

**UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL  
INSTITUTO DE BIOCÊNCIAS  
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

**Dissertação de Mestrado**

**Efeito de borda e de distúrbio antrópico sobre a fauna de  
insetos galhadores em transições floresta-campo**

Tiago Shizen Pacheco Toma

Porto Alegre, Fevereiro de 2012

# **Efeito de borda e de distúrbio antrópico sobre a fauna de insetos galhadores em transições floresta-campo**

Tiago Shizen Pacheco Toma

Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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“À luz do conhecimento já adquirido, o resultado obtido parece quase normal e qualquer estudante inteligente o adivinha com facilidade. Assim a pesquisa procede por momentos distintos e prolongados, intuição, cegueira, exaltação e febre. Vem dar, um dia, nesta alegria e conhece tal alegria aquele que viveu estes momentos incomuns.”

Albert Einstein – *Mein Weltbild*

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## Resumo

O efeito de borda em florestas é bastante estudado, porém pouco se sabe sobre as respostas das interações entre espécies a este efeito. O mesmo acontece quando se trata de distúrbios antrópicos, muitas vezes presentes após o processo de fragmentação. Apesar de não terem sido originadas por tal processo, as transições floresta-campo existentes nas florestas com *Araucaria* do sul do Brasil são submetidas aos distúrbios causados pelo pastejo e manejo por fogo, possuindo características semelhantes às bordas florestais mantidas no seu ponto de criação. No Capítulo 1, o efeito de borda e de distúrbios antrópicos sobre a fauna de insetos galhadores foi testado em transições floresta-campo, em termos de riqueza e composição destes organismos, comparando-se tanto bordas e interiores florestais quanto graus de distúrbio (com distúrbio e em regeneração), e adicionalmente foram feitas comparações entre manchas florestais naturais e a floresta contínua. Considerando as hipóteses propostas para os padrões de distribuição dos insetos galhadores, espera-se que existam mais espécies nas bordas de florestas comparadas ao interior, e que os distúrbios afetem estas respostas. Apesar das bordas em geral não terem apresentado maior riqueza de espécies que o interior, o padrão foi oposto ao esperado em locais com presença de distúrbio, com interiores mais ricos que bordas. A composição de espécies foi diferente entre os habitats e entre graus de distúrbio, e as porções de floresta contínua amostradas foram mais ricas que manchas florestais. Além disso, a fauna de insetos galhadores das manchas florestais foi um subconjunto da floresta contínua. Os resultados reforçam a relação dos padrões de distribuição da vegetação com os insetos galhadores, que indiretamente responderam ao efeito de borda e de distúrbios antrópicos atuando sobre suas plantas hospedeiras. No Capítulo 2 é apresentado de forma pioneira um inventário das galhas de insetos da Floresta com Araucária, referente às galhas coletadas para o estudo apresentado no primeiro capítulo. São listadas as espécies de insetos galhadores e suas plantas hospedeiras, com informações sobre a morfologia das galhas e a ocorrência nos locais amostrados. Foram encontradas 57 espécies de insetos galhadores (a maioria Diptera: Cecidomyiidae), em 43 espécies de plantas pertencentes a 18 famílias botânicas. As galhas foram predominantemente caulinares ou em gemas, glabras, isoladas, fusiformes e de coloração verde. Myrtaceae, Asteraceae e Melastomataceae foram as famílias de plantas mais representativas. Os valores brutos totais de galhas por habitat ou local

mostraram-se semelhantes entre borda e interior, porém foram relativamente maiores na área sem distúrbio e na floresta contínua, esta última abarcando um grande número de galhas que ocorreram nas manchas. A existência de áreas sem distúrbio do pastejo e manejo por fogo se mostrou relevante para a conservação da fauna de insetos galhadores, que podem se estabelecer e manter suas populações. O conhecimento da diversidade destes organismos é um fator chave para o desenvolvimento de ações mais claras visando sua preservação.

**Palavras-chave:** diversidade, Floresta com Araucária, galhas de insetos, manchas florestais.

## Abstract

The edge effect on forests is widely studied, however little is known about species interactions responses to this effect. The same is true for anthropogenic disturbances, many times present after the fragmentation process. Despite not originated by this process, forest-grassland boundaries of Araucaria forests in southern Brazil are under disturbance by cattle grazing and fire, presenting characteristics similar to forest edges maintained at their point of creation. In Chapter 1, edge and anthropogenic disturbance effects on the galling insect fauna were tested in forest-grassland boundaries, in terms of richness and composition of this organisms, comparing both forest edges and interiors as degrees of disturbance (disturbed and recovering), and additional comparisons were performed between natural forest patches and a continuous forest. Considering hypotheses proposed to distribution patterns of the galling insects, it is expected that forest edges would harbor more species compared to forest interior, and that disturbances would affect the outcome. Although edges in general did not present higher species richness than forest interiors, the pattern was opposite to the expected in disturbed sites, with forest interiors richer than edges. Species composition differed between habitats and disturbance degrees, and portions of continuous forest were richer than forest patches. Furthermore, the galling fauna of forest patches was a subset of the continuous forest. Results strengthen the relation between vegetation distribution patterns and galling insects, which indirectly responded to edge and disturbance effects acting on their host plants. In Chapter 2 it is pioneering presented an inventory of insect galls from Araucaria forest, referring to the galls collected to the study presented in first chapter. Galling insect species and their host plants are listed, with information about gall morphology and occurrence in sites sampled. Fifty seven galling insect species were found (mostly Diptera: Cecidomyiidae), in 43 host plants belonging to 18 plant families. Galls were predominantly induced on stem or buds, glabrous, isolated, fusiform and green. Myrtaceae, Asteraceae e Melastomataceae were the most representative plant families. Total raw values of galls per habitat or site were similar between forest edge and interior, but were relatively higher in the recovering area and in continuous forests, the latter embracing a great number of galls occurring on forest patches. The existence of areas without disturbance by cattle grazing and fire management was important to the conservation of galling insect fauna, which can establish and



keep their populations. Knowledge of the diversity of these organisms is a key factor to the development of clearer actions seeking its preservation.

**Key-words:** Araucaria forest, diversity, forest patches, insect galls.

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## Introdução

### Efeito de borda e distúrbios antrópicos em florestas

Os ecossistemas encontram-se distribuídos no espaço de forma que, ao longo de sua extensão, existem zonas de transição com ecossistemas adjacentes, inicialmente denominadas ecótonos (Clements 1907). Diferente desta situação natural, grande parte dos ecossistemas encontra-se fragmentada devido a processos de eliminação da cobertura vegetal original (desmatamento, queimadas) e substituição por monoculturas ou áreas construídas (Saunders et al. 1991, Ehrlich, 1997). Os remanescentes de habitats naturais acabam imersos nestas áreas, denominadas matrizes antropizadas (Saunders et al. 1991). As zonas de transição entre os componentes desta paisagem fragmentada são denominadas bordas, e caracterizam-se por serem transições abruptas cuja influência sobre os organismos é conhecida como efeito de borda (Murcia 1995).

Desde a criação do termo referindo-se ao maior número de espécies cinegéticas em paisagens compostas por diversas manchas de habitat (Leopold 1933), a visão sobre o efeito de borda vem mudando (Ries et al. 2004). As bordas passaram de benéficas, por ocasionarem o incremento da diversidade, chegando a ser recomendadas em manejo conservativo (Harris 1988, Yahner 1988), para armadilhas ecológicas (Gates & Gysel 1978, Chasko & Gates 1982), locais de baixa qualidade para espécies especialistas (Mills 1995, Burke & Nol 1998) e porta de entrada para espécies exóticas em áreas protegidas (Morgan 1998, Honnay et al. 2002).

Diante do crescente aumento do processo de fragmentação de habitats, diversos estudos tem sido desenvolvidos acerca do efeito de borda sobre os organismos, principalmente aves e plantas, tanto em termos de riqueza quanto de abundância (Murcia 1995, Ries et al. 2004). A resposta dos organismos é avaliada em vários tipos de bordas, seja com relação ao tempo de criação (recém-criadas ou mais antigas), ao manejo (sem manejo ou com desbaste da vegetação regenerante), ao tipo de matriz adjacente, e à fisionomia dos ecossistemas limítrofes (Ries et al. 2004, Harper et al. 2005).

As bordas certamente não são estáticas (Murcia 1995), e o mesmo pode ser dito da degradação por atividades antrópicas das florestas fragmentadas (Cochrane & Laurance 2002).

Tais atividades afetam consideravelmente as florestas, podendo até mesmo alterar a frequência de distúrbios naturais em escala regional (Cochrane & Schulze 1999). O efeito de borda, combinado aos distúrbios antrópicos e naturais, pode resultar na regressão das bordas e na diminuição do tamanho dos remanescentes florestais que, em último caso, podem entrar em colapso (Gascon et al. 2000).

