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DINÂMICA DA METACOMUNIDADE DE BRIÓFITAS EPIFILAS EM FLORESTAS  
FRAGMENTADAS NA AMAZÔNIA

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MANAUS, AMAZONAS

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FRAGMENTADAS NA AMAZÔNIA

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### **Sinopse:**

Realizou-se a atualização da flora de briófitas epifilas das reservas do PDBFF como fonte taxonômica para futuros estudos ecológicos e de monitoramento da flora briofítica. Além disso, foi avaliado o impacto da fragmentação sobre as comunidades epifilas na Amazônia Central em longo prazo por meio da comparação da estrutura das comunidades coletadas no ano 2000 e 2016. Com isso, sugeriu-se como as espécies respondem à fragmentação utilizando traços de história de vida.

**Palavras-chave:** Briófitas, Lejeuneaceae, dispersão, fragmentação.

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*Onde quer que você vá, vá com todo o coração.*

Confúcio

## **RESUMO**

Estudos de comunidades de plantas tropicais que tentam separar os principais mecanismos que influenciam suas distribuições (conectividade e qualidade do habitat) por meio de paisagens fragmentadas são escassos. Briófitas epifilas devido a suas comunidades espacialmente delimitadas, altamente dinâmicas e grande diversidade dos sistemas sexuais é um modelo excelente de estudo, com o qual se combinam dados da comunidade e demográficos, tendo em conta os traços adaptativos para abordar quais são os mecanismos que controlam distribuições das plantas terrestres. Este trabalho é um estudo sobre uma meta comunidade altamente dinâmica de briófitas epifilas, para investigar mudanças temporais na estrutura da comunidade em fragmentos florestais e relacionar as alterações aparentes com diferença nos traços adaptativos em relação a dispersores mais eficazes e maior tolerância fisiológica. Para tal, foi utilizado como base para comparação, dados sobre a estrutura da assembleia de epifilas publicadas em um estudo realizado no PDBFF há 15 anos atrás. Assim, foram amostradas comunidades de briófitas epifilas, a fim de avaliar se as mudanças na riqueza de espécies, abundância e composição ocorreram nos anos seguintes. Com base em resultados anteriores foi testada a seguinte hipótese: a estrutura da comunidade de epifilas mudou nos fragmentos pequenos (1 ha e 10 ha) para as espécies com traços adaptativos com maior capacidade de dispersão e tolerância fisiológica. Para as briófitas epifilas observamos nos fragmentos pequenos (1- e 10-ha) um nível de recuperação na abundância, riqueza e composição de espécies, convergindo com os fragmentos de 100 ha e floresta contínua. As alterações positivas na comunidade de epifilas foram relacionadas com traços adaptativos de vida que representam maior capacidade de dispersão e tolerância fisiológica.



## **ABSTRACT**

Studies of tropical plant communities which attempt to disentangle the principle mechanisms (connectivity and habitat quality) influencing their distributions across fragmented landscapes are scarce. Epiphyllous bryophytes, due to their spatially patchy distribution, high turnover and diversity of sexual systems, are an excellent model system with which to combine community and demographic data in light of life history traits to address what mechanisms control terrestrial plant distributions. In this work I studied a highly dynamic community, epiphyllous bryophyte, to investigate temporal changes in community structure in forest fragments and relate apparent changes with difference in life history traits in relation to more effective dispersers and physiological tolerance. By using baseline data on epiphyll assembly structure published from a study conducted at BDFFP over a decade ago, I sampled epiphyllous community in order to evaluate whether changes in species richness, abundance and composition have occurred in the intervening years. Based on previous results I test the following hypothesis: epiphyll community structure has changed in small (1- and 10-ha) to bias species presenting life history traits which favor increased dispersal capacity and physiological tolerance. For epiphyllous bryophytes we observed a degree of recovery in the abundance, species richness and composition in small fragments (1- and 10-ha), converging with 100 ha fragments and continuous forests. Positive changes in the epiphyllous community are related to adaptive life history traits related to species with greater dispersal capacity and physiological tolerance.

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## **Introdução Geral**

### **Fragmentação das florestas tropicais**

Compreender os efeitos da fragmentação do habitat em florestas tropicais é uma questão crítica para prever como isso poderá causar algum impacto sobre a biodiversidade tropical e a dinâmica das comunidades (Laurance *et al.*, 2011). Estudos anteriores realizados nas reservas do Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF) na floresta amazônica têm abordado o efeito da fragmentação em diversos níveis (Sintetizado por Laurance *et al.*, 2002; Laurance *et al.*, 2011). Para as comunidades de plantas vasculares, a fragmentação tem mostrado um efeito de redução na riqueza de espécies quando comparadas com a floresta contínua, assim como também tem causado mudanças nas condições físicas e ecológicas nos fragmentos florestais (Laurance *et al.*, 1998a; 1998b; 2001a; 2001b; 2006a; 2007; 2014; Lovejoy *et al.*, 1986).

Alterações na dinâmica dos fragmentos fizeram com que fragmentos de tamanhos similares divergissem em sua composição e estrutura ao longo do tempo (Laurance *et al.*, 2007; 2006b). Os mecanismos que contribuem na dinâmica dos fragmentos são amplos e variados que vão desde efeitos de borda no sucesso de plântulas de espécies tolerantes à sombra (Benítez-Malvido, 1998; Benítez-Malvido e Martinez-Ramos, 2003a; Benítez-Malvido *et al.*, 2005), incremento na abundância de lianas (Laurance *et al.*, 2014), redução no crescimento e sucesso de plântulas de ervas do sub-bosque (Bruna, 1999; Bruna, 2002; Bruna *et al.*, 2002; Bruna e Kress 2002) e até perturbação na dinâmica de dispersão, conforme observado para algumas espécies de briófitas epífilas (habitam folhas vivas) (Zartman e Shaw, 2006).

Entretanto, florestas secundárias vêm gradualmente substituindo as pastagens na paisagem do PDBFF (Laurance *et al.*, 2011) diminuindo os efeitos da fragmentação para alguns taxa quando a matriz (i.e., área circundante aos fragmentos) torna-se menos hostil e os fragmentos menos isolados, explicando a dinâmica observada nos fragmentos ao longo do tempo. Como consequências desse processo, podemos citar trabalhos com diferentes grupos de organismos, os quais voltaram a recolonizar esses fragmentos após o crescimento da floresta secundária circundante, como as aves insetívoras (Stouffer e Bierregaard, 1995; Stouffer *et al.*, 2011) que também tiveram suas taxas de extinção reduzida (Stouffer *et al.*, 2008; 2011). Outros organismos, como aranhas florestais (Mestre e Gasnier, 2008),

escaravelhos (Andresen, 2003; Quintero e Roslin, 2005), abelhas Euglossina (Becker *et al.*, 1991) e macacos (Boyle e Smith, 2010) têm recolonizado alguns fragmentos.

Os efeitos fortes da dinâmica da matriz sobre as comunidades fragmentadas (Antongiovanni e Metzger, 2005; Stouffer *et al.*, 2008), a divergência da composição da comunidade de plantas nos diferentes fragmentos, aumento de lianas na borda da floresta (Laurance *et al.*, 2007; Laurance *et al.*, 2014), e os efeitos contrastantes da fragmentação sobre espécies raras ou de vida longa (Benítez-Malvido e Martinez-Ramos, 2003b; Ferraz *et al.*, 2007), são pontos que começamos a compreender melhor após de 35 anos de pesquisa no PDBFF. No entanto, estudos equivalentes a longo prazo com comunidades de plantas altamente dinâmicas, como as comunidades de plantas epifitas e epifilas ainda não foram realizados.

### **Comunidades epifilas**

Epifilas são organismos fotossintéticos que habitam as folhas de plantas vasculares e atingem sua maior diversidade e abundância em regiões tropicais úmidas, onde líquens, briófitas, e as algas podem coexistir na mesma folha (Gradstein, 1997; Lücking, 1999). A família Lejeuneaceae corresponde a 90% da brioflora epifílica representada (Gradstein, 1997; Sonnleitner *et al.*, 2009).

Organismos que habitam folhas representam um substrato efêmero com um curto período de vida (em torno de 1-4 anos) compõem um sistema modelo com os quais podemos examinar como as mudanças nos processos bióticos e abióticos resultantes da fragmentação impactam estes grupos de plantas menos visíveis em florestas tropicais (Arnold e Lutzoni, 2007; Cornelissen e ter Steege, 1989).

As briófitas epifilas são um grupo ideal para avaliar os efeitos de fragmentação de habitat porque são abundantes, taxonomicamente diversas, apresentam altas taxas de colonização-extinção, e são altamente sensíveis as condições ambientais locais (Coley e Kursar, 1996; Monge-Nájera, 1989). Além disso, as briófitas apresentam um ciclo de vida curto e suas dinâmicas populacionais especialmente delimitadas à superfície da folha (Pharo e Zartman, 2007), deste modo favorecem a coleta de dados em uma escala de tempo curta.

Zartman (2003) mostrou que as briófitas epifilas dentro do PDBFF apresentaram abundância e riqueza das comunidades significativamente menor nos fragmentos pequenos (1- e 10-ha) quando comparado com fragmentos de 100-ha e florestas contínuas. A análise de

transplantes experimentais de forófitos com duas espécies epífilas comuns do PDBFF, *Radula flaccida* e *Cololejeunea surinamensis* (Zartman e Shaw 2006), e em conjunto com padrões de estrutura da metacomunidade (Zartman e Nascimento 2006) concluíram que a explicação mais provável para a riqueza e abundância reduzida em fragmentos pequenos deve-se à capacidade reduzida de dispersão em pequenos fragmentos ao invés do aumento das taxas de extinção. Apesar da redução na colonização observada em pequenos fragmentos, a estrutura genética não diferiu entre os fragmentos e as florestas contínuas, sugerindo que os impactos demográficos de dispersão reduzida ameaçam mais a possibilidade de sobrevivência local do que as consequências evolutivas de deriva genética para esta metacomunidade transitória (Zartman *et al.*, 2006). Contudo, permanece ainda a questão se essas comunidades de briófitas epífilas têm sofrido mudanças nos fragmentos ao longo do tempo, como foram observados para outros organismos.

### **Traços adaptativos**

A fragmentação tem o efeito sob espécies limitadas pela dispersão deixem de ser espécies núcleo (core) para se tornarem espécies urbanas ou satélites ao longo do tempo (Hansson *et al.*, 1992; Zartman, 2003; Alvarenga e Pôrto 2007; Alvarenga *et al.*, 2010). Demandas conflitantes entre traços adaptativos (i.e., tempo de vida, estratégias reprodutivas e capacidade de dispersão) podem determinar a frequência da espécie além da persistência ou extinção da espécie na metacomunidade (Murray *et al.*, 2002; Austrhein *et al.*, 2005; Löbel e Rydin, 2009; Söderstörn e Durante, 2005).

Traços adaptativos são ferramentas importantes para compreender os efeitos ecológicos e evolutivos da fragmentação sobre os organismos, e comunidades (Lebrija-Trejos *et al.*, 2010; Johansson *et al.*, 2012). Estudos utilizando sistemas sexuais por Patiño *et al.*, (2013) e Laenen *et al.*, (2015) relacionando assim a capacidade de dispersão com a distribuição biogeográfica global das espécies de hepáticas. Em uma escala ecológica Löbel *et al.*, (2009) também utilizaram traços adaptativos para explicar a distribuição de espécies de briófitas epífitas na paisagem fragmentada na floresta temperada. Enquanto Johansson *et al.*, (2012) explicaram os padrões observados na dinâmica meta populacional de epífitas por traços das espécies (i.e., nicho e capacidade de dispersão) além da conectividade e dinâmica das manchas. Austrhein *et al.*, (2005) explicaram a diferença na frequência das espécies em dois ambientes diferentes em regiões alpinas utilizando traços adaptativos. Já para populações de uma espécie de musgo em diferentes altitudes, Hassel *et al.*, (2005) observou que há

diferenças nas taxas de crescimento e reprodução. No entanto, não encontramos estudos que tenham relacionado os padrões da metacomunidade epifilas com traços adaptativos das espécies em florestas fragmentadas nos trópicos.

