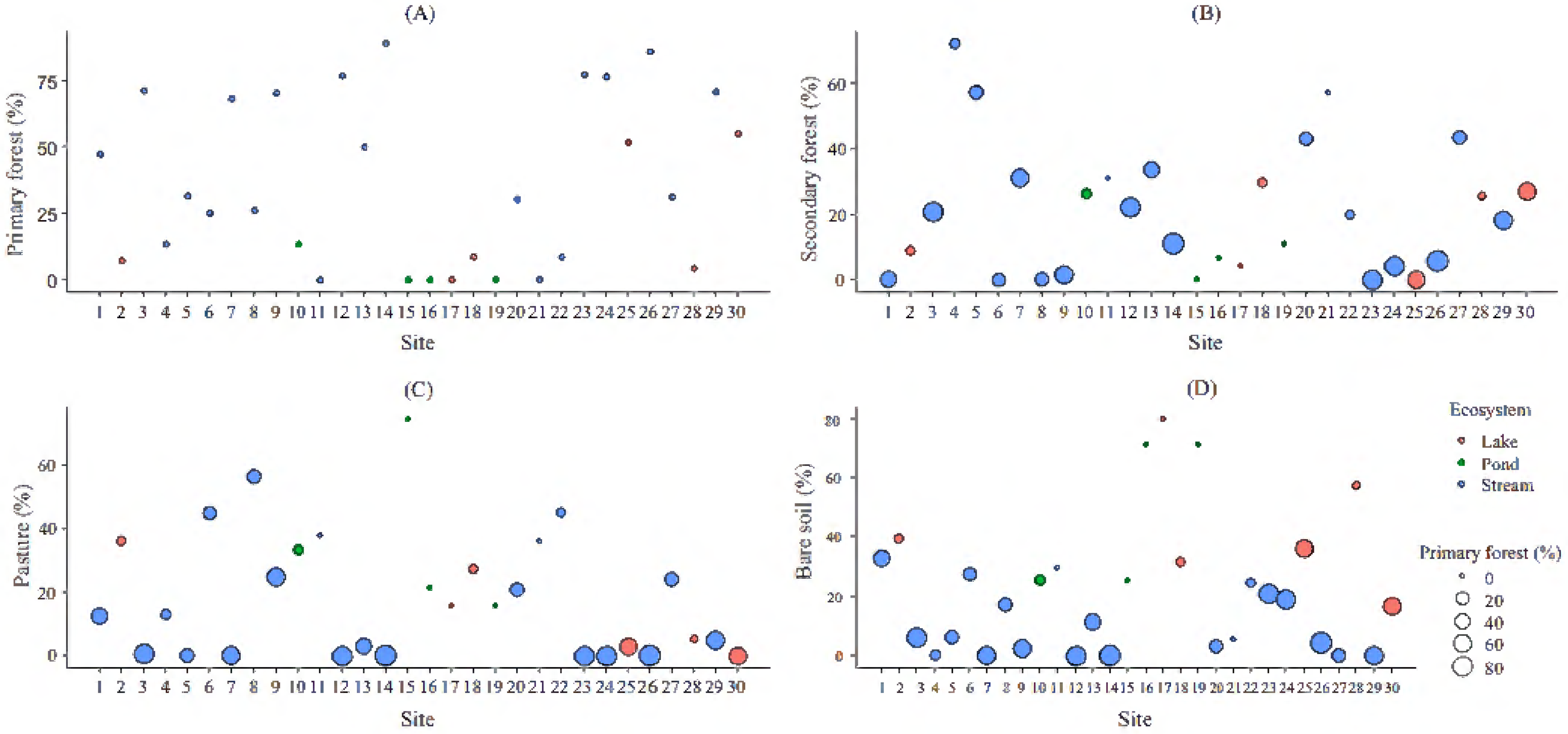


Figure 2: Graphs showing the percent of each land-use class by sampling site. a) A scatter plot of percentage (%) of Primary forest per site. b) A bubble plot of percentage (%) of secondary forest per site. c) A bubble plot of percentage (%) of bare soil per site. d) A bubble plot of percentage (%) of pasture per site. The dots are colored according to the type of ecosystem. The sizes of the dots on graphs b-d are according to the Primary forest cover on each site, to represent how much of it was lost due to the increase of other uses.