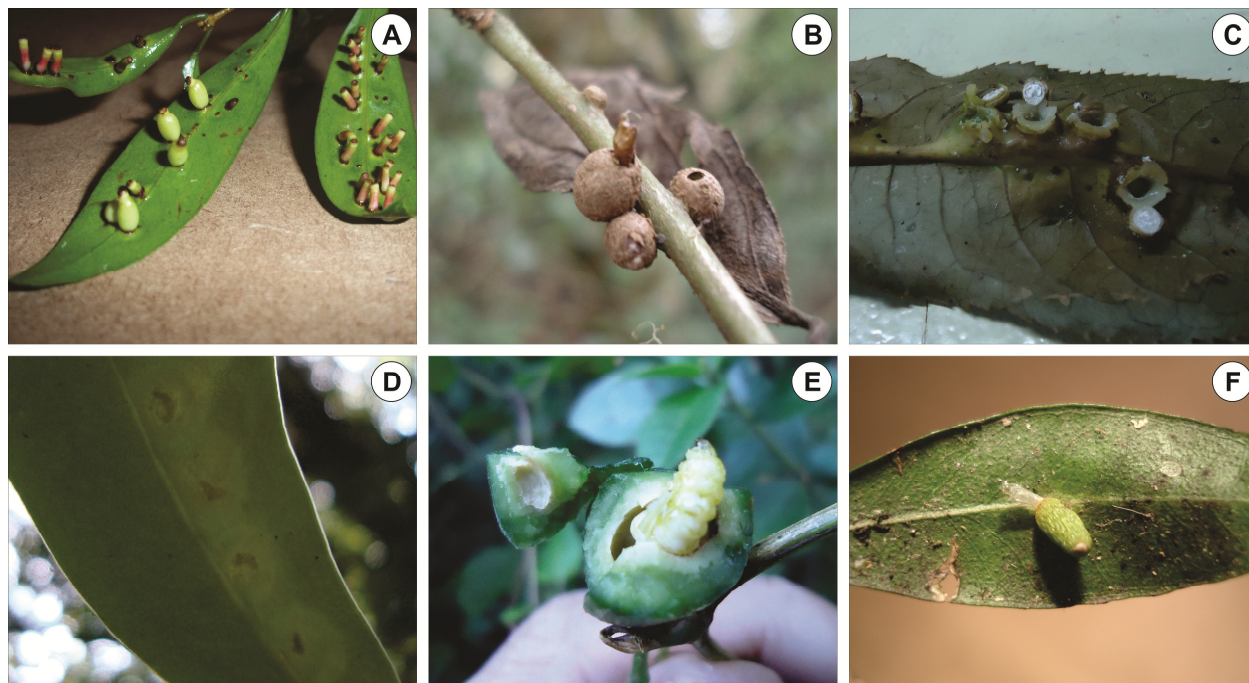
Os padrões de resposta variáveis e a dificuldade em se estabelecer comparações entre os estudos sobre o efeito de borda resultaram em algumas tentativas de se criar um arcabouço conceitual comum que permitisse entendê-los e compará-los (Murcia 1995, Cadenasso 2003, Ries & Sisk 2004, Ries et al. 2004). Modelos que contemplam a variedade de características associadas às bordas foram propostos (Ries et al. 2004, Ewers & Didham 2006), além de sugestões de como abordar tais características nos estudos (Murcia 1995, Harper et al. 2005). Considerei, para o presente estudo, os conceitos sugeridos para o efeito de borda segundo Murcia (1995).

Estudos sobre o efeito de borda envolvendo interações entre espécies, na revisão publicada por Murcia (1995), foram considerados escassos e restritos principalmente a interações entre aves e os predadores e parasitas de seus ninhos. Nos anos seguintes à referida publicação surgiram diversos sobre o assunto (e.g. Meiners et al. 2000, Ferguson 2004, Benítez-Malvido & Lemus-Albor 2005, Valladares et al. 2006). A especialização caracterizada por algumas interações entre espécies, característica que pode ser relacionada à maior probabilidade de extinção (McKinney 1997), reforça a importância dos estudos sobre efeito de borda envolvendo interações. Interações entre insetos herbívoros e plantas, por exemplo, são em sua maioria específicas (Bernays & Graham 1988), mas tem recebido pouca atenção, apesar de poderem afetar propriedades ecossistêmicas de forma significativa (Wirth et al. 2008).

### As galhas de insetos: hipóteses e mecanismos explicando padrões de distribuição

Os organismos escolhidos para conduzir as pesquisas foram os insetos indutores de galhas (Fig. 1). Galhas são estruturas formadas em plantas a partir do crescimento anormal dos tecidos, devido a uma atividade parasita, sendo que a maioria é induzida por insetos (Mani 1964, Darlington & Hirons 1975). As galhas proporcionam à larva dos insetos nutrição e abrigo de condições ambientais adversas e inimigos naturais (Price et al. 1987). Por serem conspícuas,





**Fig. 1.** Exemplos de galhas de insetos encontradas na Floresta com Araucária, São Francisco de Paula, RS, Brasil. A) Galhas foliares em *Eugenia pluriflora* DC.; B) galhas caulinares em *Chamissoa altissima* (Jacq.) Kunth; C) galhas foliares após a emergência dos insetos indutores em *Sapium glandulosum* (L.) Morong; D) galhas foliares translúcidas em *Rudgea parquioides* (Cham.) Müll. Arg.; E) galha de gema em *Cayaponia* sp., mostrando a larva do inseto indutor; F) galha foliar em *Siphoneugena reitzii* D.Legrand.

persistentes, morfologicamente diversas (Price et al. 1998) e hospedeiro-específicas (Carneiro et al. 2009), as galhas de insetos constituem uma ótima ferramenta para estudos ecológicos, de identificação de padrões geográficos e dos possíveis mecanismos que produzem tais padrões (Fernandes & Price 1992).

Diversas são as hipóteses sobre o valor adaptativo do hábito galhador (Price et al. 1987) e sobre diferenças na riqueza de insetos galhadores nos ecossistemas (Fléck & Fonseca 2007). Para a compreensão dos padrões esperados para a riqueza de galhas em relação ao efeito de borda, selecionamos três hipóteses. A hipótese da sincronização de recursos prevê que ecossistemas caracterizados pelo brotamento sincronizado das plantas apresentariam maior riqueza de insetos galhadores (Mendonça 2001). Já a hipótese da concentração de recursos se baseia na relação positiva entre densidade de recursos e riqueza de insetos herbívoros (Root 1973). Por fim, a hipótese do estresse higrotérmico propõe que a riqueza de insetos galhadores é maior em áreas caracterizadas por altas temperaturas, baixa umidade do ar, e vegetação escleromórfica (Fernandes & Price 1988). Plantas pioneiras são favorecidas nas bordas de florestas, por serem

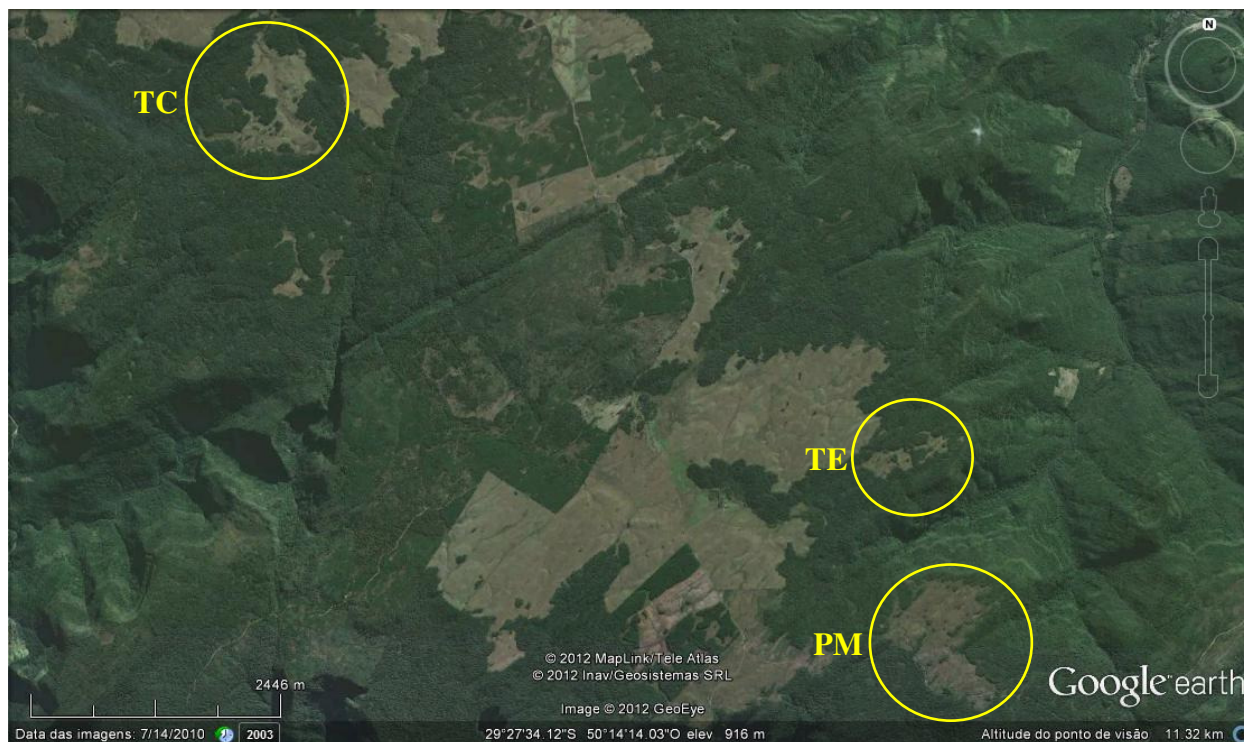
intolerantes à sombra (Nascimento et al. 2006, McDonald & Urban 2006), e além disso caracterizadas por rápido crescimento, com alta produção de folhas ao longo do ano (Coley 1983) e crescimento agregado (Melo & Tabarelli 2003). Consequentemente, espera-se que bordas de florestas possuam maior diversidade de galhas.

## Influência do efeito de borda e distúrbios antrópicos sobre a fauna de insetos galhadores

O efeito de borda sobre a fauna de insetos galhadores é um tema pouco abordado, presente em somente dois estudos (Julião et al. 2004, Martinez et al. 2005) em uma revisão (Wirth et al. 2008), e um estudo recentemente publicado (Araújo et al. 2011). Os estudos demonstraram tanto maior riqueza e abundância de galhas em uma única espécie de planta hospedeira (Martinez et al. 2005, Araújo et al. 2011), quanto valores semelhantes destes parâmetros para a fauna de galhadores no bioma Pantanal (Julião et al. 2004).

Para testar o efeito de borda sobre a fauna de insetos galhadores, desenvolvi estudos em bordas existentes em um mosaico campo-floresta, com foco para as florestas. Este mosaico vegetacional é característico de uma região conhecida como Campos de Cima da Serra, no Planalto Nordeste do Estado do Rio Grande do Sul, e é constituído por manchas de Floresta com Araucária (regionalmente conhecidas como capões) imersas em áreas de campo (Oliveira & Pillar 2004, Behling & Pillar 2007). Os capões são considerados núcleos de avanço da floresta sobre o campo, e não remanescentes de uma floresta contínua preexistente (Pillar & Quadros 1997, Behling 2002, Oliveira & Pillar 2004, Behling & Pillar 2007). Vale ressaltar que este mosaico vem sendo mantido por atividades antrópicas tais como queimadas, criação de gado e atividade madeireira (Behling & Pillar 2007).