Diante do que foi exposto este projeto teve o objetivo de responder as seguintes perguntas: 1. Qual é o efeito da fragmentação na dinâmica da metacomunidade de briófitas epifilas em florestas fragmentadas ao longo do tempo? 2. Os padrões da metacomunidade nas florestas fragmentadas são explicados pelas diferenças nos traços adaptativos das espécies? Como previsões para nossas perguntas têm que a nos fragmentos ao longo do tempo vai se observar uma diminuição na abundância e riqueza de espécies epifilas, e se observara maior diferença na composição de espécies entre os fragmentos pequenos que nos fragmentos de 100-ha e floresta contínua. Para as espécies que persistem nos fragmentos vamos observar traços adaptativos, relacionados com maior capacidade de dispersão (Monóicos, esporos pequenos, propágulos assexuados) e tolerância ao stress ambiental (pigmentação escura, ocelos, margen hialino, papilas, etc.), a diferença com as que só ocorrem em floresta contínua (Austrhein *et al.*, 2005; Johansson *et al.*, 2012; Letcher e Chazdon, 2012).

## **Objetivos**

### **Objetivo geral**

- a) Avaliar as comunidades de briófitas epifilas e sua dinâmica ao longo prazo em florestas fragmentadas na Amazônia.

### **Objetivos específicos**

- a) Atualizar a flora de briófitas epifilas das reservas do PDBFF como fonte taxonômica para futuros estudos ecológicos e de monitoramento da flora briofítica.
- b) Comparar as mudanças na abundância, riqueza e composição de espécies de briófitas epifilas ao longo do tempo em florestas fragmentadas nas reservas do PDBFF.
- c) Explicar a distribuição das espécies nos fragmentos florestais e mudanças na sua abundância ao longo do tempo com base na diferença interespecífica nos traços adaptativos das espécies de briófitas epifilas.



## Capítulo 1

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Sierra A. M. & Zartman C. E. 2018. An updated key and synopsis to the epiphyllous bryophytes from the bdfp reserves in the amazon forest. Manuscrito em preparação para *The Bryologist*

**AN UPDATED KEY AND SYNOPSIS TO THE EPIPHYLLOUS  
BRYOPHYTES FROM THE BDFFP RESERVES IN THE AMAZON  
FOREST**

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## **Abstract**

We present a total of 84 species (15 mosses and 69 liverworts), of which 11 species names are updated, and 21 species are recorded for the first time in the BDFFP reserves. As an effort to update the flora of the BDFFP reserves, we listed the accepted epiphyllous bryophytes species recorded to date, include the previous species now considered as synonyms. An identification dichotomous key with all the epiphyllous bryophyte in the BDFFP reserves is presented.

## **Resumo**

Apresentamos um total de 84 espécies (15 musgos e 69 hepáticas), das quais 11 nomes de espécies foram atualizados e 21 espécies são registradas pela primeira vez nas reservas do PDBFF. Com o objetivo de atualizar a flora das reservas do PDBFF, enumeramos as espécies aceitas de briófitas epifilas registradas até o momento, incluindo os nomes de espécies que atualmente consideradas sinônimos. Uma chave de identificação dicotômica com todas as espécies nas reservas do PDBFF é apresentada.

## INTRODUCTION

Epiphyllous communities hold an incredible high local and regional diversity, of bryophyte, lichen, cyanobacteria, fungi and bacteria (Pócs 1996; Verholt 2012; Zartman 2003). Bryophytes are the more conspicuous epiphyllous organism in humid tropical forest, with 90% represented by the single family Lejeuneaceae (Gradstein 1997; Sonnleitner et al. 2009).

Research on the ecology of bryophytes have increased substantially with the recent publication of taxonomic local floras, and monographs of diverse and difficult taxa (Lücking 1998; Gradstein & Costa 2003; Gradstein & Ilkiu–Borges 2007; Zartman & Ilkiu–Borges 2007; Dauphin 2003; Pócs et al. 2014). Nevertheless, bryophyte ecologists usually must identify small, undeveloped and unfertile individuals with the objective to detect all species that occur locally, that otherwise would be overlooked in general floristic surveys (Lücking 1995). Due to its small size and short life cycle, bryophyte individuals can't be tag for long term monitoring studies, and species identification depend greatly on the literature that is use and the floristic experience of the ecologist identifying the species in the field. For the later reason, is essential the use of taxonomic tools, like dichotomous keys, and updated list with valid species names of the local flora in ecological reserves to facilitate long term monitoring studies in tropical forest.

The Biological Dynamic of Forest Fragments Project reserves (BDFFP) harbors various forest fragments of different size (1-, 10- and 100-ha) and vast continuous forest in one of the most diverse tropical forest in the Neotropics (Amazonas, Brazil). Various ecological studies were published on the impacts of fragmentation on epiphyllous bryophytes (Zartman 2003; Zartman & Shaw 2006; Zartman & Nascimento 2006; Zartman et al. 2006). Consequently, as a result of the large inventories from ecological studies, the local flora of the PDBFF was described and illustrated with a total of 55 species (Zartman & Ilkiu–Borges 2007). Recently we sampled all the forest plots studied 15 years ago, and recorded various species absent in Zartman & Ilkiu–Borges (2007). As an effort to update the flora of the BDFFP reserves, we list accepted epiphyllous bryophytes species recorded to date, include the previous species now considered as synonyms and present a dichotomous key with all the species recorded so far.

**Dichotomous Key of the Epiphyllous bryophytes at the Biological Dynamics of Forest Fragmentation Project (BDFFP), Manaus, Brazil.**

1. Leaves spirally arranged (rarely in 2–3 rows). Rhizoids multicellular. Cells without oil bodies (Bryophyta).....2
1. Leaves arranged in 2–3 rows, *or* reduced to single-celled projections originating from the stem, *or* plants thalloid. Rhizoids unicellular. Oil bodies present in cells (Marchantophyta)..... 16
2. Gametophyte trailing, prostrate generally forming loose tufts. Archegonia produced on short lateral branches (pleurocarpous)..... 3
2. Gametophyte growing in erect tufts, little branched. Archegonia terminal (acrocarpous).....9
3. Leaves with double costa. Costa apex ending in a sharp spine. Median and lateral leaves differentiated.....4
3. Leaves with either a single costa or ecostate. Median and lateral leaves undifferentiated .....5
4. Laminal cells short, isodiametric to short oblong (2–3:1). Leaf cells papillose.....*Callicostella pallida*
4. Laminal cells elongate (5–10:1). Leaf cells usually porose.....*Brymela acuminata*
5. Alar cells present, inflated, oval to oblong, mostly thick walled, dark yellow or golden-red.....6
5. Alar cells absent or if present, then not inflated or oval, mostly subquadrate or quadrate.....7
6. Leaf cells with a single papillae on the cell lumen.....*Trichosteleum*
6. Leaf cells smooth.....*Semathophyllum*
7. Costa single. Stem and branch leaves undifferentiated but conspicuously seriate ranked. Asexual propagula absent from leaf bases.....*Meteoridium remotifolium*
7. Costa short and fork or absent; Plants complanate with differentiated lateral and dorsal leaves. Asexual propagule present or absent.....8
8. Alar cell differentiated, unequally distributed with cells on one side more numerous; Asexual propagule absent .....*Pilosium chlorophyllum*
8. Alar cell undifferentiated; Asexual propagule commonly in clusters at leaf bases ..... *Crossomitrium patrisiae* (Brid.) C. Müll.
9. Plants dark green with involute leaves. Leaf lamina unistratose, with conspicuous cancellinae at the base.....10
9. Plants light green to glaucous without involute leaves. In cross section, leaf multi-stratose composed of leucocyst and chlorocyst cells.....15

10. Leaf margin bordered all around or only at base by long hyaline cells.....11
10. Leaf margin not bordered by long hyaline cells; intramarginal border present at base (Teniolae).....14
11. Leaf apex bluntly rounded or retuse; cells of upper lamina pluripapillose; leaves ligulate .....*Syrrhopodon ligulatus*
11. Leaf apex acute; leaves oblong to broadly linear or lanceolate.....12
12. Cells of upper lamina large, with firm walls; dorsally smooth or some cells inconspicuously bluntly unipapillose .....*Syrrhopodon flexifolius*
12. Cells of upper lamina smaller; dorsally unipapillose or pluripapillose; margins of upper lamina—where unbordered—serrulate by papillae and cell angle.....13
13. Cells of upper lamina unipapillose dorsally; upper lamina to many time lengths of lower .....*Syrrhopodon cymbifolius*
13. Cells of upper lamina pluripapillose dorsally; upper lamina ca. 2 times length of lower .....*Syrrhopodon graminicola*
14. Leaves at shoulder region, with distinct intra—marginal border composed of a narrow band elongate cells (Teniolae).....*Calymperes afzelii*
14. Leaves at shoulder region bordered by 8 or more elongate cells. Teniolae lacking .....*Calymperes mitrafugax*
15. Limb of leaves flat or plano—convex on upper surface; apex mucronate base of leaves often ovate or obovate.....*Octoblepherum pulvinatum*
15. Limb of leaves channeled; apex acute to acuminate; base ovate—oblong or —elliptical .....*Leucobryum sp.*
16. Gametophytes thalloid, light green in color and generally one—cell thick throughout except along the central axis.....*Metzgeria sp.*
16. Gametophytes leafy, color variable.....17
17. Leaves succubous. Lobules absent.....*Plagiochila montagnei*
17. Leaves incubous. Underleaves and lobules generally present.....18
18. Rhizoid pads arising from lobules. Underleaves absent. Perianths trumpet—shaped .....*Radula flaccida*
18. Rhizoid pads arising from stems. Underleaves generally present. Perianth morphology variable.....19
19. Gametophytes usually with reddish pigmentation. Lobules utriculiform, almost free from the lobe, keel lacking or indistinct (extending much less than ¼ the leaf lobe length). Multiple archegonia per gynoecium..... *Frullania apiculata*

19. Gametophyte color variable (green to dark red or glossy brown). Lobules varying from vestigial to well developed, attached to the leaf lobe along a keel extending at least ¼ the leaf lobe length. A single archegonium per gynoecium.....Family **Lejeuneaceae**

**Dichotomous key to Epiphyllous Lejeuneaceae**

- 1. Underleaves entire or emarginated.....2
- 1. Underleaves divided or absent.....14
- 2. Leaf margins dentate and/or with sharp apical tip (formed by more than two–four cells) .....3
- 2. Leaf margins entire.....7
- 3. Ocelli absent.....4
- 3. Ocelli present.....5
- 4. Leaf margins irregularly serrate throughout. Underleaves serrate with two prominent postical (tail–like) teeth arising from its base. Perianth five–keeled, and wings irregularly toothed.....*Odontolejeunea lunulata*
- 4. Leaf margins with teeth restricted to the apex. Leaf apex apiculate. Underleaves weakly emarginate and dentate. Keels extend greater than ½ length of leaf. Perianth five–keeled, more or less smooth.....*Thysananthus amazonicus*
- 5. Ocelli arranged in a row from the leaf base to apex. Lobules inflated and large (extending ½ the leaf length). Distal margin of lobule with a sharp, falcate apical tooth .....*Neurolejeunea seminervis*
- 5. Ocelli grouped (generally in pairs) at leaf bases. Lobules variable.....6
- 6. Leaf lobe and perianth wing margins sharply dentate. Perianth dorsiventrally flattened .....*Cyclolejeunea convexistipa*
- 6. Leaf lobe marginal teeth restricted to leaf apex. Perianth with four, horn–like projections .....*Ceratolejeunea desciscens*
- 7. Underleaves distinctly emarginate, leaves apiculate. Plants dark green.....  
.....*Caudalejeunea lehmanniana*
- 7. Underleaves entire. Plant color variable.....8
- 8. Plants tiny (less than 1 mm wide). Lobules well–developed, inflated and covering more than 2/3 leaf lobe area. Hyaline papilla distal to the tooth.....*Cheilolejeunea holostipa*
- 8. Plants larger. Lobules various but not covering more than 1/3 leaf lobe area. Leaf cells various. Hyaline papilla proximal to the apical tooth.....9
- 9. Underleaves large (more than 3 times stem width) inserted along a conspicuous arc. Plant robust (2–3 mm wide). Proximal portion of lobule strongly inflated; distal free margin of lobule flattened.....10