2.3.2. Effects of land-use on macrophyte species richness

The model 1 results showed that macrophyte species richness associates positively with the land-use gradient (Estimate= 0.007, P<0.025), represented by the PCA axis, increasing with the loss of riparian vegetation and increase in bare soil and pasture activities (Table 4).

Results of model 2 shows that, among all the local environmental variables, macrophyte species richness is associated negatively with canopy cover (Estimate= -0.373, P<0.001), increasing with the loss of riparian vegetation (Table 4).

Explanatory Variable	Estimate	Std. Error	*t*	*p*
Model 1				
Intercept	2.022	0.093	21.649	<0.001***
Land-use	0.007	0.003	2.372	0.025*
Random effect				
Intercept	<0.001			
Residual	1.342			
Model 2				
Intercept	1.980	0.087	22.701	<0.001***
Canopy Cover	-0.373	0.091	-4.087	<0.001***
pH	0.045	0.106	0.424	0.675
Conductibility	-0.110	0.101	-1.098	0.283
Turbidity	-0.049	0.090	-0.539	0.595
Dissolved Oxygen	-0.065	0.108	-0.598	0.556
Random effect				
Intercept	<0.001			
Residual	1.113			

Table 4: Results of Generalized Additive Mixed Models testing the contribution of land-use and local environmental variables to explain macrophyte species richness

2.3.3. Effects of land-use on macrophyte species composition

We performed dbRDA to detect if macrophyte community composition changes along a land-use gradient, and which environmental variables best explained those changes along the sites. This model showed that the environmental variables and the land-use gradient explained 22.79% of the community structure, while the type of ecosystem (conditioned variable) explained 16.09% of the variance (F=1.305; P=0.035; Df=6). The first dbRDA axis explains 53.69% of variance, and is negatively correlated to canopy cover (-0.75) and positively related to the land-use gradient (0.57), while the second axis explained 16.54% of variation, and is positively related to pH (0.71).

The triplot shows that *Cabomba aquatica*, *Eleocharis interstincta*, *Fuirena umbellata*, *Nymphaea amazonica*, *Urochloa arrecta*, and *Utricularia* sp were positively associated with the land-use gradient. In that case, their cover increased with the loss of primary vegetation and increase in bare soil and pasture activities. *Urochloa arrecta*, the invasive species, was positively correlated with the first axis, which is positively correlated to land-use and negatively correlated to canopy cover. *Apalanthe granatensis*, *Cyperus haspan*, *Eleocharis plicarhachis*, *Ludgwigia leptocarpa*, *Sauvagesia erecta* and *Xyris jupicai* occurred in sites with increased pH. *Borreria verticillata*, *Ceratopteris* sp, *Leersia hexandra* and *Rhynchospora corymbosa* occurred in sites that had increased dissolved oxygen. The species *R. corymbosa* was correlated positively with the second axis, which is positively correlated with pH (Figure 3).