Em um dos locais estudados, o Centro de Pesquisas e Conservação da Natureza Pró-Mata (PM, Fig. 2), pastejo e manejo por fogo estão excluídos desde 1994 (Oliveira & Pillar 2004), o que é uma situação peculiar para a região. As bordas ali presentes podem ser classificadas como sem manejo (*advancing edges*, Murcia 1995), caracterizadas pelo avanço da floresta sobre o campo através de substituição e estabelecimento de espécies arbustivas e arbóreas em lugar das gramíneas adjacentes (Machado 2004, Oliveira & Pillar 2004). Nas fazendas vizinhas ao PM amostradas, Fazenda Três Estrelas (TE) e Três Cachoeiras (TC, Fig. 2), assim como na maioria



**Fig. 2.** Vista aérea das áreas de estudo. Centro de Pesquisas e Conservação da Natureza Pró-Mata (PM), Fazenda Três Estrelas (TE) e Fazenda Três Cachoeiras (TC). Fonte: Google Earth (2012), disponível em <http://earth.google.com>

das propriedades rurais da região, a criação de gado e o manejo por fogo persistem, e os capões são mantidos para utilização do gado devido ao sombreamento que proporcionam. Desta forma, pude comparar bordas em processo de recuperação e bordas ainda sob o efeito de tais distúrbios.

Alguns estudos apontam que, quando possuem tamanho muito reduzido, fragmentos ou manchas florestais podem ser constituídos inteiramente por ambientes característicos de bordas (Ries et al. 2004, Ewers & Didham 2006). Uma vez que as manchas florestais existentes nos locais de estudo são pequenas (menores que 1 ha.), foram amostradas também regiões de borda da floresta contínua circundante, de forma a estabelecer comparações entre as bordas nestas formações florestais.

A dinâmica da vegetação nas manchas de Floresta com Araucária sem influência de fogo e pastejo indicam a expansão radial das manchas e um processo de reestruturação interna (Machado 2004, Duarte et al. 2006). Mesmo com a influência dos distúrbios, a partir do histórico de formação das manchas e dos padrões de colonização da vegetação (Duarte et al. 2006), é possível presumir que estas constituam subconjuntos da floresta contínua vizinha, caracterizando

um padrão aninhado das comunidades. Assim, espera-se que a fauna de insetos galhadores apresente um padrão semelhante ao da vegetação, uma vez que sua riqueza e distribuição são diretamente relacionadas à composição da vegetação.

Diante das respostas esperadas para a fauna de insetos galhadores ao efeito de borda e a distúrbios, testei se a riqueza de galhadores é maior na borda quando comparada ao interior de formações florestais (floresta contínua e manchas florestais) em áreas submetidas a distúrbio por pastejo e manejo por fogo e uma área em regeneração após a exclusão do distúrbio. Além disso, testei diferenças na composição de galhadores entre borda e interior, e também entre formações florestais e tipos de distúrbio. A conformação da vegetação em mosaico me permitiu testar, adicionalmente, se a fauna de galhadores das manchas apresentava o padrão aninhado em relação à da floresta contínua circundante. Estes testes são apresentados no Capítulo 1.

## Conhecimento taxonômico dos insetos galhadores

Os insetos são um grupo relativamente pouco conhecido (Chapman 2009), e o mesmo acontece para a fauna de insetos galhadores, com uma estimativa de 132,000 espécies existentes (Espírito-Sando & Fernandes 2007). No entanto, a família Cecidomyiidae (Diptera), o táxon mais representativo dentre os insetos galhadores, possui somente 6,131 espécies descritas (Gagné 2010). Seguindo o preceito de que a riqueza de insetos galhadores está ligada à riqueza de plantas, a região Neotropical, com uma flora megadiversa, permanece com uma representatividade muito abaixo da esperada, com seis vezes menos espécies de Cecidomyiidae descritas que a da região Paleártica (Gagné 2007).

Diante deste panorama, estudos sobre a diversidade de insetos galhadores são de fundamental importância. Apesar do aumento do número de publicações de listas de espécies de insetos galhadores, nem sempre os pesquisadores avançam na identificação dos organismos além do nível de família. Taxonomistas de Cecidomyiidae recomendam que ecólogos esforcem-se para obter as fases do desenvolvimento dos insetos necessárias para a sua devida identificação e descrição taxonômica, e não fiquem restritos somente ao registro da diversidade destes insetos através de suas galhas (VC Maia, comunicação pessoal). Seguindo esta recomendação, e com o intuito de contribuir para o conhecimento taxonômico desta fauna pouco conhecida, procedi à obtenção do material necessário à identificação dos galhadores quando possível, além de

fornecer a identificação das plantas hospedeiras e dados sobre a morfologia das galhas, os quais apreseto no Capítulo 2.

# **Capítulo 1. Edge and anthropogenic disturbance effects on gall-inducing insects in natural forest-grassland boundaries<sup>1</sup>**

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## Abstract

Forest-grassland boundaries in South Brazil, despite naturally occurring over thousands of years, are sharp forest edges commonly maintained by cattle grazing and anthropogenic fire. The vegetation dynamics of these boundaries is well known, but the same is not true for insect-plant interactions. Insects that induce galls on plants are expected to be more diverse on forest edges and affected by disturbances on the vegetation. We tested these predictions and compared Araucaria forest patches and portions of continuous forest (forest types), and also disturbed and recovering (17 years without grazing or anthropogenic fires) forest areas both for galling insect species richness and composition. We also tested the nestedness pattern between forest types for the galling faunas. We sampled 20 sites with equal number of samples for each combination of factors, conducting 60 min transects searching for galls at the edge and interior for each site. We conducted analysis for habitat (edge vs. interior) and site (edge and interior combined) species richness and composition. Disturbed forest interiors were richer than edges; recovering forest interiors were as rich as the edges; species composition differed between habitats and types of disturbance, but not between forest types. For sites, portions of continuous forest were richer than patches, while species composition only differed for disturbance. Galls of forest patches were a subset of the continuous forest only when there was vegetation recovery. We stress the importance of sampling reference areas, the continuous forest as opposed to forest patches or remnants. Areas without disturbance seem important to herbivores such as galling insects by allowing suitable hosts to persist. Edge effects, grazing and fire disturbances are determinant to the galling fauna of natural forest-grassland boundaries, which is strongly linked to vegetation patterns.

**Keywords:** Araucaria forest, cattle grazing, edge effect, forest patches, insect galls

## Resumo

As transições floresta-campo no sul do Brasil, apesar de ocorrerem naturalmente há milhares de anos, são bordas florestais abruptas comumente mantidas por pastejo e fogo antrópico. A dinâmica da vegetação destas transições é bem conhecida, mas o mesmo não se aplica para interações inseto-plantas. Espera-se que insetos indutores de galhas em plantas sejam mais diversos em bordas de florestas e afetados por distúrbios sobre a vegetação. Nós testamos estas predições e comparamos manchas de Floresta com Araucária e porções de uma floresta contínua (tipos florestais), e também áreas com distúrbio e em regeneração (17 anos com exclusão de pastejo e fogo), tanto para riqueza quanto composição de insetos galhadores. Nós também testamos o padrão de aninhamento da fauna de insetos galhadores entre os tipos florestais. Amostramos 20 locais com igual número de amostras para cada combinação de fatores, através de transecções de 60 min procurando por galhas, na borda e no interior de cada local. Fizemos análises para riqueza e composição de espécies para habitat (borda *vs.* interior) e local (borda e interior combinados). Os interiores de florestas com distúrbio foram mais ricos que as bordas; os interiores de florestas em regeneração foram tão ricos quanto as bordas; a composição de espécies diferiu entre habitats e graus de distúrbio, mas não entre tipos florestais. Para locais, porções de floresta contínua foram mais ricas que manchas, enquanto a composição de espécies só diferiu para graus de distúrbio. Galhas de manchas florestais foram um subconjunto da floresta contínua somente em caso de regeneração da vegetação. Reforçamos a importância de amostrar áreas de referência, tal como a floresta contínua em relação às manchas ou remanescentes florestais. Áreas sem distúrbio parecem ser importantes para herbívoros tais como os insetos galhadores por permitirem que hospedeiros apropriados persistam. Efeito de borda e distúrbio por pastejo e fogo são determinantes para a fauna de insetos galhadores em transições floresta-campo naturais, que é fortemente relacionada aos padrões da vegetação.

**Palavras-chave:** efeito de borda, Floresta com Araucária, galhas de insetos, manchas florestais, pastejo.



## Introduction

Forest edges are often ecologically different from the forest core since they are exposed to different conditions such as higher temperature and lower humidity (Williams-Linera 1990, Laurance 2001, Ries et al. 2004). Furthermore, energy, material and organisms flow through edges between adjacent ecosystems (Cadenasso et al. 2003), and the consequence of this interaction is known as the edge effect (Murcia 1995). This might result in an altered community structure and composition near the edge, as primary and secondary responses to the edge creation (Harper et al. 2005). These observed edge responses can be influenced by a series of ecological factors and any ecological characteristics of the organism, but when edge type is maintained the responses are quite consistent (Ries et al. 2004).

Edges differ depending on the age and maintenance process involved. Newly created edges are more open and less developed than older ones (Harper et al. 2005). Maintained edges are often abrupt and do not show a regeneration structure that could in that case form a buffer (Murcia 1995, Harper et al. 2005). There are few studies on edges that are not maintained, also called regenerating edges (Harper et al. 2005), on which a decay in edge penetration 5-10 years after edge creation is expected (Williams-Linera 1990, Camargo & Kapos 1995). Edge maintenance factors like grazing (Williams-Linera 1990, Buxton et al. 2008) or fire (Heringer & Jacques 2001) can affect the woody regeneration process in many grassland-forest ecotones. Under intense grazing and fire regimes, patch contrast between forests and the surrounding grassland holds, but without these factors the contrast is softened while grasses and shrubs regenerate (Williams-Linera 1990, Oliveira & Pillar 2004).