9. Underleaves of various sizes, and insertion shallowly arched or transverse.....	11
10. Plants 2–3 mm wide. Ventral surface of perianth randomly covered with short spines, cilia or lacinae.....	<i>Symbiezidium barbiflorum</i>
10. Plants 3–5 mm wide. Ventral surface of perianth smooth or with ciliate/lacinate in 1–2 shrap rows, never random. ....	<i>Symbiezidium transversale</i>
11. Lobules with 2 teeth on the free margin. Plant robust (3–5 mm from leaf tip to leaf tip), and dark–green to black when dried. Antheridia borne on distinct, raised branches .....	<i>Mastigolejeunea innovans</i>
11. Lobules with 0–1 teeth on the free margin. Color various (light green, brown to blackish) .....	12
12. Plants dark brown to blackish. Distal end of lobule free margin connected to the lobe surface across 2–3 cells. Perianth keels ciliate–lacinate. Innovations lacking. .....	<i>Lopholejeunea subfusca</i>
12. Plants green or brown (rarely blackish). Distal end of lobule free margin connected to the lobe surface across 1 cells. Perianth keels smooth, rarely ciliate. Innovation present. .....	13
13. Plants yellow–brown. Underleaves imbricate; width 4–7 times greater than stem width. Innovations pycnolejeuneoid.....	<i>Archilejeunea fuscescens</i>
13. Plants light green. Underleaves distant or sub–imbricate; width 2–4 times the stem width. Innovations lejeuneoid.....	<i>Archilejeunea parviflora</i>
14. Underleaves absent ( <i>Cololejeunea</i> incl. <i>Aphanolejeunea</i> ).....	15
14. Underleaves present.....	23
15. Polymorphic leaves on the same branches, lobules present or absent. Secondary branches without athecal collar at the branch base.....	16
15. Leaves monomorphic on the same branch. Secondary stems with athecal collar at branch bases. Hyaline cells commonly present along leaf lobe margins.....	20
16. Most leaves reduced to a single filament of two cells wide. Developed leaves with large inflated lobule covering ca 70% of the leaf.....	<i>Cololejeunea gracilis</i>
16. Reduced leaves more than 3 cells wide, usually similar in shape and size of developed leaves.....	17
17. Leaf apices sharp–tipped.....	18
17. Leaf apices rounded.....	19
18. Lobulate leaves common, and inflated lobules generally extending ¼ length of the leaf. Lobules and keels with conically projecting cells.....	<i>Cololejeunea sicifolia</i>
18. Lobulate leaves rare. Leaves distant, with smooth surface (only the margins slightly crenulate by rounded cells). Leaves broadly elliptic, rhombic, or lanceolate, almost	



symmetrical, widest near the middle, apex acute, ending in a one-celled tip .....	<i>Cololejeunea camillii</i>
19. Marginal leaf cells 1.5 times larger than interior cells. Leaf generally elliptic (widest at midpoint). Lobules, when present, covering less than 1/3 the leaf surface area .....	<i>Cololejeunea crenata</i>
19. Marginal leaf cells more or less the same size as the interior cells. Developed leaves spatulate (widest portion of leaf lobe distal to midpoint). Inflated lobules covering at least 1/2 leaf surface area.....	<i>Cololejeunea winkerli</i>
20. Marginal hyaline cells present on leaves.....	21
20. Marginal hyaline cells absent. Lobule and leaf margins frequently with conically-projecting cell walls.....	<i>Cololejeunea obliqua</i>
21. Marginal hyaline cells two rows deep and extending to near leaf lobe base. Lobules vestigial or composed of 3–5 cells.....	<i>Cololejeunea surinamensis</i>
21. Marginal hyaline cells restricted to the leaf apex, hyaline margin formed by 1 row of cells .....	22
22. Developed lobules plane lanceolate (3–5 cells long) .....	<i>Cololejeunea microandroecia</i>
22. Developed lobules saccate with two apical teeth.....	<i>Cololejeunea cardiocarpa</i>
23. An underleaf per leaf.....	24
23. An underleaf per each leaf pair.....	28
24. Upper part of the leaf lobe forming an inflate sac. Ocelli lacking.....	25
24. Upper part of the leaf lobe flattened, not forming an inflated sac. Ocelli scattered on leaves.....	26
25. Leaves cylindrical. Leaf apex sharp.....	<i>Colura tortifolia</i>
25. Leaves oblong. Leaf apex rounded.....	<i>Colura greig-smithii</i>
26. Marginal hyaline cells not restricted to leaf apex; forming a border of 2–4 cells .....	<i>Diplasiolejeunea pellucida</i>
26. Marginal hyaline cells absent.....	24
27. Second (distal) lobule tooth T-shaped.....	<i>Diplasiolejeunea buckii</i>
27. Second (distal) lobule tooth straight.....	<i>Diplasiolejeunea brunnea</i>
28. Lobules large and inflated covering more than 2/3 the area of the leaf lobe. Plants less than 1 mm wide.....	29
28. Lobules covering less than 1/2 the leaf lobe. Plants larger.....	30
29. Leaf base with 1 or more ocelli. Innovations lejeuneoid.....	<i>Microlejeunea bullata</i>
29. Leaf base without ocelli. Innovations pycnolejeuneoid.....	<i>Metalejeunea cuculata</i>

30. Ocelli present.....	31
30. Ocelli absent.....	56
31. Ocelli present in both leaves and underleaves.....	32
31. Ocelli only present in leaves, absent from the underleaves .....	34
32. Ocelli brown or black occurring in both leaves and underleaves. Leaf cells often papillose .....	<i>Pictolejeunea picta</i>
32. Ocelli colorless or gray (rarely pale brown). Leaf cells smooth.....	33
33. Leaf apex acute. Lobule funnel-shaped; apical tooth present, hyaline papilla proximal to tooth. Underleaves arising from a pair of conspicuously inflated merophyte cells .....	<i>Lepidolejeunea involuta</i>
33. Leaf apex broadly rounded. Lobule tooth lacking, hyaline papilla in a small notch at lobule apex.....	<i>Haplolejeunea amazonica</i>
34. Underleaf lobes generally uniseriate widely divergent.....	35
34. Underleaf lobes broader not widely divergent.....	44
35. Underleaf lobes with rounded tips. Leaf apex consisting of a filamentous row of 4–6 cells .....	<i>Harpalejeunea oxyphylla</i>
35. Underleaf lobes with acute tips. Leaf apex various, but never consisting of a row of 4–6 cells.....	36
36. Underleaves distinctly border by large rectangular cells, interior disk cells distinctly smaller than marginal cells. Lobule tooth short and blunt ( <i>Leptolejeunea</i> ).....	37
36. Underleaves not bordered by large rectangular cells, interior disk cells at base square and equal in size to marginal cells. Lobule tooth long and falcate ( <i>Drepanolejeunea</i> ).....	41
37. Leaf lobe margins tridentate, teeth composed by more than two cells .....	<i>Leptolejeunea tridentata</i>
37. Leaf lobe margins denticulate to smooth.....	38
38. Leaf lobe apex apiculate; margin denticulate with blunt teeth Leaf lobe ovate asymmetric .....	<i>Leptolejeunea jamaicensis</i>
38. Leaf apex rounded; margin entire. Leaf lobe elliptical or obovate.....	39
39. Leaf lobes with the maximum leaf width distal to the midpoint between base and apex (obovate).....	<i>Leptolejeunea radicata</i>
39. Leaf lobe widest at its midpoint between base and apex (elliptic).....	40
40. Ocelli reddish or orange, lowermost ocellus separated from next one by only 1 cell .....	<i>Leptolejeunea moniliata</i>
40. Ocelli colorless or pale yellowish, lowermost ocellus separated from next one by (1)3–4 cells.....	<i>Leptolejeunea elliptica</i>

41. Leaf lobe margins entire. Underleaf lobes rather long horizontally divergent. Lobule preapical tooth absent.....	<i>Drepanolejeunea polyrhiza</i>
41. Leaf lobe margins toothed. Underleaf lobes widely divergent, not horizontal. Lobule preapical tooth present.....	42
42. Leaf ventral margin with one conspicuous tooth just above the lobule junction. Leaf margin otherwise entire or crenulate. Ocelli 3–6 per leaf, occurring from base to apex. .....	<i>Drepanolejeunea orthophylla</i>
42. Leaf ventral margin with or without one conspicuous tooth above the lobule junction. Leaf margin toothed. Ocelli 1–2 at the lower half of lobe.....	43
43. Teeth on dorsal and ventral lobe margin.....	<i>Drepanolejeunea crucianella</i>
43. Teeth present on dorsal lobe margin only.....	<i>Drepanolejeunea palmifolia</i>
44. Ocelli in a row from the leaf base toward the apex.....	45
44. Ocelli basal or suprabasal (not forming a row) .....	46
45. Ocelli forming an unbroken row. Hyaline papillae distal. Perianth 4 keeled without hornlike projections.....	<i>Cheilolejeunea urubuensis</i>
45. Ocelli forming a broken row. Hyaline papillae proximal. Perianth with short horns like projection.....	<i>Ceratolejeunea ceratantha</i>
46. Plants brown. Perianth with four apical horn–like projections.....	47
46. Plants pale to dark green (not brown). Perianths without horns.....	50
47. Underleaf margin with one tooth on each side.....	<i>Ceratolejeunea minuta</i>
47. Underleaf margins entire.....	48
48. Leaf margins crenulate throughout; teeth compose of one cell. Leaves asymmetric .....	<i>Ceratolejeunea coarina</i>
48. Leaf margins only toothed at the apices; teeth compose more than two cells. Leaves symmetric .....	49
49. Underleaves ovate to almost lanceolate. Ocelli in pairs.....	<i>Ceratolejeunea cubensis</i>
49. Underleaves ovate to reniform. Ocelli single, not in pairs.....	<i>Ceratolejeunea cornuta</i>
50. Leaf margins and perianth wings entire.....	51
50. Leaf margins and perianth wings dentate to lacinate.....	54
51. Asexual reproduction by means of caducous leaves produced in specialized flageliferom branches. Underleaves distant.....	52
51. Asexual reproduction by means of caducous leaves rare, when present not produced in specialized flageliferom branches. Underleaves imbricate to continuous.....	53

52. Caducous leaves produced on specialized, upright flagelliform shoots. Leaf base with 4–10 large ocelli arranged in short rows.....*Rectolejeunea versifolia*
52. Caducous leaves produced on ordinary leafy shoots. Leaf base with fewer and less well marked ocelli.....*Rectolejeunea emarginuliflora*
53. Lobule large, more than half of lobe length.....*Pycnolejeunea macroloba*
53. Lobule smaller, 1/3 of lobe length.....*Pycnolejeunea contigua*
54. Asexual reproduction by means of gemmae. Leaf and underleaves margins strongly dentate. Perianth dorsiventrally–flattened.....*Cyclolejeunea peruviana*
54. Asexual reproduction by gemmae absent. Leaf and underleaves margin not strongly dentate. Perianth with 5–keels.....55
55. Leaf margins dentate. Ocelli 2–3 basal. Perianths with 5–keels, with double irregularly winged.....*Xylolejeunea crenata*
55. Leaf margin entire. Ocelli 2–6 subbasal. Perianth with 5–keels, with irregularly lacinate .....*Otigoniolejeunea huctumalcensis*
56. Plants tiny (< 0.5 mm wide). Dorsal surface of lobe strongly roughened by mamillose, conically projected cells.....*Lejeunea asperrima*
56. Plants larger. Dorsal surface of lobe smooth.....57
57. Leaf margin with a distinct tipped by a small papillae.....*Prionolejeunea denticulata*
57. Leaf margin smooth or weakly mamillose.....58
58. Underleaf with a pair of lateral teeth along each shoulder. Leaves apiculate .....*Lejeunea boryana*
58. Underleaf margins entire, without teeth.....59
59. Leaves more than 2x longer than wide. Lobules small and rectangular. Perianth dorsiventrally–flattened with two broadly auriculate keels.....*Otolejeunea schnellii*
59. Leaves less than 2x longer than wide. Lobules larger, saccate. Perianth with 4–5 keels, without auricles.....60
60. Lobule with two prominent teeth.....61
60. Lobule with only one prominent tooth.....62
61. Lobule elongate and curve downward. Lobule keel mamillose. Trigones large .....*Cheilolejeunea neblinensis*
61. Lobules ovate not elongate. Lobule keel smooth. Trigones small .....*Cheilolejeunea aneogyna*
62. Lobule with hyaline papilla distal to the apical tooth.....63
62. Lobule with hyaline papilla proximal to the apical tooth.....66