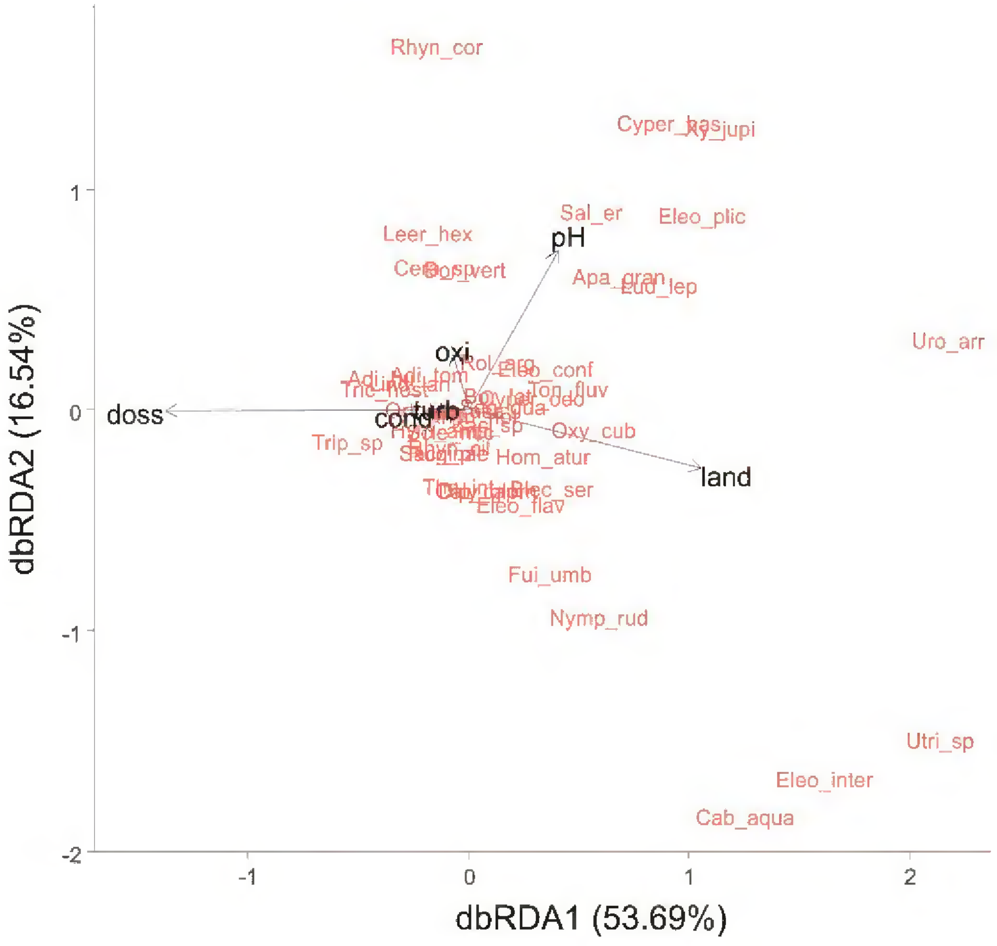
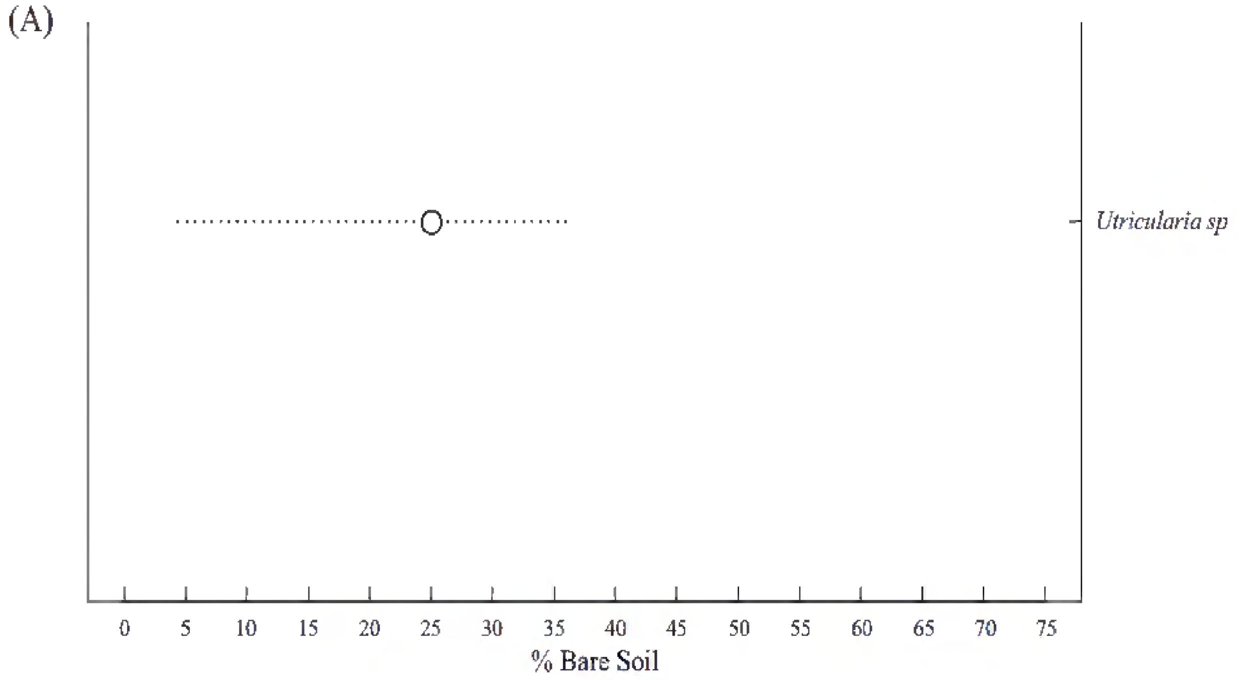


Figure 3: Distance-based Redundancy Analysis performed between macrophyte species composition and the environmental variables Canopy cover (doss), Conductivity (cond), Dissolved Oxygen (od), Land-use (land), pH (ph) and Turbidity (turb).