Edge characteristics per se can directly alter vegetation structure and composition (Harper et al. 2005) or animal distribution (Ries & Sisk 2010) separately, but can also alter animal-plant interactions (Fagan et al. 1999, Murcia 1995, Wirth et al. 2008). The same was found for edges with grazing activity (Tadey & Farji-Brener 2007) and fire (Knight & Holt 2005). However, studies concerning the effects of edges on species interactions are mostly about nest predation and brood parasitism, and much more scarce for other interactions (Murcia 1995), although more studies regarding the issue have been published since (e.g. Meiners et al. 2000, Ferguson 2004, Benítez-Malvido & Lemus-Albor 2005, Valladares et al. 2006). The interaction between gall-inducing insects and host plants is poorly evaluated for edge effects, with only two

studies (Julião et al. 2004, Martinez et al. 2005) present in a recent review (Wirth et al. 2008) and a later one (Araújo et al. 2011).

Galls are the abnormal growth of plant tissue induced by another organism, most of them insects (Mani 1964). The relationship between host plant and gall inducing insects is considered parasitic, because the galler has a negative impact on the host plant (Price et al. 1987), as well as being host-specific for most of them (Carneiro et al. 2009). Two hypotheses were suggested to best explain the adaptive significance of insect gall formation: nutrition and microenvironment (Price et al. 1987). The first one states that galls provide better nutrition to the insect larva, and the second that the insect is protected inside the gall from external variations in humidity and temperature. These hypotheses were extended to account for galling species richness patterns as a way to explain biogeographical trends. Thus higrothermally stressed ecosystems with scleromorphic vegetation would harbor a more diverse galling fauna (Price et al. 1998). Unfortunately, little is mentioned about the ecological causes of the patterns (see Mendonça 2001), while most ecological studies focus on patterns of species distributions among ecosystems (Fernandes & Price 1991, 1992, Gonçalves-Alvim & Fernandes 2001, Mendonça et al. 2010) or altitudinal gradients (Fernandes & Lara 1993, Blanche & Ludwig 2001) and present many other hypotheses to explain the patterns found (Fernandes & Price 1988, Fernandes et al. 1994, Price et al. 1998).

We considered three hypotheses on galling species richness that would best explain the edge effect on gall-inducing species richness. Firstly, the resource synchronization hypothesis predicts higher galling species richness in ecosystems with synchronous leaf flushing (Mendonça 2001). Secondly, the resource concentration hypothesis states that more concentrated resources would harbor more herbivore species (Root 1973). Higher light availability at forest edges favors pioneer plant species (Nascimento et al. 2006, McDonald & Urban 2006), which grow fast, produce more leaves per year and tend to steadily produce young leaves throughout the year (Coley 1983). These also commonly aggregate at the forest edge (Melo & Tabarelli 2003). The third hypothesis is the harsh environment hypothesis, which states that gall species richness increases with temperature and dryness (Fernandes & Price 1988). Hence, forest edges would harbor higher galling insect species richness and a distinct species composition compared to the forest interior. This prediction for galling insects is opposite to the expectation of similar

herbivore richness between pioneer and climax plant species, although the latter is based on polyphagous insects (Basset 1996, Novotny 1994), which possibly alters the outcome.

The vegetation mosaic of *Campos* grassland and Araucaria forest in South Brazil, with natural forest patches sparsely disposed in a grassland matrix, readily allows studies of natural forest-grassland boundaries (Pillar & Quadros 1997, Oliveira & Pillar 2004). This vegetation pattern is a natural process occurring over thousands of years in this region (Pillar & Quadros 1997, Behling & Pillar 2007, Silva & Anand 2011), based on forest nucleation generally triggered by *Araucaria angustifolia* (Duarte et al. 2006a). Forest usually expands over grasslands, resulting from a vegetation dynamics that consists on the replacement and establishment of shrubby and woody vegetation instead of grasses (Oliveira & Pillar 2004). Furthermore, woody plants in forest patches have their dynamics associated with patch structure and development, which probably determines species establishment from the regional species pool (Duarte et al. 2006b). In some cases ‘insular fields’ are present, when a grassland matrix punctuated by forest patches is surrounded by continuous forest (Machado 2004), which would represent the species pool for the forest patches. This probably implies that the floristic composition of patches represents a subset of the surrounding forest, an idea not explicitly addressed in the above cited studies. The expected outcome from this scenery is different vegetation structure and composition along edges compared to forest interior (e.g. Fontoura et al. 2006) and in continuous forests compared to patches, possibly leading to distinct galling insect faunas in each habitat and forest type.

This landscape mosaic is subjected to anthropogenic disturbances such as grazing and human-induced fire regimes that play an important role in forest vegetation dynamics, and the exclusion of these disturbances determine marked differences on this dynamics (Oliveira & Pillar 2004). Edges under these disturbances are classified as maintained edges and as recovering edges when disturbances are absent (Murcia 1995, Harper et al. 2005). Galling insect fauna might respond differently between these edge types, due to differences in vegetation.

Studies that comprise reference areas compared to the ones undergoing anthropogenic disturbances allow valuable insights that demonstrate and reinforce the negative impacts such disturbances have on ecosystems (Kotze & Samways 2001). Moreover, looking at higher trophic levels is of capital importance as specialized consumers could be more easily lost from a given

ecosystem (McKinney 1997), especially galling insects which strictly depend on their host plants to complete their life cycle.

We tested whether galling insect species richness responds to: 1) habitat – forest edges and interiors; 2) forest type – continuous forests and forest patches; 3) type of disturbance – recovering and disturbed areas; with the expectation of being larger at the edges, for continuous forests and recovering areas. The same comparison was done for galling insect species composition. In addition, we tested whether the galling insect fauna of sites (interior and edge samples coupled) differed between forest formations and disturbance levels. The nestedness of the galling insect fauna in patches and surrounding continuous forest was also evaluated to verify whether the pattern suggested for the floristic composition is followed by the herbivores.

## Material and methods

### STUDY AREA

We conducted the study at São Francisco de Paula municipality, Rio Grande do Sul state, Brazil, in three localities: the Research and Nature Conservation Centre Pró-Mata (Centro de Pesquisas e Conservação da Natureza Pró-Mata, 29°29'05'' S, 50°12'25'' W, henceforth PM), Três Estrelas Farm (29°28'08'' S, 50°12'38'' W, TE), and Três Cachoeiras Farm (29°26'21'' S, 50°16'21'' W, TC). Regional climate is classified as Cfb according to Köppen's system (Moreno 1961), which corresponds to a subtropical rainy climate, with a uniformly distributed precipitation throughout the year, and warm summers. Annual mean temperature is 15.1 °C, and annual mean rainfall is 2086 mm (Hijmans et al. 2005).

The localities were chosen for their similar areas with natural forest patches surrounded by grasslands, themselves surrounded by a continuous *Araucaria* forest, characterizing what is known as insular fields. The areas differed in terms of type of disturbance. Only PM has no cattle grazing or burning practices (recovering area), which stopped in 1994, allowing an increase in forest regeneration and forest nucleation processes (Oliveira & Pillar 2004). The two other localities, TC and TE have extensive cattle grazing and periodic burning as disturbance factors (disturbed areas). The latter are representative examples of the regional landscape, where most natural patches are located in farms and maintained amidst grasslands to be used by cattle for protection from insolation and wind. There were clear visual differences in the vegetation

between recovering and disturbed areas. Even though we did not collect data to confirm the differences, disturbed areas had forest formations affected by cattle trampling, with a much sparser understory, also reported by Duarte et al. (2006b) for the same region, and shorter grasslands and abrupt edges compared to recovering areas.

## SAMPLING

We sampled 20 sites classified in two forest types – ten portions of continuous forest and ten natural forest patches – five of each at PM, three at TC and two at TE (i.e. ten sites for each type of disturbance). Samples were performed in five occasions: December 2010, and April, May, June and September 2011; there is apparently no clear seasonality for galls of this region (Dalbem & Mendonça 2006). The patches ranged in size from 0.06 to 0.56 ha. At each site we sampled edge and interior. Edge was defined as the transition between the trees and grassland, following an imaginary line connecting the plant individuals over 2m tall that touched the crown of at least another such plant. The interior of continuous forest portions was restricted to a strip until 25 m away from the edge transect inspected, while patch interior was the area surrounded by the edge, in order to standardize the samples in terms of range inspected for each forest type. Each forest interior and edge pair comprised a forest site; the latter were at least 500 m far from each other to ensure independence.

At each sampled site we performed a 60 min transection at the edge and another at the interior actively searching for galls, following the methodology proposed by Julião et al. (2004). We collected galls and plant branches for identification. Galls were separated in morphotypes, dissected under stereomicroscope and put in plastic pots to rear adults. Gall inducers were identified down to order or family whenever possible, or to more specific taxonomic levels helped by specialists.

## DATA ANALYSES

Because samples were paired for each site, we treated species richness in two different ways: 1) *habitat species richness* meaning richness recorded in each sample (edge and interior habitats) at each site (patch or forest portion); and 2) *site species richness* as habitat species richness coupled for each site, considering co-occurrence as a single record. Similarly, composition considering sites resulted from a combination of composition for habitats of the

same site, co-occurrence being a single record as well. All analyses were performed in the R environment (R Development Core Team 2011).