63. Caducous leaves present (rhizoids projecting from leave margin). Lobule apical tooth long and hyaline.....*Cheilolejeunea adnata*
63. Caducous leaves absent. Lobule tooth short or long but not hyaline.....64
64. Leaf apex acute to apiculate, keels with thickened cell walls, lens shape  
.....*Cheilolejeunea oncophylla*
64. Leaf apex obtuse to rounded.....65
65. Underleaves sub-imbricate, wider than long (underleaf width > 2.5x stem width), base strongly auriculate.....*Cheilolejeunea trifaria*
65. Underleaves distant, obcordate, longer than wide and < 2x stem width  
.....*Cheilolejeunea rigidula*
66. Leaf lobes acute-tipped. Perianth keels laciniate .....*Lejeunea controversa*
66. Leaf lobes obtuse. Perianth with 5 smooth keels.....67
67. Underleaves imbricate, more than 2x stem width, base cordate. Underleaves sinus V shape  
.....*Lejeunea flava*
67. Underleaves distant, less than 2x stem width, base cuneate. Underleaves sinus U shape  
.....*Lejeunea adpressa*

### Updated synopsis of epiphyllous bryophytes from the PDBFF reserves

The synopsis contains all validly published species of epiphyllous bryophyte including mosses (Bryophyta) and liverworts (Marchantiophyta) separately. Species are classified by family following Cox et al. (2009) for mosses, considering Octoblepharaceae as a separate family (Santos & Stech 2017), and Stotler et al. (2009) for liverworts. For each family, species are listed in alphabetical order. Corrected names and synonyms previous recorded for the PDBFF reserves are listed. Species with \* were recorded by Zartman & Ilkiu-Borges (2007) and are updated here. Species with \*\* are recorded for the first time in the PDBFF reserves.

Bryophyta (Mosses)

#### Calymperaceae

\*\**Calymperes afzelii* Sw.

\*\**Calymperes mitrafugax* Florsch.

\*\**Syrrhopodon cymbifolius* Müll. Hal.

\*\**Syrrhopodon flexifolius* Mitt.

\*\**Syrrhopodon graminicola* R.S. Williams

\*\**Syrrhopodon ligulatus* Mont.

### **Hookeriaceae**

*Brymela acuminata* (Mitt.) W.R. Buck

\*\**Callicostella pallida* (Hornsch.) Ångström

*Crossomitrium patrisiae* (Brid.) Müll. Hal.

### **Leucobryaceae**

\*\**Leucobryum* sp.

### **Meteoriaceae**

\*\**Meteoridium remotifolium* (Müll. Hal.) Manuel

### **Octoblepharaceae**

*Octoblepharum pulvinatum* (Dozy & Molk.) Mitt.

### **Stereophyllaceae**

\*\* *Pilosium chlorophyllum* (Hornsch.) Müll. Hal. ex Broth.

### **Sematophyllaceae**

\*\**Sematophyllum* sp.

\*\**Trichosteleum* sp.

### **Marchantiophyta (Liverworts)**

#### **Frullaniaceae**

\**Frullania apiculata* (Reinw., Blume & Nees) Nees

Describe and illustrated as *Frullania* sp. 1. (Plate 3. G–H)

#### **Lejeuneaceae**

*Archilejeunea fuscescens* (Hampe ex Lehm.) Fulford

*Archilejeunea parviflora* (Nees) Steph.

*Caudalejeunea lehmaniana* (Gottsche) A. Evans

\*\**Ceratolejeunea ceratantha* (Nees & Mont.) Steph.

*Ceratolejeunea coarina* (Gottsche) Steph.

*Ceratolejeunea cornuta* (Lindenb.) Schiffn.

*Ceratolejeunea cubensis* (Mont.) Schiffn.

*Ceratolejeunea desciscens* (Sande–Lac.) Schiffn.

*Ceratolejeunea minuta* Dauphin

*Cheilolejeunea adnata* (Kunze ex Lehm.) Grolle

\*\**Cheilolejeunea aneogyna* (Spruce) A. Evans

*Cheilolejeunea holostipa* (Spruce) Grolle & R.–L.Zhu

\**Cheilolejeunea neblinensis* Ilkiu–Borges & Gradst.

Illustrated as *Pycnolejeunea* sp. (Plate 20. C–E)

*Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner

*Cheilolejeunea rigidula* (Nees ex Mont.) R.M. Schust.

*Cheilolejeunea trifaria* (Reinw., Blume & Nees) Mizut.

\**Cheilolejeunea urubuensis* (Zartman & I.L. Ackerman) R.L. Zhu & Y.M. Wei

≡*Vitalianthus urubuensis* Zartman & I.L. Ackerman

\**Cololejeunea camillii* (Lehm.) A. Evans

=*Aphanolejeunea camillii* (Lehm.) R. M. Schust.

*Cololejeunea cardiocarpa* (Mont.) A. Evans

\**Cololejeunea crenata* (A. Evans) Pócs

≡*Aphanolejeunea crenata* A. Evans

\**Cololejeunea gracilis* (Jovet–Ast) Pócs

≡*Aphanolejeunea gracilis* Ast

*Cololejeunea micrandroecia* (Spruce) Schiffn. ex Mizut.

*Cololejeunea obliqua* (Nees & Mont.) Schiffn

\**Cololejeunea sicifolia* (Gottsche ex Steph.) Pócs et Bernecker

≡*Aphanolejeunea sicifolia* (Gottsche ex Steph.) A. Evans

*Cololejeunea surinamensis* Tixier

\**Cololejeunea winkleri* (M.I. Morales & Lücking) Bernecker & Pócs

≡*Aphanolejeunea winkleri* M. I. Morales et Bernecker

*Colura greig-smithii* Jovet–Ast

*Colura tortifolia* (Nees & Mont.) Trevis.

*Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A. Evans

*Cyclolejeunea peruviana* (Lehm. & Lindenb.) A. Evans

*Diplasiolejeunea brunnea* Steph.

*Diplasiolejeunea buckii* Grolle

*Diplasiolejeunea inermis* Tixier

*Drepanolejeunea crucianella* (Tayl.) A. Evans

*Drepanolejeunea orthophylla* (Nees & Mont.) Bischl.

*Drepanolejeunea palmifolia* (Nees) Steph.

*Drepanolejeunea polyrhiza* (Nees) Grolle & R.–L. Zhu

\*\**Haplolejeunea amazonica* Ilkiu-Borges & Gradst.

*Harpalejeunea oxyphylla* (Nees & Mont.) Steph.

\**Lejeunea adpressa* Nees

Described and illustrated as *Lejeunea* sp. 2 (Plate 14. G–H)

*Lejeunea asperrima* Spruce

*Lejeunea boryana* Mont.



*Lejeunea controversa* Gottsche

*Lejeunea flava* (Sw.) Nees

*Lepidolejeunea involuta* (Gottsche) Grolle

\**Leptolejeunea jamaicensis* Schust

Described and illustrated as *Leptolejeunea maculata* (Plate 15. A–B).

*Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffn.

\*\**Leptolejeunea moniliata* Steph.

*Leptolejeunea radicata* (Nees ex Mont.) Grolle

*Leptolejeunea tridentata* Bischl.

\*\**Lopholejeunea subfusca* (Nees) Schiffn.

*Mastigolejeunea innovans* (Spruce) Steph.

\*\**Metalejeunea cuculata* (Reinw. et al.) Grolle

*Microlejeunea epiphylla* Bischl.

*Neurolejeunea seminervis* (Spruce) Schiffn.

*Odontolejeunea lunulata* (Weber) Schiffn.

\**Otigoniolejeunea hutumalcensis* (Lindenb. & Gottsche) Y.M. Wei, R.L. Zhu & Gradst.

Described and illustrated as *Lejeunea* sp 1 (Plate 14. A–C)

*Otolejeunea schnellii* (Tixier) R.L. Zhu & M.L. So

\**Prionolejeunea denticulata* (Weber) Schiffn.

Illustrated as *Prionolejeunea* sp. (Plate 19. I)

*Pycnolejeunea contigua* (Nees) Steph.

\*\**Pycnolejeunea macroloba* (Nees & Mont.) Schiffn.

*Rectolejeunea emarginiflora* (Schiffn.) A. Evans

*Rectolejeunea versifolia* (Schiffn.) L. Söderstr. et Hagborg

=*Rectolejeunea berteriana* (Gottsche ex Steph.) A. Evans

\*\**Symbiezidium barbiflorum* (Lindenb. & Gottsche) A. Evans

*Symbiezidium transversale* (Sw.) Trevis

*Thysananthus amazonicus* (Spruce) Schiffn

### **Metzgeriaceae**

*Metzgeria* sp.

### **Radulaceae**

*Radula flaccida* Lindenb. & Gottsche

### **Plagiochilaceae**

*Plagiochila montagnei* Nees

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## Capítulo 2

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Sierra A. M., J. J. Toledo, M. R. Pereira & C.E. Zartman. 2018. A fifteen-year reappraisal of habitat fragmentation impacts on epiphyllous bryophyte metacommunities in central Amazonia. Manuscrito em preparação para *The Bryologist*

**A FIFTEEN-YEAR REAPPRAISAL OF HABITAT FRAGMENTATION  
IMPACTS ON EPIPHYLLOUS BRYOPHYTE METACOMMUNITIES  
IN CENTRAL AMAZONIA**

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## **Abstract**

Forest fragmentation clearly impacts population abundance and community diversity at both local and regional scales over time. Understanding the resilience of tropical forest to anthropogenic impact and the time lapse for land to recover are critical steps for conservation policy implementation. We took advantage of a highly dynamic terrestrial land plant group, tropical epiphyllous bryophytes, and examined temporal changes in their abundance, species richness and community composition between forest fragments over a period of 15 years in the Biological Dynamics of Forest Fragmentation Project (BDFFP) in central Amazon. We observe an increase in abundances and species richness of epiphyllous bryophytes in small fragments (1- and 10-ha) over 15 years. Also, we observed more compositional change of epiphyllous communities in small fragments than on large fragments and continuous forest, with an increased in the core species in smaller fragments. The occupancy patterns in fragments and changes in relative abundance over time are related to interspecific differences in life history traits entailing higher dispersal capacity and physiological tolerances. These results suggest some level of recovery of the phyllosphere biodiversity in smaller fragments (1- and-10 ha) over the past decade and a half. But even for this group with extremely fast generation times and putatively high dispersal abilities their community structure has yet to reach characteristics indicative those documented in continuous forest. Species relative abundance in fragmented forest and their temporal changes herein, were explained by differences in life history traits, positive related to species with higher dispersal capacity and physiological tolerance. Therefore, the interplay of both, dispersal capacity and physiological tolerances, play a significant role shaping the distributional patterns of epiphyllous bryophytes in fragmented forest.

**Keywords:** Community dynamic; demography; dispersal; disturbance; Lejeuneaceae; life history traits; physiological tolerance; resilience; tropics.

## INTRODUCTION

Forest fragmentation is among the major threats for biological diversity as it alters habitats quality and isolates small local populations (Laurance & Peres 2006). Understanding the impacts of habitat fragmentation is critical for predicting the persistence and subsequently the fates of species. How these long-term changes impact tropical ecosystems are still something not completely understood on ecosystem processes (Laurance et al. 2011).