2.3.4. Indicator species and life-forms of land-use change

The TITAN analyses detected three species that are indicators of one type of land-use and land-cover. *Utricularia* sp, a free submerged macrophyte, had a positive response (z+) and was selected as an indicator of increase in bare soil (Figure 4a), with a change-point observed at 24.980% of bare soil and a *z* score of 4.42. Three species had a negative response (z-), and were recorded as indicators of decrease in primary forest: *Cabomba aquatica* (rooted submerged), *Eleocharis interstincta* (emergent) and *Utricularia* sp (Figure 4b). The change points were observed between 8.83%, for *C. aquatica (z* score: 6.09) and *Utricularia* sp (*z* score: 5.73), and 11.20%, for *E. interstincta* (*z* score: 4.29), of primary forest present in the sampling sites. No species were selected as indicators of secondary vegetation and pasture activities.

(A)



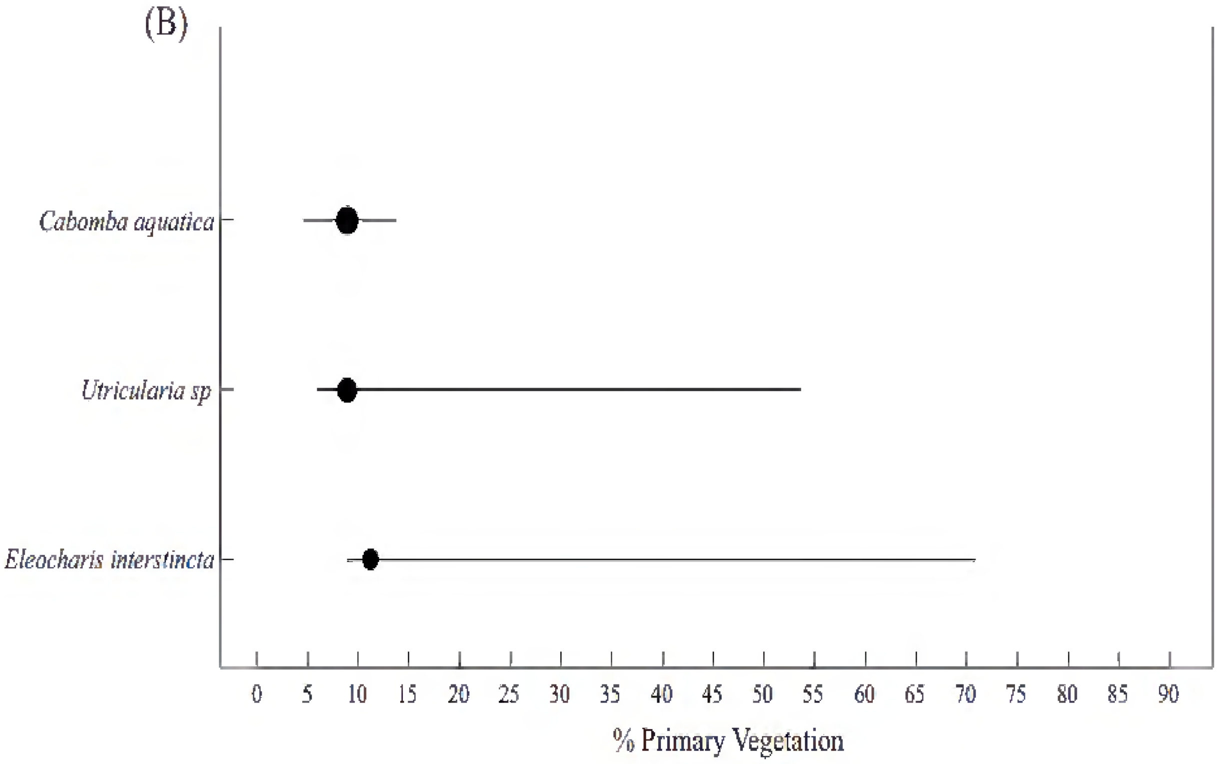


Figure 4: Result of the TITAN on individual species abundance in response to land-use and cover gradients. A) Indicator species of % of Bare Soil. B) Indicator species of % of Primary Forest. Black circles indicate the species that declined (z-) as the environmental gradient increased, while white circles indicate those that increased (z+). The size of the circles is proportional to the response's magnitude (*z* score). The horizontal lines represent the 5th and 95th quantiles of Primary Forest and Bare soil values that resulted in the largest change in species z-scores among 500 bootstraps.