#### *Edge effect on habitat species richness and composition*

We performed a two-way ANOVA using the difference (D) between edge (E) and interior (I) richness ( $D = E - I$ ) as the response variable and forest formation and type of disturbance as predictor variables. The edge effect on galling insect composition was accessed with a permutational multivariate analysis of variance (permutational MANOVA, Anderson 2001) using the Sørensen index (9999 permutations) including three factors (habitat, forest formation and disturbance) and the interactions among them (Vegan package v. 1.17-9, Oksanen et al. 2011). The same analysis was performed for host plant species composition. All analyses involving galling insect species composition were explored with ordination diagrams resulting from Principal Coordinates Analyses (PCoA) of qualitative data (Sørensen dissimilarity index).

#### *Site species richness and composition*

The test for paired samples of edge and interior of each forest unit in terms of forest formation and disturbance affecting galling species richness was performed using a two-way ANOVA. Likewise, we compared species composition under the same factors using a permutational MANOVA (Sørensen dissimilarity index, 9999 permutations).

#### *Nestedness tests for continuous forests and forest patches*

We evaluated whether patch species composition is a subgroup of the surrounding continuous forest with a nestedness metric based on overlap and decreasing fill (NODF; Almeida-Neto et al. 2008). We used site species composition for this analysis separated for recovering and disturbed areas because they were distinct in terms of composition (see results). Our interest was to evaluate nestedness between patches and continuous forests, so we calculated NODF only for rows of 50 matrices corresponding to all possible pairs of a forest portion and a patch (25 for each type of disturbance), with the row of a portion of continuous forest placed above the row of a forest patch. We used a 1-tailed paired *t*-test to verify whether the observed nestedness was larger than the expected, which was obtained by two null models. The null models, SIM1 (rows equiprobable, columns equiprobable) and SIM3 (rows equiprobable,

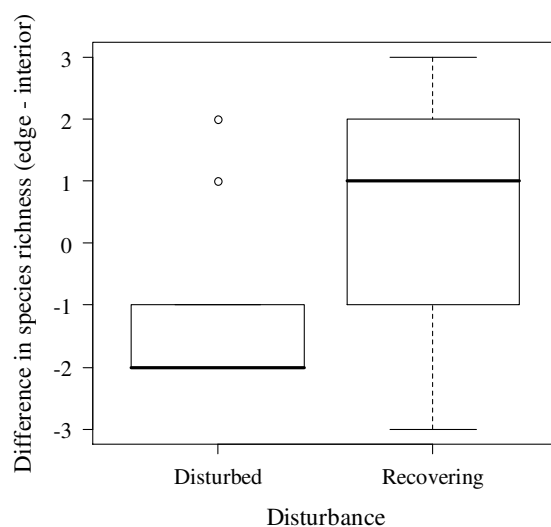
columns fixed), differed in rearrangement possibilities, while SIM1 is less conservative than SIM3 (Gotelli 2000), and were both used as recommended by Ulrich (2009). The expected nestedness values were the averages of 10 random matrices generated by each null model for each pair, totaling 50 values to be compared to the observed nestedness.

## Results

We found 57 galling insect species on 43 host plant species, belonging to 18 plant families. Overall, 39 galling insect species occurred at the edge and 37 in the interior, 19 occurring on both. Forests together had 49 species, patches totalized 33 and 25 occurred on both. Recovering sites had 43 species, while disturbed sites had 31 and 17 were found on both. For host plants: 30 were at the edge and 26 in the interior, 13 occurring on both habitats; 38 were in continuous forests and 23 in patches, 18 in both forest types; 33 were in recovering sites and 24 in disturbed ones, 14 in both types of disturbance (see Chapter 2).

### *Edge effect on habitat species richness and composition*

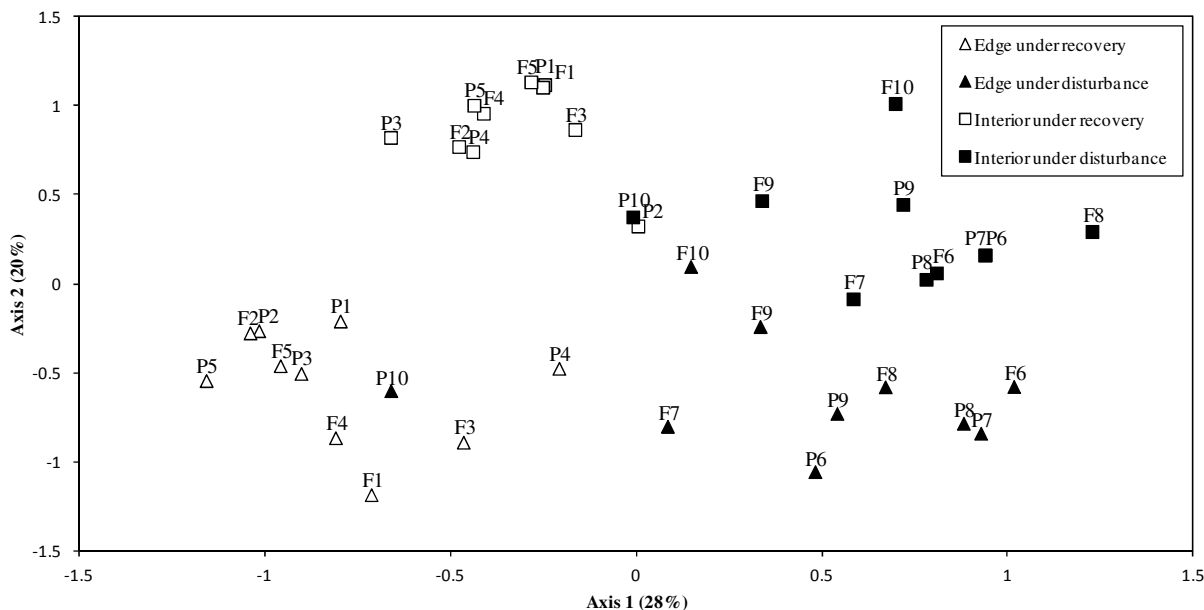
Using the difference between edge and interior richness as the response variable, disturbance was returned as a significant factor ( $F_{1,16} = 4.98$ ;  $p = 0.040$ ; Fig. 1), but not forest



**Fig. 1.** Boxplot of differences between edge and interior galling insect species richness among types of disturbance (recovering and disturbed).

formation ( $F_{1,16} = 0.55$ ;  $p = 0.467$ ) with no interaction among factors either ( $F_{1,16} = 0.98$ ;  $p = 0.336$ ). This meant that the forest interiors in disturbed sites were richer than edges, while there was no difference between habitats for recovering sites.

Species composition differed between edge and interior ( $F_{1,32} = 14.33$ ;  $p < 0.001$ ), and also between types of disturbance ( $F_{1,32} = 17.82$ ;  $p < 0.001$ ), but not for forest type ( $F_{1,32} = 1.47$ ;  $p = 0.196$ ) or for any interaction among factors (Fig. 2).



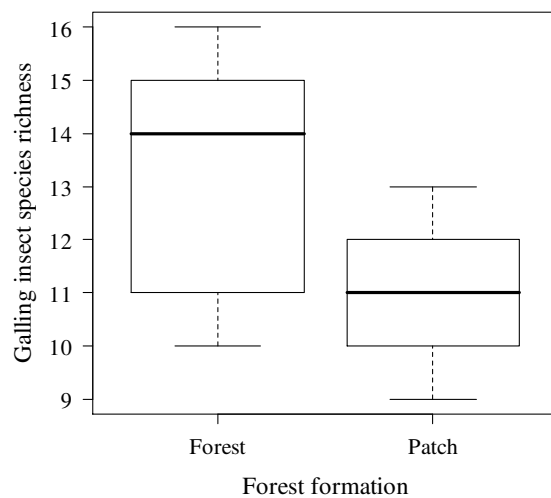
**Fig. 2.** Principal Coordinates Analysis (PCoA) plot of habitat (edge or interior) galling insect species composition on recovering (open symbols) and disturbed areas (solid symbols). Letters indicate forest type, F: continuous forest, P: patches, and numbers (1-10) indicate site sampled.

For host plants, species composition also differed between habitats ( $F_{1,32} = 16.33$ ;  $p < 0.001$ ), and also types of disturbance ( $F_{1,32} = 20.60$ ;  $p < 0.001$ ), but not for forest types ( $F_{1,32} = 1.66$ ;  $p = 0.140$ ) or any interaction among factors.

### *Site species richness and composition*

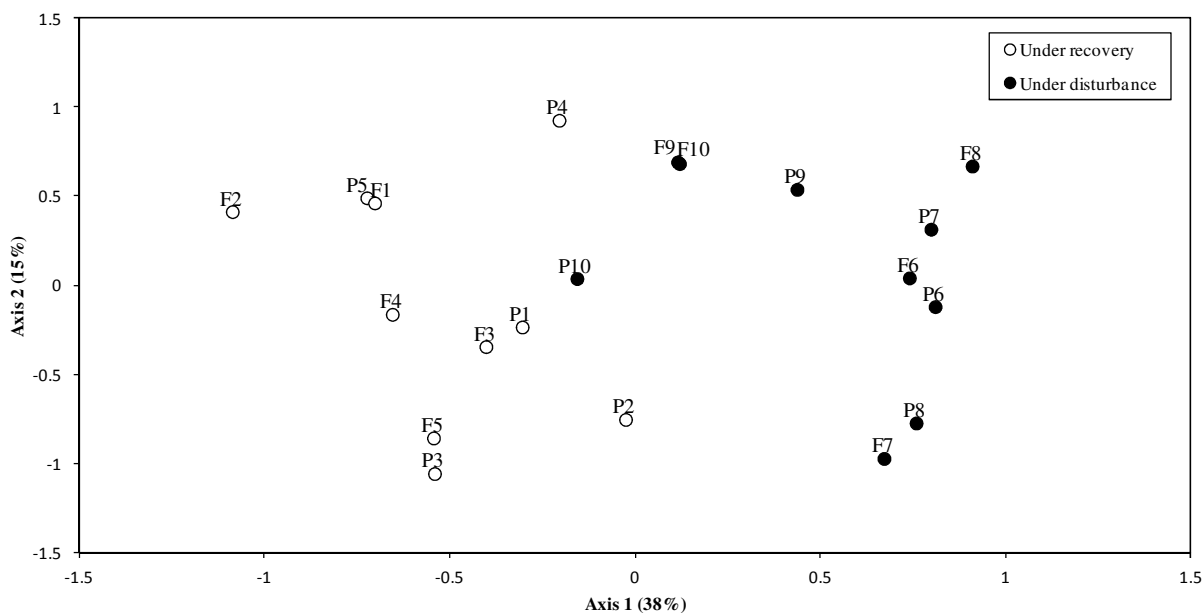
Galling species richness was statistically different among forest types ( $F_{1,16} = 8.42$ ;  $p = 0.010$ ; two-way ANOVA; Fig. 3), but not for type of disturbance ( $F_{1,16} = 3.41$ ;  $p = 0.083$ ) or the interaction between factors ( $F_{1,16} = 1.11$ ;  $p = 0.307$ ).