The Amazon basin is one of the largest and more diverse ecosystems in the world and in the recent past suffered some of the highest global rates of deforestation (Laurance 1998). Currently the amazon have been transformed into vast region of a mosaic landscape of pasture, degraded, secondary forests and mature forest fragments. The Biological Dynamics of Forest Fragmentation Project (BDFFP), is the largest and longest experimental study of habitat fragmentation located in the Amazon forest. Previous studies have addressed the effect of fragmentation in tropical forests across many levels resulting in complex and occasionally inconsistent outcomes (see reviews in Laurance et al. 2002 and Laurance et al. 2011). For example, long term tree census studies reported variation in tree community structure and ecological function on fragmented Amazonian landscapes, altering ecosystem dynamic in complex and unpredictable ways (Laurance et al. 2007). Among other groups, for example, where population success and recruitment rate of shade-tolerant trees and understory herbs has decreased in small (1- and 10 ha) fragments (Bruna et al. 2002; Benítez-Malvido & Martinez-Ramos 2003a; 2003b; Benítez-Malvido et al. 2005). Furthermore, a wide variety of organisms including monkeys, insectivorous birds, euglossine bees, dung beetles and forest spiders, locally extinct immediately following isolation, re-colonized at varying rates forest fragments where secondary forest growth reduces the negative impacts of border environments (Stouffer & Bierregaard 1995; 2011; Stouffer et al. 2008; 2011; Mestre & Gasnier 2008; Quintero & Roslin 2005; Becker et al. 1991; Boyle & Smith 2010).

Despite the unique long term experimental design of the BDFFP, long term impacts of habitat fragmentation are slow to be understood principally due to the difficulties in evaluating demographic processes in organisms (such as lignaceous plants) with slow generation times and low local densities at the species level (Laurance et al. 2006a; 2007). Indeed, demographic parameters offer an essential tool to assess population viability, when measurements of population structure differ inconsistently but differences in demographic structure are obvious (Bruna et al. 2002; Bruna & Kress 2002). Accurate measurements of

demographic parameters are hard to generate, but it is possible by using organisms with short generation times like epiphyllous bryophytes (Zartman & Shaw 2006; Zartman et al. 2012).

Epiphyllous are a model example of communities with short generation times which offer an ideal system to assess the effects of habitat fragmentation due to their high local abundance, taxonomic diversity, high colonization-extinction rates, and sensitivities to local environmental conditions (Coley & Kursar 1996; Monge-Najera 1989; Sonnleitner et al. 2009; Zartman et al. 2012). Their short generation times and spatially delimited habitats (e.g., leaf surfaces), make epiphyllous bryophytes an ideal system to collect data at the community level in a short time scale (Zartman 2003). Epiphylls present interspecific differences in life history traits, displaying varying dispersal capacities and physiological tolerance (Gradstein, 1997; Schuster, 1988), which give the opportunity to look at the different respond of epiphyllous species to fragmentation.

At the community level, immediate fragmentation events impact both abundance and species richness, as epiphyllous bryophytes are significantly reduced in small (1- and 10-ha) fragments when compared to 100-ha and continuous forests (Zartman 2003). The decreased abundance and species richness based on evidence from experimental transplants (Zartman & Shaw 2006) in combination with patterns of metacommunity structure (Zartman & Nascimento 2006) subsequently identified that reduced colonization rate in small fragments, rather than increased rates of patch extinction, is the most likely explanation. Studies from temperate regions also have related the importance of dispersal capacity and broad niche tolerance to the suppress patterns of abundance observed in isolate habitats, by looking to interspecific difference in life history traits (Löbel et al. 2009; Johannson et al. 2012). Indeed, metacommunity theory suggest that distribution patterns on isolated habitat may be explained by differences in species dispersal abilities (Leibold et al. 2004), a result which has also been supported by biogeographic studies at global scales (Patiño et al. 2013; Laenen et al. 2015).

To date, no re-evaluation of epiphyllous bryophyte community structure has been conducted in the subsequent 15 years since the original work of Zartman (2003) at the BDFFP, thus offering a unique opportunity to re-census this highly dynamic group of plants following a decade and a half with the objective of evaluating how epiphyllous community structure may have change in the intervening time period (Zartman 2003; Zartman & Nascimento 2006). Moreover, by investigating differences in life history traits related to species responses to fragmentation, will enable us to understand the interplay of dispersal



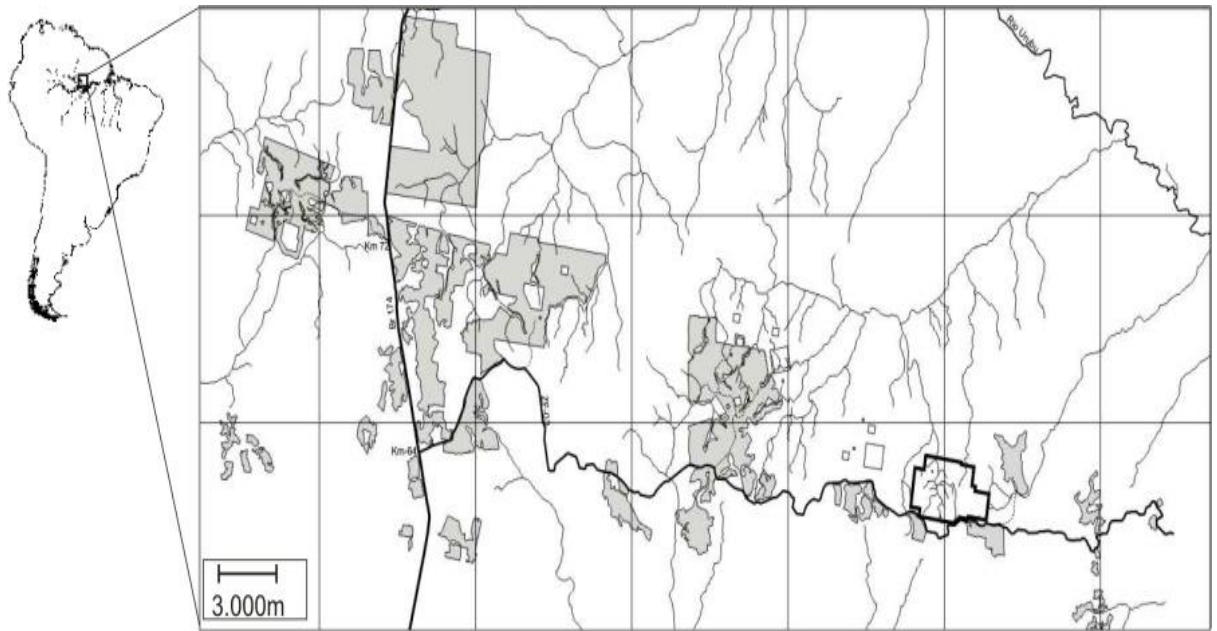
capacity and physiological tolerance determining the distributional patterns, and further predict the persistence and subsequently the fates of species in fragmented landscape (Löbel et al. 2018).

With the objective to evaluate the long-term impacts of habitat fragmentation on epiphyll communities in the BDFFP reserves, we compared species richness, abundance and distribution of epiphyllous bryophytes in a time lapse of fifteen year in relation to the size of remnant habitat patches. Specifically, we test the following predictions: 1) abundance of epiphyllous bryophytes are reduce in smaller fragments (1- and 10-ha), due to the decrease colonization rate and suitable habitat for epiphylls; 2) species richness is reduce in smaller fragments (1- and 10-ha), due to lack of rescue events and enough time-lag for population to pass the extinction threshold, consequently local community become less diverse with the local extinction of rare species; 3) community structure have suffered more change in small fragments than on large fragments, since overall tree community have been under higher dynamic in small fragments, affecting forest structure and ecosystem processes (Laurance et al. 2007); 4) species life history trait related to higher dispersal capacity and physiological tolerance, determine distribution patterns in fragmented forest and dynamic over time, due to the species adaptive capacity to overcome the decrease in habitat connectivity and tolerate the harsh environment present in small fragments (1- and 10-ha).

## **METHODS**

The Biological Dynamics of Forest Fragmentation Project (BDFFP) is located at the BR-174, ~80 km north of Manaus, Brazil, in central Amazonia (2°30 S, 60° W) (**Fig. 1**) with elevation ranging between 100 and 150 m. The rainy season occurs from November to June and rainfall ranges from 190 to 250 cm annually (MME 1978). Since the early 1980s, replicate 1-, 10-, and 100-ha fragments have been isolated from continuous forest by distances ranging from 70 to 1000 m. Primary forests in the reserves include canopies ranging from 30 to 37 m in height and harbour some of the most floristically diverse tree communities in the world (Oliveira & Mori 1999). The forest fragments were surrounded by cattle pasture and secondary forest characterized by *Vismia* and *Cecropia* spp., but currently secondary forests have gradually overtaken most pastures around the fragmented landscape (Laurance et al. 2011). For the epiphyllic bryophyte flora 67 species were recorded in the forest of the BDFFP reserves, 95% of which are member of the single liverwort family Lejeuneaceae (Zartman &

Ilkiu-Borges 2007). From June to August 2016, we re-sampled 21 permanent 1-ha study plots in thirteen fragmented and eight continuous forest reserves sampled in 2000 (Zartman 2003).



**Fig. 1.** The Biological Dynamics of Forest Fragmentation Project (BDFFP) in the state of Manaus, Amazonas, Brazil.

Of the thirteen fragment plots sampled, three are located in three different 1-ha fragments, four in three different 10-ha fragments (one plot located in the fragment interior and three located along the fragment edge), and six plots are located in two 100-ha fragments (two plots located in the interior and four along the fragment edge).

### *Field Sampling*

In order to, compare the epiphyll communities in forest fragments at the BDFFP reserves, we re-sampled using a standardize methodology implemented by Zartman (2003) for 1-ha study plots. We randomly collected epiphylls from entire branches from host plants in 25 (all) of the 400-m<sup>2</sup> quadrats comprising the 1-ha study plots in fragments borders and 13 (half) in fragments interior plots and in continuous forest. We made branch collections in proportion to the estimated abundances of epiphylls in each quadrat and selected only branches with more than one-third of their leaves occupied by epiphyll communities. We identified a total of 17342 individuals from 2523 randomly selected leaves to species or morpho-species using Gradstein & Costa (2003), Zartman & Ilkiu-Borges (2007) and references therein. Vouchers are housed at INPA herbarium. For each 1-ha study plot, we estimated epiphyll densities by counting the total number of understory plant (shrub, palm or

seedling) up to 2 m above ground in each 400-m<sup>2</sup> quadrat hosting epiphyll colonies. This estimating scheme is considered accurate, as epiphyllous bryophyte densities in lowland rain forest decline precipitously 2 m above ground level (Montford & Ek 1990; Zartman 2003).

### *Species Life History Trait*

For all species we quantified the life history trait in two classes (i.e., Reproductive traits and vegetative traits), with values reflecting lower (0) or higher (1) dispersal capacity or physiological tolerance. Spore size take values from lower (0), to higher (1 and 2) dispersal capacity. For reproductive traits associated with dispersal capacity we evaluate sexual system, specialized asexual propagules, and spore size. Vegetative traits associated with physiological tolerance we look at plant sizes, leaf surface, hyaline margin, neotenic features, ocelli, and dark pigmentation. The life history traits were mainly collected from bibliographic search on monograph and species descriptions. When data was not available in the literature, we record life history traits from material collected at the PDBFF and herbarium specimens deposited in INPA. A quali-quantitative database was generated for all traits coded as follow:

1. Reproductive trait: Sexual system (Bisexual=0 or Unisexual=1), specialized asexual propagules (absence=0 or presence=1), and spore size (1–20  $\mu\text{m}$ =2, 20–60  $\mu\text{m}$ =1 or > 60  $\mu\text{m}$ =0) following Laenen et al. (2015).

2. Vegetative traits: Plant sizes (<1 mm wide small=0 or >1.5 mm wide large=1), leaf surface (smooth=0 or papillose including mamillose=1), hyaline margin (absence=0 or presence=1), neotenic features (absence=0 or presence=1) following Gradstein et al. (2003), ocelli (absence=0 or presence=1), and dark pigmentation (absence=0 or presence=1).

### *Statistical analyses*

We compile data of the community structure (epiphyll abundance, presence/absence data, species relative abundance) for all plots in fragments sampled in 2000 and 2016. We tested differences of mean epiphyll abundance and species richness in two spatial scales (individual leaf and 1 ha study plot) using repeated measure ANOVA with an unbalanced design.