2.4. Discussion

Our hypotheses were that i) macrophyte species richness would increase in multiple land-use gradients, due to canopy openness, while ii) macrophyte species composition would change along land-use gradients, where less altered sites would have more life-form diversity than more altered sites, since altered sites would favor amphibious and emergent species dominance, especially the pioneers in ecological succession, due to change in water quality. According to the results, hypotheses (i) was corroborated, as aquatic macrophyte species richness was affected positively by a land-use gradient of decrease in primary forest and increase in bare soil and pasture activities, and the main local factor affecting species richness was light availability. However, hypothesis (ii) was partially corroborated, since macrophyte species composition did change along a land-use gradient, and the land-use gradient, canopy cover and pH were the main drivers of community composition structure, but the response was contrary to what we expected. Life-form diversity increased in sites that had increased bare soil and pasture activities. Moreover, three species were selected as indicators of land-use change: *Cabomba aquatica* and *Eleocharis interstincta* as indicators of decrease in primary forest, and *Utricularia sp* as indicator of both loss of primary forest and increase in bare soil.

2.4.1. Species Richness

In general, macrophyte richness was affected positively by the land-use gradient, meaning that species richness increased in sites where bare soil and pasture also increased, and primary forest cover decreased. Several studies (Alahuhta et al., 2014; Bleich et al., 2015; Elo et al., 2018; Mikulyuk et al., 2011) showed that land use, when in moderate to high stages, could increase macrophyte species richness due to several factors (e.g.: increased light incidence, sediment load, and nutrient input on water). Those factors change macrophyte's habitats, providing more microhabitats that could favor species that otherwise would not be able to occur there.

Canopy cover was the local environmental variable that affected species richness positively. Light incidence is considered one of the most important limiting factor of macrophyte occurrence in freshwaters (Bando et al., 2015; Bornette and Puijalon, 2011; Lacoul and Freedman, 2006), and species richness increases when there is more light availability (Bando et al., 2015; Bleich et al., 2015; Wood et al., 2012). This also reinforces the result of the land use model, as the loss of forest cover, especially of the riparian vegetation on more altered sites are a cause of increased light incidence (Allan, 2004; Heartsill-Scalley and Aide, 2003). This could be the reason why species richness increased.

2.4.2. Community composition

Canopy cover, pH and the land-use gradient were the main drivers of macrophyte community structure on this study. The shade created by the riparian vegetation can be considered an environmental filter for macrophyte occurrence (Bando et al., 2015; Wood et al., 2012). Different species are associated with different ranges of light incidence; some species thrive in shaded habitats, whereas others occur only in light-saturated habitats (Bornette and Puijalon, 2011). Thus, it is not surprising that, on this study, macrophyte community composition changed along a light gradient. Moreover, Mackay et al. (2010), while investigating the use of macrophytes as indicators of tropical stream condition in Queensland (Australia), suggested that the condition of the riparian vegetation could be used as a first form of macrophyte assessment, since, on their study, macrophytes responded more strongly to canopy and riparian vegetation metrics than to land use metrics. On the present study, macrophytes responded to both canopy cover and land-use.