**Fig. 3.** Boxplot for galling insect species richness between forest types (continuous forest and patches).

When we considered site species composition, type of disturbance was the only significant factor ( $F_{1,16} = 8.58$ ;  $p < 0.001$ ), with forest type ( $F_{1,16} = 1.02$ ;  $p = 0.378$ ) and factor interaction insignificant ( $F_{1,16} = 1.29$ ;  $p = 0.241$ ; Fig. 4).



**Fig. 4.** Principal Coordinates Analysis (PCoA) plot of site (portion of continuous forest or patch) galling insect species composition on recovering (open symbols) and disturbed areas (solid symbols). Letters indicate forest type, F: continuous forest, P: patches, and numbers (1-10) indicate site sampled.

### *Nestedness tests for continuous forests and forest patches*

Galling species composition of patches were a subset of the forest composition only for sites placed on the recovering area (mean nestedness = 48.35), for the rows equiprobable/columns equiprobable (paired  $t$  test:  $t_{24} = 2.26$ ,  $p = 0.033$ ) and for rows equiprobable/columns fixed null models (paired  $t$  test:  $t_{24} = 2.45$ ,  $p = 0.010$ ). However, composition was not nested for sites placed on the disturbed areas (mean nestedness = 41.95), for the rows equiprobable/columns equiprobable (paired  $t$  test:  $t_{24} = 1.62$ ,  $p = 0.118$ ) or for rows equiprobable/columns fixed null models (paired  $t$  test:  $t_{24} = 1.23$ ,  $p = 0.115$ ).

## Discussion

The higher species richness found for interior habitats in sites with disturbance was opposite to what we expected. This could be due to vegetation changes brought by cattle activity as visually noticed in the field and observed for mammalian herbivores in general (Tadey & Farji-Brener 2007 and references therein). In our case, edges were probably more strongly affected by cattle, which have a reflection on insect gall occurrence in this habitat compared to the forest interior. For some plants there might be a minimum plant size to be gall maker inducer-prone (Collevatti & Sperber 1997), which can be a determinant factor for gall occurrence in frequently grazed edges. Furthermore, fire favor grasslands instead of forests (Mayer & Khalyani 2011) and coupled with cattle grazing this is probably responsible for the maintenance of grasslands in this region – the current hypothesis is that forests should prevail considering the region climate with high precipitation levels (Pillar & Quadros 1997). Thus, areas where fire and grazing are excluded are characterized by forest expansion over grassland, with strong shifts in vegetation (Oliveira & Pillar 2004). The consequence of vegetation recovery on undisturbed edges seems to be that galling insect species can colonize their hosts and an equivalence of edge and interior richness is reached. Indeed, an increase in vegetation cover, richness and abundance of woody species, woody seedlings and herbaceous plants was recorded for a similar edge between *Araucaria* forest-grassland five years after cattle and fire exclusion (Fontoura et al. 2006).

Despite the similar species richness between habitats, edge and interior had different species composition, as we expected. Habitat species composition also differed between areas

under grazing and burning practices and the recovering ones. This reiterates the disturbance effect on the galling fauna, probably reflecting differences in vegetation composition: not only galling insect species composition differed but also host plant composition. Another study also found no differences in species richness between habitats for insect galls (Julião et al. 2004), albeit with no considerations about species composition or disturbance. The authors suggested the small size of patches justify similar richness between habitats. However, edge effect seems to affect species composition even in small forest patches. Sobrinho & Schoereder (2007) pointed out that ant species composition allowed them to notice a fragmentation effect that species richness alone would not. Additionally, similarities in species composition between edge and interior were not greater than 50% for small remnants, besides having a negative relation with remnant area.

Recovering and disturbed sites differed in species composition, once more showing the effect of disturbance on the galling insect fauna. Forests were richer in gallers than patches, as expected, but disturbance did not influence species richness despite the supposed impoverishment of vegetation and the lower total richness between disturbance types. Another mechanism that could affect galling species richness is based on plant species richness and composition (Fernandes 1992, Blanche & Westoby 1995, Wright & Samways 1998), which we did not consider for the expected differences between forest edge and interior habitats, but appears to have a great influence upon gallers on different forest types and disturbance degrees. In a study of land restoration using galls as bioindicators, Moreira et al. (2007) found an increase of 66% in galling insect species richness five years after restoration management started, and the authors attributed this to the increment in number of host plants and habitat complexity. Despite similar mean richness considering disturbance in our study, total richness was 39% higher for recovering sites compared to disturbed ones. This might indicate that disturbed sites maintain high species richness per site, with species evenly distributed in space.

Galling insect fauna followed the nestedness pattern expected for the floristic composition of this region, but only for recovering areas. For instance, nestedness of terrestrial gastropods was reported to increase after large-scale disturbances (Bloch et al. 2007). The large effect grazing and fire exert on patch plant composition might indirectly affect the galling fauna, which affects the expected nested pattern between patches and the surrounding continuous forest, reflecting the evenness in species distribution stated above.

It seems to be important to sample reference areas while studying fragments or patches, because an outcome like richness equivalence between edge and interior could be mistakenly interpreted as an artifact of patch size. For instance, here we report no difference between edge and interior for continuous forest either. We conclude that edge effects, grazing and fire disturbance are determinant to the galling fauna of natural forest-grassland boundaries. Furthermore, species composition is probably a better indicator of edge effects than species richness in the study of the galling insect fauna providing more detailed information on the extent and nature of the effects, as revealed in the faunal nestedness pattern as well. The three hypotheses on galling species richness considered as possible explanations for this outcome remain untested regarding insect galls and edge effects, but this study represents an evidence of their validity. Maintenance of areas without disturbance seem thus to be important to herbivores, especially host-specific ones such as galling insects, so that suitable hosts persist and avoid local extinctions of insects. In addition, galling insects and vegetation patterns appear strongly linked, strengthening the notion that at the community level the response shown by gallers mirrors that of the vegetation.

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## **Capítulo 2. Gall-inducing insects of an Araucaria Forest in South Brazil<sup>2</sup>**

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## ABSTRACT

Gall-inducing insects of an Araucaria Forest in South Brazil. Diversity of galling insects is reported for the first time in an Araucaria Forest. We address gall characteristics, host plant identification and the inducer identification and provide additional information about gall occurrence in forest edge and interior habitats and local forest types, either recovering or still under disturbance by fire and cattle grazing. After 40h of sampling we found 57 species of five insect orders, the majority of them Diptera (Cecidomyiidae), galling 43 host plant species, which in turn belonged to 18 host families. Stem and buds together, compared to leaves, harbored more galls, which were mostly glabrous, isolated, fusiform and green. Myrtaceae, Asteraceae and Melastomataceae were the most representative host families. Number of galls per habitat was proximately similar between forest edge and interior, but higher in recovering sites and continuous forests, the latter overlapping patches, probably indicating disturbance effects and that patches represent subsets of the continuous forest galling fauna. Similarities in gall characteristics probably result from spatial correlation in a larger scale driven by ecological and evolutionary processes and are worthy of further studies.

**KEYWORDS:** Cecidomyiidae, diversity, forest patch, host plant, insect galls.

## RESUMO

Insetos indutores de galhas em Floresta com Araucária no sul do Brasil. A diversidade de insetos galhadores é registrada pela primeira vez em Florestas com Araucária. Apresentamos características das galhas, identificação das plantas hospedeiras e dos indutores, incluindo informações sobre a ocorrência das galhas em bordas e interiores de florestas nas formações florestais locais, tanto em regeneração quanto ainda com presença de distúrbio por fogo e pastejo. Após 40h de amostragem encontramos 57 espécies de cinco ordens de insetos, a maioria delas de Diptera (Cecidomyiidae), induzindo galhas em 43 espécies de plantas hospedeiras, sendo estas pertencentes a 18 famílias botânicas. Caules e gemas em conjunto, comparados às folhas, tiveram mais galhas, que foram em sua maioria glabras, isoladas, fusiformes e verdes. Myrtaceae, Asteraceae e Melastomataceae foram as famílias de plantas hospedeiras mais representativas. O número de galhas por habitat foi aproximadamente similar entre a borda e o interior florestal, mas maior em locais em regeneração e florestas contínuas, esta última sobrepondo-se às manchas, provavelmente indicando os efeitos do distúrbio e o fato das manchas representarem subconjuntos da fauna de insetos galhadores da floresta contínua. As similaridades nas características das galhas provavelmente resultam de correlação espacial em uma escala maior, devido a processos ecológicos e evolutivos, e deveriam ser mais estudadas.

**PALAVRAS-CHAVE:** Cecidomyiidae, diversidade, galhas de insetos, mancha florestal, planta hospedeira.

## Introduction

Galls are the result of an abnormal growth induced on plants by different organisms, most of them insects (Mani 1964). The formation of a gall is essential to the inducers and is part of their life cycle, most of them being host-specific, especially those belonging to the dipteran family Cecidomyiidae (Carneiro *et al.* 2009a).