To investigate temporal changes in community structure on the 1-ha study plot in relation to fragment size, a test for homogeneity of multivariate dispersions was used (Anderson 2006) which employs the distances from centroids, obtained from Principal Coordinate Analysis (PCoA), in a permutation test (999 permutations) to generate null

distribution of F and calculate *p*-values. We test for differences in the homogeneity of multivariate dispersion among small fragments (1- and 10-ha) and large reserves (100-ha fragments and continuous forest) between the year sampled.

To evaluate if changes in relative abundance of species in fragmented and continuous forest are explain by difference in life history traits, we calculate the mean trait proportion by 1 ha study plot for all species. Mean trait proportion was calculated using the following equation:

$$y = \bar{X}(\textit{life history trait})(\textit{species freq.}/n)$$

Where *y* is the average trait per 1-ha study plot; *life history trait* is the value of each trait for each species; *species freq.* is the number of times a species was registered in one 1-ha study plot and *n* the total number of sample per 1-ha study plot. We test for difference in average trait among small fragments (1- and 10-ha) and large reserves (100-ha fragments and continuous forest) and among year sampled using repeated measure ANOVA.

All analyses were carried out using R software (version 3.2.5) (2016). The *vegan* (Oksanen et al. 2016) package was used to run PERMANOVA, permutation tests for homogeneity of multivariate dispersion, and ordination analyses, and the *Biodiversity R* package (Kindt & Coe 2005) was used to build dominance-diversity curves.

## RESULTS

### *Community structure*

The epiphyllous flora of the PDBFF reserves is represented by 87 species, which more than 90% of the taxa are members of the liverwort family Lejeuneaceae (For more detail of the species see **Capítulo 1**). Eight species registered in 2000 were not found in 2016, while 20 species were recorded only in 2016. Various species were either absent or newly recorded in all fragment size (1-, 10-, 100-ha) and continuous forest in the year 2016 when compared to the year 2000 (**Table 1**). Of the 87 species, 59 in 2000 were absent from all 1 ha fragments, while 51 spp. in 2016. In 10 ha fragments 49 spp. were absent in 2000, but only 28 in 2016. For all small fragments (1- and 10-ha), we still observed the absence of 19 species when compared to large fragments and continuous forest, and the presence of six species only present in small fragments.

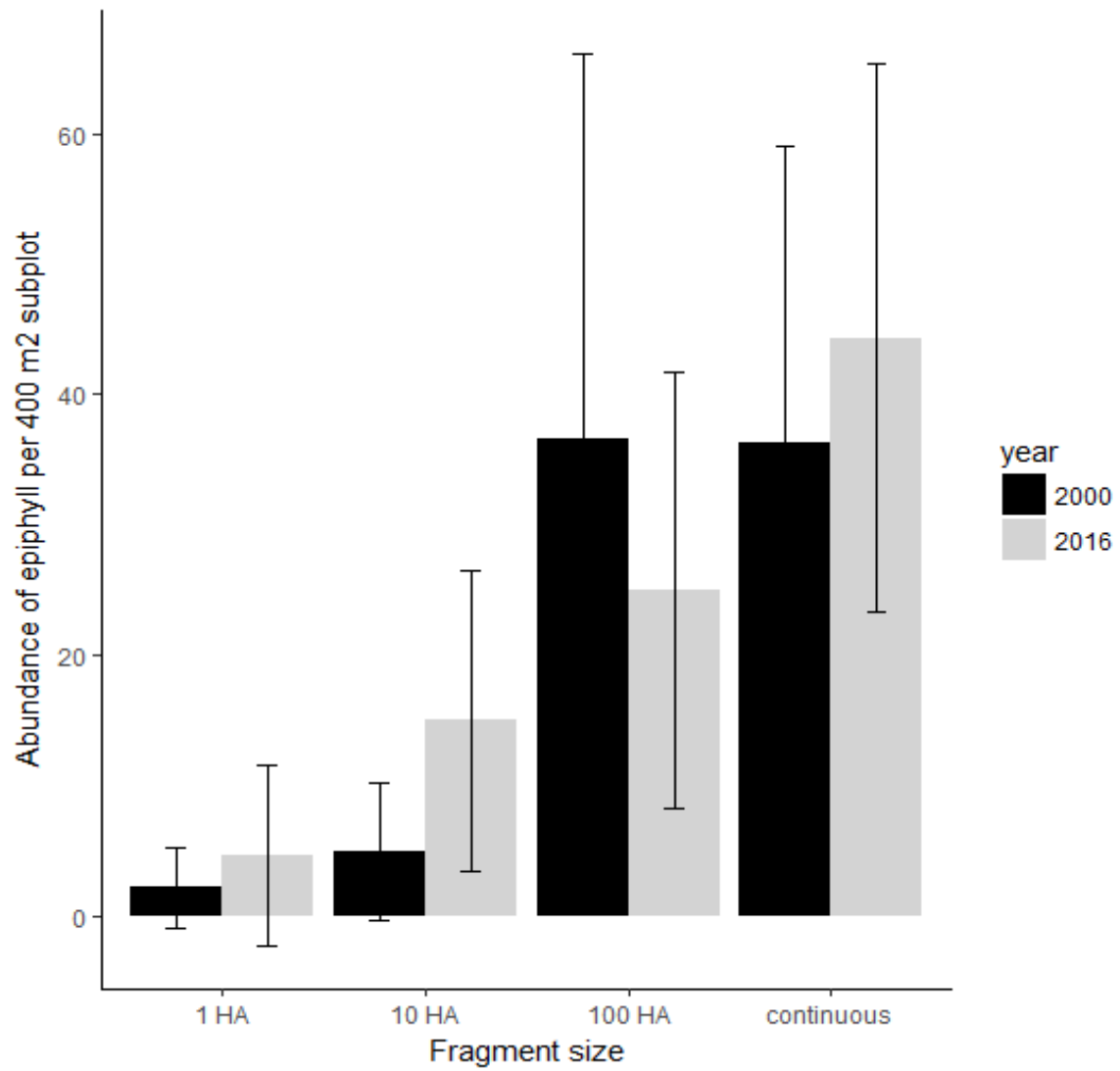
**Table 1.** Overall species loss/gain on the fragmented and continuous forest in the year 2016

Reserves sizes	Number of species absent in 2016	Number of species newly present in 2016
1 ha	9	18
10 ha	9	26
100 ha	11	19
Continuous	6	20

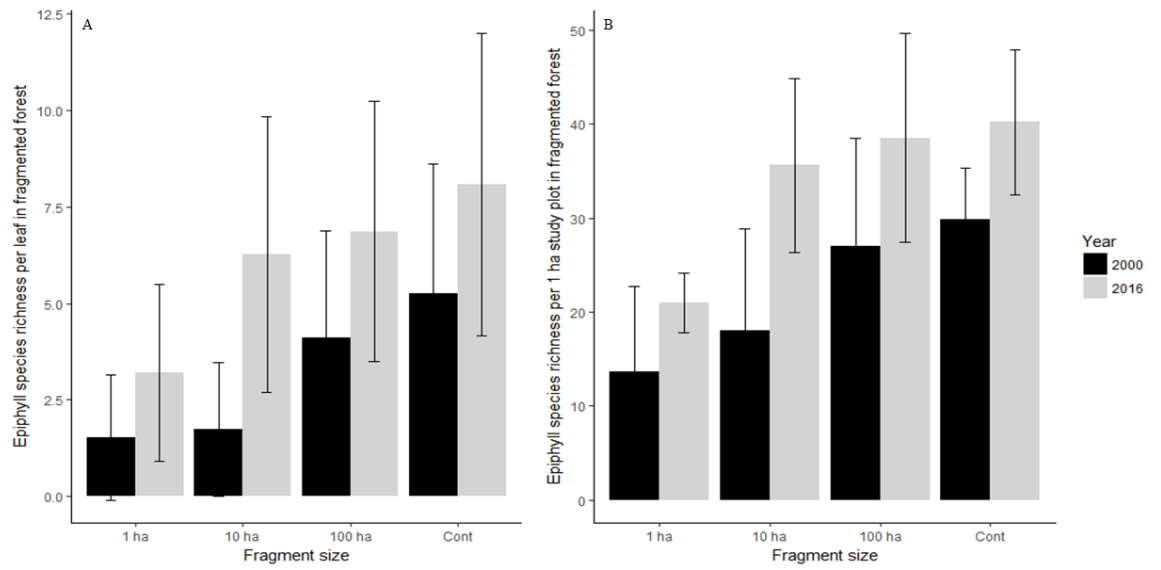
Based on dominance diversity curve we observed that core species in epiphyllous communities on 100-fragments and continuous forest were similar in the two years sampled, but they differ based on their relative abundance. In small fragment, core species in epiphyllous community were dominated by two species (*Radula flaccida* and *Cololejeunea surinamensis*) in 2000, but 11 species dominated epiphyllous communities in 2016, close to the observed in 100 ha fragments and continuous forest (**Fig. 5**).

*Patterns and temporal changes in abundance and species richness*

Epiphyll abundance (**Fig.2**) were significantly different in fragments of different size when compared between the two-year sampled (Repeated measure ANOVA:  $F=18.086$   $p<0.001$ ) (**Table 2**). Epiphyll abundance in 10-ha were significantly higher in 2016 when compared with the year 2000, but in 100-ha fragments abundance was significantly reduce in 2016. Species richness significantly increased in all fragments size and continuous forest when compare between the two-year sampled for individual leaf (**Fig. 3 A**) (Repeated measure ANOVA:  $F=10.60$ ,  $p<0.001$ ); but was not significant for differences among 1-ha study plot (**Fig. 3 B**) (Repeated measure ANOVA:  $F= 0.4955$ ,  $p=0.69$ ) (**Table 2**).



**Fig. 2.** Abundance of epiphyll per 400 m<sup>2</sup> subplot in fragment and continuous forest sampled in the years 2000 (Black) and 2016 (Grey).



**Fig. 3.** Species richness at two spatial scales: A. individual leaf and B. 1 ha, in relation to fragment size in the years 2000 (Black) and 2016 (Grey).

**Table 2.** Repeated measure ANOVA summary statistic for Epiphyll abundance, species richness per study leaf and 1 ha study plot.

	F Value	Pr(>F)	
<i>Epiphyll abundance</i>			
Fragment size	108.086	<0.000000000000000022	***
Year	0.9726	0.3243	NS
Fragment size :			
Year	18.0405	2.30E-11	***
<i>Species richness per leaf</i>			
Fragment size	10.575	6.58E-07	***
Year	15.763	7.39E-05	***
Fragment size :			
Year	10.606	6.29E-07	***
<i>Species richness per 1 ha plot</i>			
Fragment size	3.424	0.02695	*
Year	1.2823	0.26476	NS
Fragment size :			
Year	0.4955	0.68766	NS

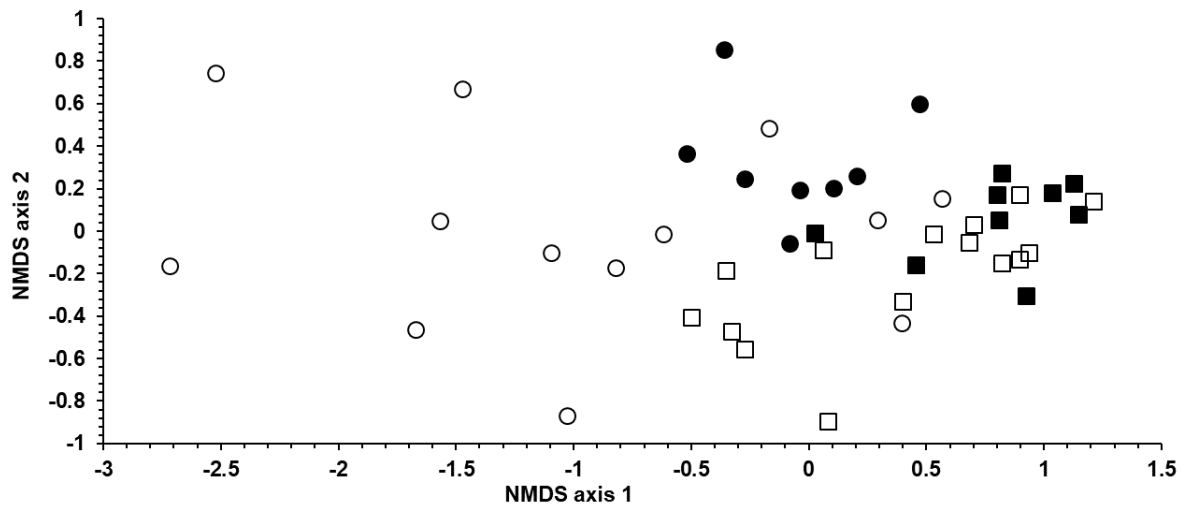
#### *Patterns in epiphyll community composition*

Community composition of epiphyllous bryophytes in 1-ha study plot in small fragments (1- and 10-ha) showed greater significant compositional dispersion over the past 15 years than 100-ha fragment and continuous forest (**Table 3**). Composition in small fragments sampled in 2016 tend to diverge from small fragments sampled in 2000; and become more similar to large fragments (100-ha) and continuous forest (**Fig. 4**). Species rank also showed an increase in the number of dominant species in smaller fragments between year sampled (**Fig. 5 A**); while in large fragments and continuous forest the number of dominant species didn't change between the year sampled (**Fig. 5 B**).