The variable pH is a factor associated with alkalinity, which reflects on carbon (both organic and inorganic) availability in water (Esteves, 2011), which are important to primary production (Toivonen and Huttunen, 1995), and therefore affect community composition. Additionally, macrophytes have the ability to utilize different carbon sources available on water and air, and as such, they can occur on different pH ranges, but that varies among taxonomic groups, and between species belonging to the same life form (Alexander et al., 2008; Bornette and Puijalon, 2011; Vestergaard and Sand-Jensen, 2000). The species *Apalanthe granatensis*, *Cyperus haspan*, *Eleocharis plicarhachis*, *Ludgwigia leptocarpa*, *Sauvagesia erecta* and *Xyris jupicai* were most associated to pH, as their cover increased in sites with higher pH values. These species belong to various life forms (amphibious, emergent and submerged), but most of them are emergent and amphibious species (Table 1). On this study, pH varied mildly along the scale, but remained more acidic, getting close to neutral (Min: 3.927; Max: 6.157; Table 2), which is common for freshwaters of tropical regions (Ríos-Villamizar et al., 2013). On this pH range, carbonic acid (and dissolved CO_2) is the most dominant source of inorganic carbon on water (Esteves, 2011), and could limit other submerged species as it gets close to neutral, since most of those species are adapted to more acidic waters characteristic of the Amazon Basin (Junk and Howard-Williams, 1984). The species *A. granatensis* could be tolerant to an ample range of alkalinity, thus occurring in sites where pH increases and gets close to neutral. This does not affect carbon uptake of emergent and amphibious species, who mostly rely on atmospheric carbon (Bornette and Puijalon, 2011), which is why they were also favored by increasing pH.

Macrophytes mostly affect dissolved oxygen rather than get affected by it, since they are one of the main sources of oxygen on water (Bornette and Puijalon, 2011). Usually the submerged macrophytes oxygenate water more efficiently than floating-leaved species (Bornette and Puijalon, 2011; Carpenter and Lodge, 1986). On this study, *Borreria verticillata*, *Ceratopteris sp*, *Leersia hexandra* and *Rhynchospora corymbosa* were correlated with dissolved oxygen. All those plants are either emergent or amphibious. This could have occurred because emergent species, even if do not provide oxygen to water, have a complex role on oxygen dynamics in freshwaters (Rose and Crumpton, 1996).

Interestingly, land-use affected community composition positively. The fact that macrophyte assemblages changed as primary forest decreased and bare soil and pasture activities increased could be due to light availability (caused by loss of riparian vegetation; Bleich et al., 2015; Mackay et al., 2010), and slight nutrient input (Mikulyuk et al., 2011; Sass et al., 2010). We expected that amphibious and emergent species, which are more tolerant (Akasaka et al., 2010; Kolada, 2010; Quinn et al., 2011), would dominate on more altered sites, indicating a successional stage on those communities, but it was not the case. Indeed, the species that correlated with land-use (*Cabomba aquatica*, *Eleocharis interstincta*, *Fuirena umbellata*, *Nymphaea rudgeana*, *Urochloa arrecta*, and *Utricularia sp*), belonged to a range of four life-forms, showing that more altered sites can actually provide habitat heterogeneity and the resources to different life-forms, and increase life-form diversity, even though some of them are considered species of early stage succession (*E. interstincta* and *F. umbellata*).

Another result is that an invasive species (*Urochloa arrecta*) was positively associated with decrease of primary forest and increase in bare soil and pasture activities. Several studies showed that land-use pressure increases invasive species cover (Gołdyn, 2009; Lougheed et al., 2008; Mackay et al., 2010; Quinn et al., 2011; Sass et al., 2010), providing them more niche opportunities, due to propagule pressure, disturbance, and eutrophication, processes that facilitate invasion (Shea and Chesson, 2002). In addition, the presence of an invasive macrophyte harms native macrophyte communities (Michelan et al., 2010), resulting in the loss of several native taxa that provided services to those ecosystems, which means that they affect not only macrophyte diversity, but also the diversity of all other organisms (i.e. fish, insects and periphyton) that depend on them (Lougheed et al., 2008).

Even so, studies with macrophytes and human-induced disturbances show an increase of species diversity, that, as time passes (and the impact increases), disappear due to competition with algae (Moore et al., 2010; Theissen et al., 2012) and invasive species (Gołdyn, 2009). or simply due loss of habitat caused by channel siltation and drought, as the systems become inhospitable for plant life (Gołdyn, 2009; Mikulyuk et al., 2011; Moore et al., 2010). The results obtained on those studies seem to indicate that the diversity observed now on this study might as well be lost if those conditions continue to increase in the near future. It seems that the communities in this area could be experiencing an early stage of succession, in which there is an increase in life-form diversity, before the community begins to shift to other stages of succession (from submerged to emergent and amphibious; Gołdyn, 2009; Moore et al., 2010). The appearing of invasive species could be an indicative of the start of a decrease in diversity as the consequences of land-use become abrasive (too many nutrients, water turbidity, etc).