The host specificity implies a positive relationship between gall-inducing insect richness and plant richness, and an estimate of the global richness of gall-inducing insects based on this assumption reached an average of 132,930 species (Espírito-Santo & Fernandes 2007). Unfortunately, the family Cecidomyiidae (Diptera), the most speciose group of gall-inducing insects, has only 6,131 described species (Gagné 2010). Considering the remarkable seed plant richness in the Neotropical region, little is known of the Cecidomyiidae fauna there. Compared to other parts of the world, this fauna is about six times less rich than that of the Palearctic (Gagné 2007).

Gall inventories in Brazil increased in number in the last decades, and most biomes of the country were surveyed at least once (Santos *et al.* 2011 and references therein). However, most surveys focus on the Southeastern region (including cerrado, atlantic forest and peculiar ecosystems within these biomes) due to the concentration of taxonomists and research groups there.

In southern Brazil the first studies on gall-inducing insects were conducted by Tavares (1906, 1909) and Kieffer (1913), and since then they have been sparse. Lately, there were studies on the diversity of subtropical forests of the region (Dalbem & Mendonça 2006; Mendonça 2007; Mendonça *et al.* 2010) with a single new gall-midge genus and two species described from the region (Maia, Mendonça & Romanowski 1996; Maia *et al.* 2009). Despite the Araucaria forest being a relatively well-studied, very representative landscape (Ribeiro *et al.* 2009), its galling insect fauna remains unknown.

We report for the first time the diversity of galling insects in an Araucaria Forest, addressing gall morphological characteristics, host plant identification and the inducer identification. We provide additional information about gall occurrence at the edge and interior of continuous forests and natural patches, placed either on areas under recovery or still under disturbance by fire and cattle grazing.

## Material and methods

This research was carried out in the Pró-Mata Research and Nature Conservation Center (29°28'S, 50°13'W, henceforth PM) and two farms at the PM vicinity (Três Estrelas Farm 29°28'08'' S, 50°12'38'' W, TE; and Três Cachoeiras Farm, 29°26'21'' S, 50°16'21'' W, TC), all located at the municipality of São Francisco de Paula, Rio Grande do Sul State, southern Brazil. The study sites are located on a plateau at ca. 900 m a.s.l. with vegetation characterized by “Campos” grassland and Araucaria forest. PM has no cattle grazing or burning practices since 1994, but these are still happening at the nearby farms. Hence, forest types have been regenerating in the former (Oliveira & Pillar 2004) while management practices are still adopted constantly in the latter farms. The regional climate is classified according to Köppen as Cfb (Moreno 1961), which is a subtropical rainy climate, with a uniformly distributed precipitation throughout the year, and warm summers. The annual mean temperature is 15 °C, and annual mean rainfall is 2086 mm (Hijmans *et al.* 2005).

We sampled two forest types, continuous forests and natural forest patches. Samples were performed in five occasions: December 2010, and April, May, June and September 2011; which we consider not to affect our samples given the absence of seasonality for the gallers of this region (Dalbem & Mendonça 2006). Five of each forest type were in a recovering area (PM) and five were in disturbed areas (three at TC and two at TE), totalizing ten sampling sites. For continuous forests we considered portions of the forest adjacent to the grassland at least 500 m apart to guarantee independence. Forest patches were relatively small forest formations surrounded by grasslands ranging in size from 0.06 to 0.56 ha.

At each site we took one sample at the edge and one at the interior. In this study, we defined edge as the transition between the trees and grassland, following an imaginary line connecting the plant individuals over 2m tall that touched the crown of at least another such plant. In order to standardize the samples in terms of range inspected at the interior for each forest formation, this was restricted to a strip until 25 m away from the edge transect inspected on continuous forest portions, while it was the area surrounded by the edge for patches.

Edge and interior samples consisted of 60 min transections following the methodology proposed by Julião *et al.* (2004). During the sampling period we collected galls and plant branches for identification. Galls were separated in morphotypes (from now on called species; see Carneiro *et al.* 2009a) and later dissected under stereomicroscope. Galls were also placed in

plastic pots to rear adult insects. Gall inducers were identified down to the lowest taxonomic level possible, including the help of specialists on each group when available.

## Results

We found 57 galling insect species on five insect orders, of which 14 were undetermined. Galls occurred on 43 host plant species, belonging to 18 host families (Table I).

Most galls were induced by Diptera species, all belonging to the family Cecidomyiidae (54.4%), followed by Lepidoptera (8.8%), Hemiptera (7.0%), Thysanoptera (3.5%) and Coleoptera (1.7%), and unidentified inducers (24.6%). The galls were induced almost equally on leaves (36.8%) and stems (33.3%), but also buds (28.1%), and on both leaves and stems (1.7%). Mostly, galls were glabrous (78.9%) and occurred isolated from one another (80.7%). The most common shape was fusiform (43.9%), followed by globoid (26.3%), discoid (12.3%), conical (8.8%), cylindrical (5.3%) and amorphous (3.4%). The majority of galls were green (70.2%).

The most representative host plant families were Myrtaceae with 20 galls (35.0%), Asteraceae with eight (14.0%) and Melastomataceae with five (8.7%), totaling more than a half of all morphotypes. The same families had the highest number of host plant species, 12 (27.9%), eight (18.6%) and four (9.3%), respectively, likewise comprising together more than a half of all host plant species. The most representative genera in number of gall morphotypes were *Myrcia* with seven (12.3%), *Myrceugenia* with six (10.5%), and *Siphoneugena* with four (7.0%), all three belonging to Myrtaceae. The host plant species that harbored more gall morphotypes were *Siphoneugena reitzii*, with four, and *Myrcia guianensis* and *Ilex microdonta* with three morphotypes each.

Overall, 39 galling insect species occurred at the edge and 37 in the interior of forest formations, 19 occurring on both habitats. Recovering sites had 43 species, while disturbed ones had 31, with 17 common to both. Portions of continuous forests together had 49 species, while forest patches totaled 33 and 25 occurred on both (Fig. 4A). For host plants: 30 were at the edge and 26 in the interior, 13 occurring on both habitats; 38 were in continuous forests and 23 in patches, 18 in both forest types; 33 were in recovering sites and 24 in disturbed ones, 14 in both types of disturbance (Fig. 4B).

**Table I.** Gallling insect species and host plants of an Araucaria Forest in South Brazil. Host plants, gall morphology, gall maker and sites of occurrence (numbers represent sum of occurrences for the combination of factors, 10 is the maximum value).

Host plant Family and species	Gall morphology			Gall inducer	Site of occurrence				Figure
	Organ	Shape	Color		Recovering		Disturbed		
					Edge	Interior	Edge	Interior	
<b>Amaranthaceae</b>									
<i>Chamissoa altissima</i> (Jacq.) Kunth	stem	globoid	green	Cecidomyiidae		1 <sup>P</sup>	1 <sup>F</sup>	6	1A
	leaf / stem	amorphous <sup>1,2</sup>	green	<i>Clinodiplosis</i> sp. (Cecidomyiidae)	1 <sup>P</sup>	2	6	10	1B
<b>Anacardiaceae</b>									
<i>Lithraea brasiliensis</i> Marchand	stem	fusiform <sup>2</sup>	brown	Unidentified				1 <sup>P</sup>	1C
<b>Aquifoliaceae</b>									
<i>Ilex microdonta</i> Reissek	leaf	discoïd	green	Cecidomyiidae	6	4 <sup>P</sup>			1D
	leaf	globoid	green	Hemiptera	3		1 <sup>F</sup>		1E
	bud	globoid	green	Cecidomyiidae	5	8	1 <sup>F</sup>	2 <sup>P</sup>	1F
<b>Asteraceae</b>									
<i>Baccharis semiserrata</i> DC.	stem	globoid	green / brown	Unidentified	1 <sup>P</sup>				1G
<i>Baccharis</i> sp.	stem	fusiform <sup>2</sup>	green	Alycaulini (Cecidomyiidae)	3		8		1H
<i>Eupatorium serratum</i> Spreng.	stem	fusiform	green / brown	Unidentified	1 <sup>F</sup>				1I
<i>Mikania campanulata</i> Gardner	bud	globoid <sup>2</sup>	green / purple	Cecidomyiidae	1 <sup>F</sup>				1J
<i>Mikania paranensis</i> Dusén	stem	fusiform	green	Cecidomyiidae	1 <sup>F</sup>				1K
<i>Pentacalia desiderabilis</i> (Vell.) Cuatrec.	bud	conical	green	<i>Asphondylia</i> sp. (Cecidomyiidae)			1 <sup>F</sup>		1L
<i>Piptocarpha axillaris</i> (Less.) Baker	leaf (rib)	fusiform <sup>1</sup>	brown	Unidentified	2 <sup>F</sup>				1M
<i>Piptocarpha notata</i> (Less.) Baker	stem	globoid	green	<i>Resseliella</i> sp. (Cecidomyiidae)	1 <sup>F</sup>	3 <sup>F</sup>			1N
<b>Clethraceae</b>									
<i>Clethra uleana</i> Sleumer	bud	globoid	brown	Cecidomyiidae	2				1O
<b>Curcubitaceae</b>									
<i>Cayaponia</i> sp. 1	bud	fusiform <sup>1</sup>	green	Coleoptera	1 <sup>F</sup>				1P
<i>Cayaponia</i> sp. 2	bud	fusiform <sup>1</sup>	brown	Lepidoptera	1 <sup>F</sup>				1Q
<b>Euphorbiaceae</b>									
<i>Croton</i> sp.	bud	globoid	brown	Cecidomyiidae	2 <sup>F</sup>				1R
<i>Sapium glandulosum</i> (L.) Morong	leaf	conical	red	Psyllidae (Hemiptera)	3	1 <sup>P</sup>			1S
<b>Fabaceae</b>									
<i>Mimosa scabrella</i> Benth.	leaf	amorphous <sup>1,2</sup>	orange	Cecidomyiidae	1 <sup>F</sup>				1T
<b>Lauraceae</b>									
<i>Nectandra grandiflora</i> Nees	stem	fusiform <sup>2</sup>	brown	Unidentified		1 <sup>F</sup>			1U



Table I. Continued...