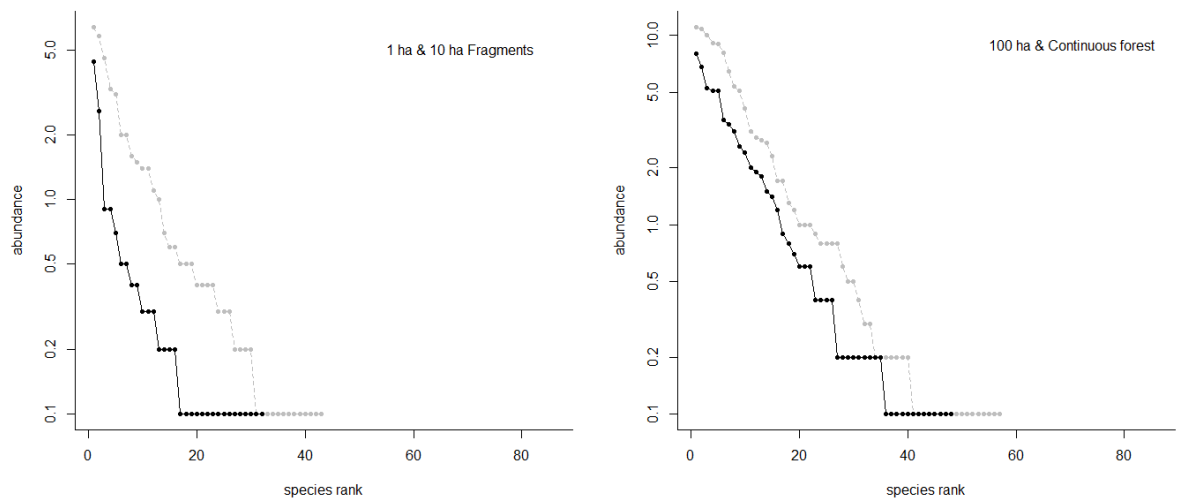


**Table 3.** Summary of homogeneity of multivariate dispersion measurements among small fragments (1- and 10-ha) and large reserves (100- ha fragments and continuous forest) between the year sampled.

	Average distance to		F value	P value	
	median				
	2000	2016			
Small	0.3899	0.671	6.8389	0.022	*
Large	0.5373	0.6097	1.2343	0.285	



**Fig. 4.** NMDS ordination of 45, 1-ha plots based on the abundance of 74 bryophyte species in fragmented (squares) and intact forests (circles) for the 2000 (open symbols) and 2016 (black symbols) inventories.



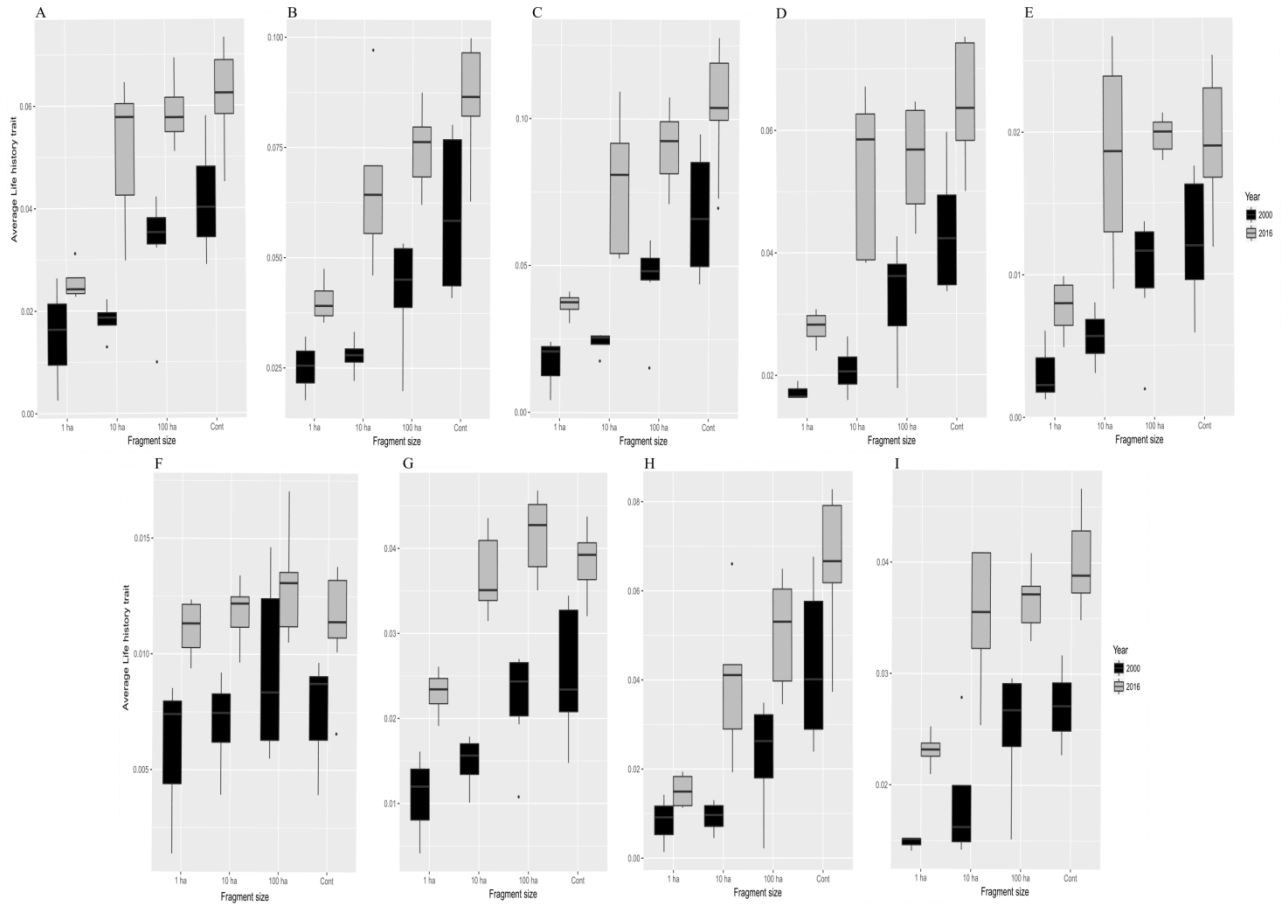
**Fig 5.** Dominance–diversity curves of epiphyll communities in A. 1- and 10-ha fragments and B. 100- ha and continuous forest, from the year 2000 (Black lines) and 2016 (Grey lines).

*Life history traits explained community changes patterns in fragmented landscape*

By calculating average trait differences for each 1 ha study plot and comparing it between fragments size and year sampled, we associated changes in relative abundance and composition (species loss or immigration of new species) with interspecific differences in life history traits associated with higher dispersal capacity and physiological tolerance to harsh environments in fragmented forest. Overall, we observed a difference in average traits values between fragment size and a shift in average traits over a fifteen-year lapse (**Fig. 6**). Reproductive traits associated with higher dispersal capacity were all significantly associated with differences in species relative abundances between fragment sizes and years sampled (**Table 4**). Pointing that the positive response in relative abundance are related to species with bisexual sexual system, presence of specialized asexual propagules, and small spores. For vegetative traits associated with physiological tolerance, were all significantly associated with differences in species relative abundances between years sampled, and for fragment size with the exception of the trait: leaves hyaline border (**Table 4**). Our results indicated that positive response in relative abundance in fragmented forest is related to species with large size, presence of neotenic features, papillae on leaf surface, ocelli, and dark pigmentation.

**Table 4.** Repeated measure ANOVA summary statistic for species life history traits as predictor of relative abundance in different size of fragmented forest and sampled year.

Predictor life history traits	Df	F value	Pr(>F)
<i>Fragment size</i>			
Sexual system	34.29	6.40E-07	***
Specialized asexual propagule	30.507	1.92E-06	***
Spore size	35.398	4.69E-07	***
Plant size	30.699	1.81E-06	***
Leaf surface	19.572	6.74E-05	***
Hyaline margin	2.1155	0.1532	NS
Neoteny	26.486	6.61E-06	***
Ocelli	33.091	9.01E-07	***
Dark color	32.708	1.01E-06	***
<i>Year (2000-2016)</i>			
Sexual system	45.934	3.03E-08	***
Specialized asexual propagule	40.462	1.20E-07	***
Spore size	42.177	7.72E-08	***
Plant size	44.41	4.40E-08	***
Leaf surface	37.683	2.51E-07	***
Hyaline margin	30.095	2.17E-06	***
Neoteny	81.549	2.15E-11	***
Ocelli	24.162	1.40E-05	***
Dark pigmentation	69.494	1.91E-10	***



**Fig. 6.** Average trait value variation for all life history traits in fragment and continuous forest sampled in the years 2000 (Black) and 2016 (Grey). A. Sexual system, B. specialized asexual propagules, C. spore size, D. plant size, E. leaf surface, F. hyaline margin, G. neoteny, H. ocelli, I. dark pigmentation.

## DISCUSSION

Forest fragmentation clearly impacts the population abundance and community diversity at both local and regional scales over time (Lovejoy et al. 1986). We took advantage of a highly dynamic terrestrial land plant group, tropical epiphyllous bryophytes, and examined temporal changes in their abundance, species richness and community composition between forest fragments. However, contrary to our predictions we observed an increase in abundances and species richness of epiphyllous bryophytes in small fragments (1- and 10-ha)

over 15 years suggesting some level of recovery. As expected we observed more composition change in epiphyllous communities in small fragments than on large fragments and continuous forest. Forest dynamics and higher species turn over in small fragments (1- and 10-ha), could be responsible for the compositional change in epiphyllous communities associated with forest structure changes with time (Laurance et al. 2006a; 2006b; 2007). Epiphyllous bryophyte characterizes by a shorter live cycle, when compared to large vascular plants, that will reveal accurate and specific demographic patterns changes in fragmented forest over time. The present results indicated positives changes in smaller fragments over a fifteen-year period. But even for highly dynamic epiphyllous communities the negatives effects appear far from recovering when compare to continuous forest. Epiphyllous species seems to respond differently to forest fragmentation, we addressed this by investigating differences in life history traits entailing dispersal capacity and physiological tolerance. Our results indicate that species relative abundance in fragmented forest and their temporal changes herein, are explained by differences in life history traits, positive related to species with higher dispersal capacity and physiological tolerance. Therefore, the interplay of both, dispersal capacity and physiological tolerances, play a significant role on the persistence of local populations of epiphyllous bryophytes in fragmented forest.