2.4.3. Indicator Species

Our results detected three species as indicators of some sort of land-use change: three were indicators of loss of primary forest, while one was indicator of increase in bare soil. *Utricularia* sp was selected as an indicator of bare soil, the type of use that is are more prone to soil erosion, channel sedimentation (Ghimire et al., 2013) and runoff pollution (Qin et al., 2010). *Utricularia* sp is a free-submerged species that occurs in places with low light incidence, low nutrients and low water flow, and is a carnivorous plant (Pott and Pott, 2000; Raynal-Roques and Jérémie, 2005). Maybe this species can thrive in sites dominated by bare soil because they are carnivorous, and do not depend on the nutrients in water to obtain resources for survival, since they can rely the carnivorous habit to obtain nutrients by consuming plankton. Studies showed that *Utricularia sp* and phytoplankton have a synergistic relationship, in which high amounts of algae were found in traps of different species of *Utricularia*, and it's possible that algae are either consumed, used to attract zooplankton to be consumed, or both (Alkhalaf et al., 2009; Díaz-Olarte et al., 2007; Koller-Peroutka et al., 2015). Altered sites (that have a high rate of nutrients on water) normally possess less submerged macrophytes and more algae (Lacoul and Freedman, 2006), and possibly more zooplankton, thus more resources for carnivorous plants (Koller-Peroutka et al., 2015).

Cabomba aquatica, *Eleocharis interstincta* and *Utricularia sp* were selected as indicators of loss of primary forest, as their cover seems to increase when there is less forest cover on the sampling sites. Those results are also congruent with the results on species composition. Most of it must be in response to loss riparian vegetation on more altered sites (Bleich et al., 2015; Mackay et al., 2010; Mikulyuk et al., 2011; Sass et al., 2010). As it has been showed on the composition results, those species associated with land-use and loss of canopy cover.

The submerged species *C. aquatica* and *Utricularia sp* co-occurred in many sites. Submerged species normally require low water flow and turbidity to establish themselves (Esteves, 2011). Interestingly enough, those species have different niche requirements: *C. aquatica* occurs in freshwaters that have lots of light incidence and high nutrients (Ørgaard, 1991; Pott and Pott, 2000), while *Utricularia sp* occurs in sites with low light incidence and low nutrients (Pott and Pott, 2000; Raynal-Roques and Jérémie, 2005). It may be that the sites in which they co-occurred had more habitat heterogeneity. Low water flow and light incidence beneficiates *C. aquatica*, and this could increase the presence of plankton, which beneficiates *Utricularia sp*. The *E. interstincta* is an emergent species that require high amounts of light availability, and often indicates an intermediate succession phase of vegetation on freshwater ecosystems, after the free-floating phase (Pott and Pott, 2000), and occurs in altered sites (Bleich et al., 2015). This species mostly increases its cover by vegetative growth, becoming dominant in the margins (Pott and Pott, 2000). *E. interstincta* could be an indicator of early succession following loss of primary vegetation.

Those results reinforce that macrophyte species are mostly indicators of altered conditions. Additionally, submerged species (either rooted or free) seem to be efficient indicators of freshwater condition. Submerged species respond more strongly to change in water quality (Akasaka et al., 2010; Moore et al., 2010; Søndergaard et al., 2010), since they depend more on water physical-chemical parameters than emergent species (Lacoul and Freedman, 2006). Because of that, many freshwater ecological assessments use only submerged species-based metrics (Søndergaard et al., 2010). Contrary to other studies, which show submerged species as indicators of freshwaters preserved conditions (Poikane et al., 2018; Søndergaard et al., 2010), the results of this study show that they can also be indicators of altered conditions, especially of loss of riparian vegetation. However, emergent species importance as indicators of land-use change should not be disregarded, as they can be strong indicators of altered conditions (Alahuhta et al., 2014, 2012; Bleich et al., 2015), and are more indicative of ecological succession on freshwaters.

Finally, another important point to emphasize is that *Utricularia sp*'s cover increased as a response of land-use change on this study, bringing to light the possible role of carnivory as an efficient strategy of survival on Amazonian freshwater ecosystems affected by land-use change. However, further studies investigating carnivorous-prey interactions in those areas are needed, to get more robust results and conclusions.