#### *Temporal changes in abundance and species richness in forest fragments*

Based on previous evidence on epiphyllous bryophytes at BDFFP, the reduced colonization rate observed in small fragments from experimental demography studies (*Radula flaccida* and *Cololejeunea surinamensis*) (Zartman & Shaw 2006) and patterns of metacommunity structure (Zartman & Nascimento 2006), with the compromised richness and abundance observed in small fragments (Zartman 2003), we expected that local populations decrease with time due to low rescue effect as connectivity and available habitat decrease in small fragments (Hanski & Gaggiotti 2004). Contrary to our expectations, our results suggested that over a period of 15 years, epiphyllous abundance and species richness have significantly increased, especially in 10-ha fragments. This could suggest that even though colonization rates were reduced, immigration have been enough to maintain local population in small fragments, or that colonization rates have increased over time recovering local populations. The disproportionally increased in epiphyll abundance in 10-ha forest fragments could also be explained by the diminishing edge effects due to re grown secondary forest around some fragments. Either of the latter explanation to the observed pattern need further empirical evidence.

Our results suggest some level of recovery in species richness in small fragments over a 15 years period, where new species have colonized the small fragments (1- and 10-ha). In the year 2000 epiphyllous communities in small fragments were dominated by a few species on both scales, single leaves and 1 ha plot (Zartman 2003). In the year 2016, we observed on both scales, an increase in the number of dominate species, closer to the one observed in continuous forest for both years. In 2000 the observed bimodal patch occupancy pattern show that the core species were lost among small fragments (1- and 10-ha) (Zartman & Nascimento 2006), but in 2016 we observed a recovery of the core species based on the species rank breaks. When there is strong rescue effect, metapopulation will show a bimodal patch-occupancy distribution (Hanski 1982), with species either core (high frequency) or satellite (low frequency), either occupying few or nearly all habitable patches within a region. The increase in core species in 2016 suggest that over the 15-year period rescue effect from nearby source populations has been re-established.

The re-colonization and increase of core species in smaller fragments points to a recovery of epiphyllous communities over a period of 35 year after isolation. This add evidence to the long term respond to fragmentation of other organisms that have shown a level of recovery as well (Stouffer & Bierregaard 1995; 2011; Mestre & Gasnier 2008; Andresen 2003; Quintero & Roslin 2005; Becker et al. 1991; Boyle & Smith 2010) as secondary forests have re grown around forest fragments and possible relaxing the effects of fragmentation for some taxa as the matrix becomes less hostile and fragments less isolated. Nevertheless, the process that drive the recovery of different groups of organisms could be diverse and complex that only with further monitoring will become better understood.

#### *Life history traits explained community changes patterns in fragmented landscape*

We observed that interspecific life history traits are related to species with high local and regional abundance in forest fragment, also temporal change of species abundance point to species with higher dispersal capacity, which agrees with the importance of dispersal to the maintenance of metacommunities in isolated habitats through rescue effect (Leibold et al. 2004). Nevertheless, species occurrence constraint of epiphyllous bryophytes has been explained by dispersal limitation (Zartman et al. 2012) and abiotic filters (Sonnleitner et al. 2009), both process related to the effects of fragmentation, isolation and edge effects respectively.

We found greater average trait proportion for all traits related to higher dispersal capacity, indicating that species with bisexual reproductive mode, small spores, presence of specialized asexual propagules are more abundant in small fragments and relative abundance of this species increase within a 15-year period. Epiphyllous bryophytes usually synchronously reproduce by asexual and sexual means, investing in both local short distance dispersal and long-distance dispersal events (Söderström & During 2005), the proportion of these two-process influencing local community dynamics is uncertain (Barbé et al. 2015). The fact that interspecific differences in life history traits related to dispersal capacity, indicates that the degree of connectivity affects species distribution differently, where species with high dispersal capacity enhances local population sizes within forest fragments through rescue effect. Otherwise, species with low dispersal capacity, rescue effect play a minor role, this is supported with the significant results of differences in averages traits between fragment size and year sampled. Also, temporal shift in averages traits among forest fragments also point to rescue effect of species with higher dispersal capacity over the 15 years. Indeed, core species are mostly bisexual, all present specialized asexual propagules and small spore size.

Epiphyllous bryophytes are highly sensitive to local environmental conditions, and different species assembly are found between dry and humid environments (Marino & Salazar 1997; Sonnleitner et al. 2009). Various morphological characteristics have been related to tolerance to dry conditions (Marino & Salazar 1997; Lücking 1995; Gradstein 1997). For example, hyaline border is suspected to help retain water as leaves create a vacuum space between the surface of the host leaves and the bryophyte leaves, diminishing evaporation of physiological water (Lücking 1995). Presence of ocelli and dark coloration have been related to desiccation tolerance and is very common characteristic in xerotolerant species (Gradstein et al. 2001). Plants with larger surface would have a larger volume-area to retain water than small plants. Papillae also create physical conditions (capillarity), that will diminish the rate of evaporation of the plant (Gradstein et al. 2001).

Our results indicated that difference in abundance of species on different fragments sizes and their temporal changes are explained by traits related to physiological tolerance. Zartman & Nascimento (2006), observed that forest edges had less abundance of epiphylls than the interior of fragments, due to the sensitivity of epiphyllous species to lower humidity and higher temperature (Sonnleitner et al. 2009). Species capable to tolerate these microenvironment conditions were associated with the presence of traits that encompass higher physiological tolerance. These traits are more important in facilitating grow and

development of bryophyte species, due to their poikylhydric conditions, in the maintenance of local populations, since in patch tracking populations stochastic extinction is unlikely (Snäll et al. 2003; Zartman & Shaw 2006).

The current recovery of the secondary forest around forest edges and changes in the microenvironment, might be factors contributing to the increase in abundance and specific positive response over time of epiphyllous bryophytes. Species with traits entailing higher dispersal capacity and physiological tolerance will favour from these changes in forest fragments that will positively impact epiphyllous communities at both local and regional scale over time (Johansson et al. 2012; Löbel & Rydin 2009; Löbel et al. 2009). Even though, the importance of dispersal has been given more attention in explaining the observed community patterns in fragmented landscape (Löbel et al. 2009), we suggest that the interplay of both mechanism (dispersal capacity and physiological tolerance) (Löbel et al. 2018), are responsible for the persistence or subsequently fate of epiphyllous species in a fragmented landscape in the tropics.

#### *Potential drivers of epiphyllous community dynamics on fragmented forest*

Habitat fragmentation lowers species regional abundance, by increasing local extinction rates and decreasing colonization rates as populations become reduced and distanced, from which immigrants may originate to maintain local population (Hanski 1999). The persistence of species will be only possible with the presence of rescue effect, where recurrent immigration reduces the rate of local extinction (Hanski & Gaggiotti 2004). The time lag between passing the extinction threshold and regional metapopulation extinction can be long, and difficult to detected until many years after there have been triggered (Ovaskainen & Hanski 2002). However, the impact of habitat connectivity and presence of rescue effect on small fragments along time can be detected in a metapopulation by looking to changes in overall abundance and species abundance patterns in fragmented landscape (Hanski 1999). Furthermore, understanding differences in life history traits related to species responses to fragmentation will enable to predict specific respond of metacommunities over time (Löbel et al. 2018).

In general, rare disturbances and stochastic process alter forest structure, dynamics, dispersal and seedling recruitment (Hubbell 2001). Habitat fragmentation drive compositional and functional changes in forest structure, increasing tree turnover, decrease survivorship of shade tolerant understory plants, affecting overall forest dynamic (Laurance et al. 2006a;



2006b; 2007; Bruna 2002; Benítez-Malvido et al. 2005). Consequently, community composition and functioning have diverged along the fragmented Amazonian landscapes in the BDFFP (Laurance et al. 2007). These compositional and functional changes in tree communities are also likely to affect canopy gap dynamics, nutrient cycling, environmental conditions and plant-animal interactions in fragmented forests, consequently altering recruitment dynamics of plants in complex and unpredictable ways (Laurance et al. 1998; Bruna 2002). Similar to other results, epiphyllous communities in smaller fragments showed higher compositional change over time when compared to large fragments and continuous forest. It is most likely that the effect of gaps formation, decrease or increase of understory plants, increase of lianas on forest edge (Laurance et al. 2014), or colonization-extinction dynamics on highly dynamic substrate are driving community composition change over time. The increase of understory plants will increase patch availability for epiphylls, with the recovery of secondary forest along forest edge, diminishing edge effects, might be responsible for the increase in epiphyll abundance and species richness, as suitable habitat is present where previously was inhabitable.

Our results suggesting that with time isolated fragments in tropical forest are recovering in abundance, species richness and species composition and becoming more similar to continuous forest, contradicts the expectations from classical metapopulation theory (Levins 1974, Hanski 1999). Empirical studies in temperate ecosystem have observed similar patterns for epiphytic lichens in old isolated patches and in Sphagnum bogs in small islands (Sundberg et al. 2006; Gjerde et al. 2012). Epiphyllous communities could be fit into patch tracking metacommunities where the colonization-extinction balance is mainly determined by the longevity of leaves of their host (*sensu* Snäll et al. 2003; Zartman et al. 2012). After fragments were isolated epiphyllous communities were drastically reduced in small fragments and edge of 100 large fragments as shown in (Zartman 2003; Zartman & Nascimento 2006). This imply that early stages of local small populations of epiphyllous bryophytes in fragments had a colonization debit and extinction credit (Jackson & Sax 2010) that will be balance with colonization events by frequent long-distance dispersal events and efficient internal colonization. Changes in species rank on small fragments present evidence of the later process, and with the given sufficient time these fragments could recover to a state close to continuous forest. We predict that this change will be more conspicuous in fragments >10 ha, which in theory will have more favourable habitat for epiphyllous bryophytes to occur (interior of fragments).

### *Conservation implications*

The strong effects of fragmentation and the matrix dynamics on plant communities (Antongiovanni & Metzger 2005; Stouffer et al. 2006), the inside forest dynamic (Laurance et al. 2007), increase of lianas on forest edge (Laurance et al. 2014) and the contrasting effects of fragmentation on the ecosystem (Benítez-Malvido & Martinez-Ramos 2003b; Ferraz et al. 2007), are complex. With the ongoing evidence of various positive respond in the PDBFF reserves along the fragmented landscape, imply that time and changes of the landscape matrix can compensate for the effects of isolations. Although, with many factors influencing colonization and extinction dynamics, including interspecific differences respond to isolation and the ongoing climate change, is difficult to generalized and predict the future of tropical forest. There is the necessity to continue monitoring various groups of organisms in fragmented landscape and the inclusion of other parameters to the current models.

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## **Conclusão geral**

O presente trabalho avaliou as comunidades de briófitas epifilas em florestas fragmentadas nas reservas do PDBFF na Amazônia Central, contribuindo para melhorar o conhecimento florístico, taxonômico e ecológico deste grupo de plantas tropicais menos visível, embora igualmente importante em florestas tropicais. Além disso, indicou novos pontos a serem avaliados sobre os impactos da fragmentação sobre a dinâmica das comunidades de plantas.

Considerando a quantidade de espécies que foram registradas pela primeira vez em uma área previamente estudada, isso indica o baixo conhecimento que temos sobre a flora de briófitas amazônicas e que o incremento em coletas em diferentes áreas da Amazônia, sem dúvida levará a novidades taxonômicas e florísticas. A flora das reservas do PDBFF atualizada fornece uma nova fonte taxonômica para futuros estudos ecológicos e de monitoramento da flora de briófitas que possibilita uma fácil identificação das espécies dentro das reservas.

A comparação das comunidades epifilas nos fragmentos florestais em um intervalo de 15 anos demonstrou uma recuperação na abundância, riqueza e composição de espécies. Os resultados indicam que os fatores que afetam as comunidades epifilas, como efeito de borda e diminuição de conectividade, tenham diminuído com o tempo, sendo a dinâmica florestal nos fragmentos e o incremento na floresta secundária na paisagem do PDBFF as possíveis causas do padrão observado nas comunidades epifilas. Nossos resultados comparando os traços adaptativos de história de vida indicam que as espécies respondem ao efeito da fragmentação com base em seus traços adaptativos, sendo menos afetadas as espécies com maior capacidade de dispersão e tolerância fisiológica. Por tanto, sugerimos que a interação de ambos os mecanismos (capacidade de dispersão e tolerância fisiológica) precisam ser consideradas na avaliação das comunidades de briófitas epifilas em florestas fragmentadas.

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