2.5. Conclusion

The aim of this study was to answer questions regarding if aquatic macrophyte diversity was affected by multiple land-use, and investigate which environmental factors were structuring the community. The results confirm that both macrophyte species richness and composition are affected along a land-use gradient of loss of primary vegetation and increase in bare soil and pasture activities, and the main local environmental driver affecting species richness was canopy cover, while canopy cover and pH affected species composition. The loss of forest cover, especially of the riparian vegetation on more altered sites increases light incidence, sediment load, and nutrient input on water, which is quite congruent with results that that attest that land-use pressure causes a cascading effect, affecting freshwater's physical-chemical structure, and thereafter the local biota. Moreover, macrophytes' responses to freshwater environmental parameters (and consequently to land-use) are taxon-specific, and vary greatly.

Additionally, we point *Utricularia* sp, *Cabomba aquatica* and *Eleocharis interstincata* as indicators of land-use change, more specifically, *C. aquatica* and *E. interstincta* are indicators of loss of primary forest, and *Utricularia sp* is an indicator not only of that, but of increase in bare soil.

Since this study brings information of macrophyte communities along a multiple land use gradient, those results reinforce the potential of macrophyte species to be considered on freshwater ecosystems assessments on the Amazon. Thus, we conclude that macrophytes are resisting the effects of multiple land use, nevertheless, even thriving on altered environments, and therefore should be used as indicators of altered conditions on Amazonian freshwaters.

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3. CONCLUSÃO GERAL

Neste estudo, buscamos responder perguntas acerca do efeito de um gradiente de múltiplos usos do solo na diversidade de macrófitas aquáticas, e investigar quais fatores ambientais locais estavam estruturando a comunidade. Os resultados confirmam que tanto a riqueza de espécies quanto a composição das comunidades de macrófitas aquáticas são afetadas ao longo de um gradiente de múltiplos usos do solo, e o fator ambiental local que mais afetou a riqueza de espécies foi a cobertura de dossel, enquanto o pH e a cobertura de dossel afetaram a composição de espécies. A perda de cobertura vegetal, especialmente da vegetação ripária em locais mais alterados causa um aumento na incidência de luz, sedimentação e carreamento de nutrientes na água, o que é um efeito congruente com os encontrados por estudos que sugerem que a pressão causada pelos usos do solo causa um efeito cascata, afetando a estrutura físico-química dos ecossistemas aquáticos, e consequentemente afetando a biota local. Além disso, as respostas das macrófitas aos parâmetros ambientais dos ecossistemas aquáticos (e, consequentemente, aos usos do solo) são táxon-específicas, e variam amplamente.

Apesar de haver uma relação positiva entre riqueza e composição de espécies e usos do solo, destacamos a possível ameaça de uma macrófita invasora nos ecossistemas aquáticos amazônicos, onde estas mudanças nos usos do solo podem estar agindo como facilitadores para que ela se estabeleça. Talvez a diversidade vista agora se perca com o passar do tempo, devido mudança na estrutura destes habitats, que podem causar a sucessão ecológica e favorecer as espécies exóticas invasoras ao invés das nativas.

Adicionalmente, apontamos as espécies *Utricularia sp*, *Cabomba aquatica* e *Eleocharis interstincata* como indicadoras de mudanças nos usos do solo. Especificamente, *C. aquatica* e *E. interstincta* são indicadoras de perda de vegetação primária, enquanto *Utricularia sp* é indicadora não só de perna de floresta primaria, mas também de aumento na porcentagem de solo exposto. Também destacamos o possível papel do modo de vida dessa última espécie (carnívora) como uma estratégia de sobrevivência em ecossistemas aquáticos amazônicos afetados por mudança nos usos do solo. Mais estudos que investiguem as interações entre plantas carnívoras e suas presas nestas áreas são necessários, para serem obtidos resultados e conclusões mais robustos.

Como este estudo traz informações acerca das comunidades de macrófitas ao longo de um gradiente de usos do solo, os resultados reforçam o potencial indicador das macrófitas, e que elas sejam consideradas em monitoramentos de ecossistemas aquáticos na Amazônia. Portanto, concluímos que as macrófitas estão resistindo aos efeitos de múltiplos usos do solo, apesar de tudo, e são até mesmo favorecidas em ambientes alterados, e, por conseguinte, devem ser utilizadas como indicadoras de condições alteradas em ecossistemas aquáticos amazônicos.

ANEXOS

Anexo I

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