Host plant	Gall morphology			Gall inducer	Site of occurrence				Figure
					Recovering		Disturbed		
					Edge	Interior	Edge	Interior	
Family and species	Organ	Shape	Color						
<b>Lauraceae (cont.)</b>									
<i>Ocotea corymbosa</i> (Meisn.) Mez	leaf	conical	brown	Unidentified		1 <sup>F</sup>			2A
	stem	fusiform	brown	Unidentified		1 <sup>F</sup>			2B
<b>Melastomataceae</b>									
<i>Leandra</i> sp.	leaf	globoid <sup>1</sup>	green	Cecidomyiidae		2 <sup>F</sup>		1 <sup>F</sup>	2C
<i>Miconia hyemalis</i> A.St.- Hil. & Naudin	stem	fusiform	brown	Unidentified			1 <sup>F</sup>		2D
<i>Miconia pusilliflora</i> (DC.) Naudin	leaf (rib)	fusiform	green	Cecidomyiidae		1 <sup>P</sup>			2E
<i>Tibouchina sellowiana</i> Cogn.	stem	globoid	green / red	Lepidoptera	5		1 <sup>P</sup>	1 <sup>F</sup>	2F
	leaf / petiole	globoid <sup>1</sup>	green / red	Lopesiini (Cecidomyiidae)	5	1 <sup>F</sup>	1 <sup>P</sup>	3	2G
<b>Myrtaceae</b>									
<i>Calyptranthes concinna</i> DC.	bud	globoid <sup>2</sup>	green	Lasipteridi (Cecidomyiidae)			4	6	2H
	leaf	discoid	green / brown	Cecidomyiidae			1 <sup>P</sup>	1 <sup>F</sup>	2I
<i>Eugenia pluriflora</i> DC.	leaf	cylindrical	green / red	Cecidomyiidae				2 <sup>F</sup>	2J
<i>Myrceugenia euosma</i> (O.Berg) D.Legrand	stem	fusiform <sup>2</sup>	brown	Cecidomyiidae	8		10	5	2K
<i>Myrceugenia mesomischa</i> (Burret) D.Legrand & Kausel	bud	conical	green	Unidentified			1 <sup>F</sup>		2L
<i>Myrceugenia miersiana</i> (Gardner) D.Legrand & Kausel	bud	fusiform <sup>1</sup>	green / purple	Cecidomyiidae				2	2M
<i>Myrceugenia myrcioides</i> (Cambess.) O.Berg	leaf	fusiform	green	Unidentified		1 <sup>P</sup>			2N
	bud	fusiform	green	Cecidomyiidae				1 <sup>F</sup>	2O
<i>Myrceugenia oxysepala</i> (Burret) D.Legrand & Kausel	bud	fusiform	brown	Cecidomyiidae		1 <sup>F</sup>			2P
<i>Myrcia guianensis</i> (Aubl.) DC.	leaf	fusiform	green / red	<i>Holopothrips</i> sp. (Thysanoptera)	2 <sup>P</sup>		1 <sup>P</sup>	1 <sup>F</sup>	2Q
	leaf (petiole)	fusiform	green	Cecidomyiidae		2			2R
	bud	globoid	green / red	Cecidomyiidae	2	1 <sup>F</sup>	3	3	2S
<i>Myrcia hartwegiana</i> (O.Berg) Kiaersk.	leaf	discoid	green	Coccoidea (Hemiptera)				1 <sup>F</sup>	2T
	bud	globoid <sup>1</sup>	brown	Cecidomyiidae				1 <sup>F</sup>	2U
<i>Myrcia palustris</i> DC.	leaf	discoid	green / yellow	Coccoidea (Hemiptera)				1 <sup>F</sup>	3A
<i>Myrcia retorta</i> Cambess.	bud	fusiform <sup>1,2</sup>	green	Lasipteridi (Cecidomyiidae)	1 <sup>F</sup>	10	8	10	3B
<i>Siphoneugena reitzii</i> D.Legrand	stem	globoid	brown	Cecidomyiidae	1 <sup>P</sup>	9	4	7	3C
	leaf	cylindrical	green / red	<i>Holopothrips</i> sp. 2 (Thysanoptera)	1 <sup>P</sup>				3D

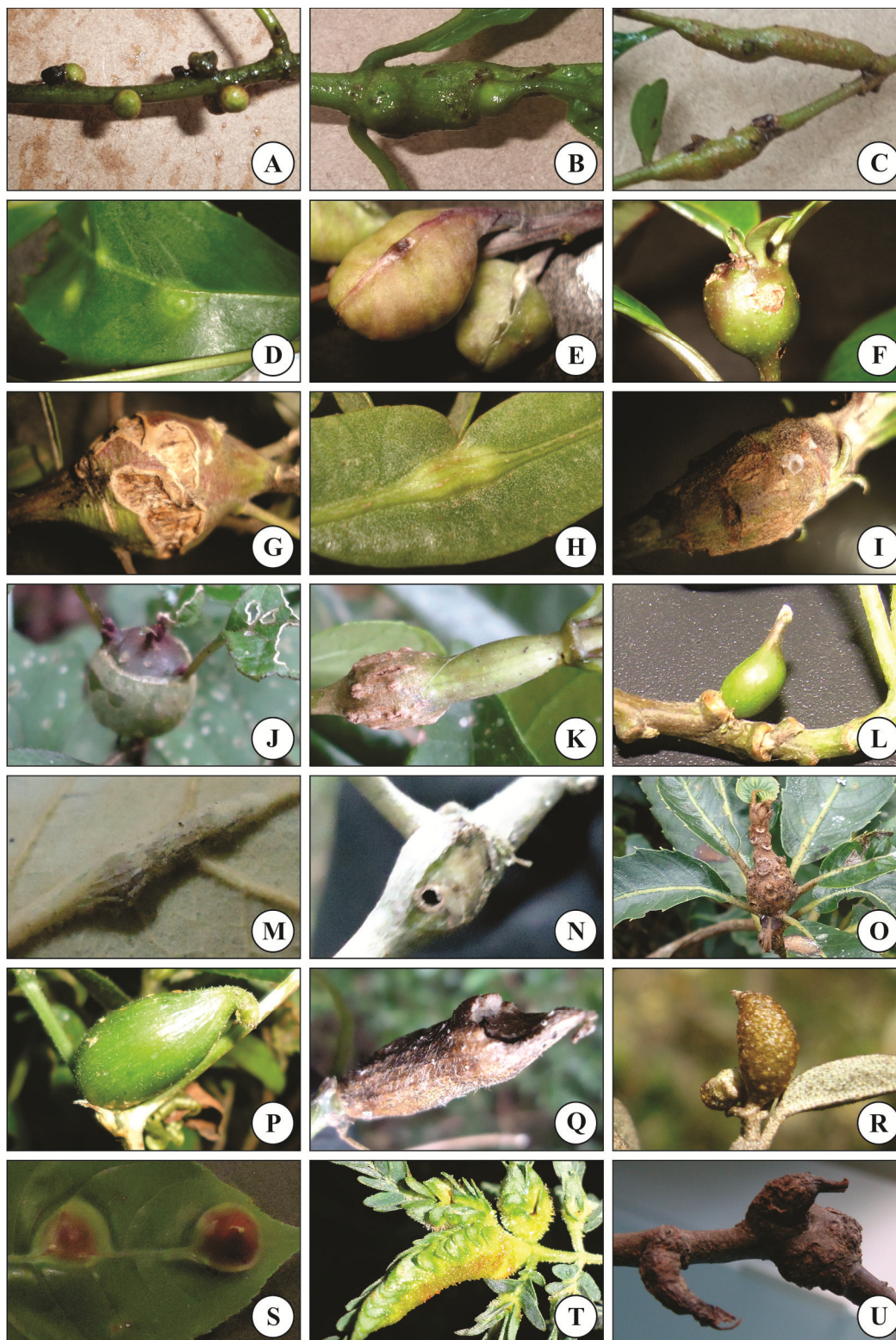
Table I. Continued...

Host plant Family and species	Gall morphology Organ    Shape    Color			Gall inducer	Site of occurrence				Figure
					Recovering		Disturbed		
					Edge	Interior	Edge	Interior	
<i>S. reitzii</i> (cont.)	leaf	cylindrical	green / yellow	Cecidomyiidae		1 <sup>F</sup>			3E
	bud	conical	green	Cecidomyiidae			8	8	3F
<b>Podocarpaceae</b>									
<i>Podocarpus lambertii</i> Klotzsch ex Endl.	stem	fusiform	brown	Cecidomyiidae	3		3		3G
<b>Primulaceae</b>									
<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	stem	fusiform	green	Lepidoptera	3	1 <sup>P</sup>	2 <sup>F</sup>		3H
<i>Myrsine lorentziana</i> (Mez) Arechav.	stem	fusiform	green / red	Lepidoptera	9	10	3	2	3I
<b>Proteaceae</b>									
<i>Roupala montana</i> Aubl.	leaf	discoid	green / brown	Unidentified	1 <sup>P</sup>				3J
	stem	fusiform <sup>2</sup>	brown	Unidentified	1 <sup>P</sup>				3K
<b>Rosaceae</b>									
<i>Rubus erythrocladus</i> Mart.	stem	fusiform <sup>1,2</sup>	green / brown	Unidentified			2		3L
<b>Rubiaceae</b>									
<i>Rudgea parquioides</i> (Cham.) Müll.Arg.	leaf	discoid	green	Cecidomyiidae		6	2 <sup>F</sup>	9	3M
<b>Sapindaceae</b>									
<i>Allophylus edulis</i> (A.St.- Hil. et al.) Hieron. ex Niederl.	stem	fusiform	green	Lepidoptera		1 <sup>F</sup>			3N
<b>Solanaceae</b>									
<i>Solanum</i> sp. L.	leaf	discoid <sup>1</sup>	green	Unidentified		1 <sup>P</sup>			3O

<sup>1</sup> pubescent gall, <sup>2</sup> gall with grouped chambers, <sup>P</sup> gall occurring only on forest patches, <sup>F</sup> gall occurring only on continuous forest.

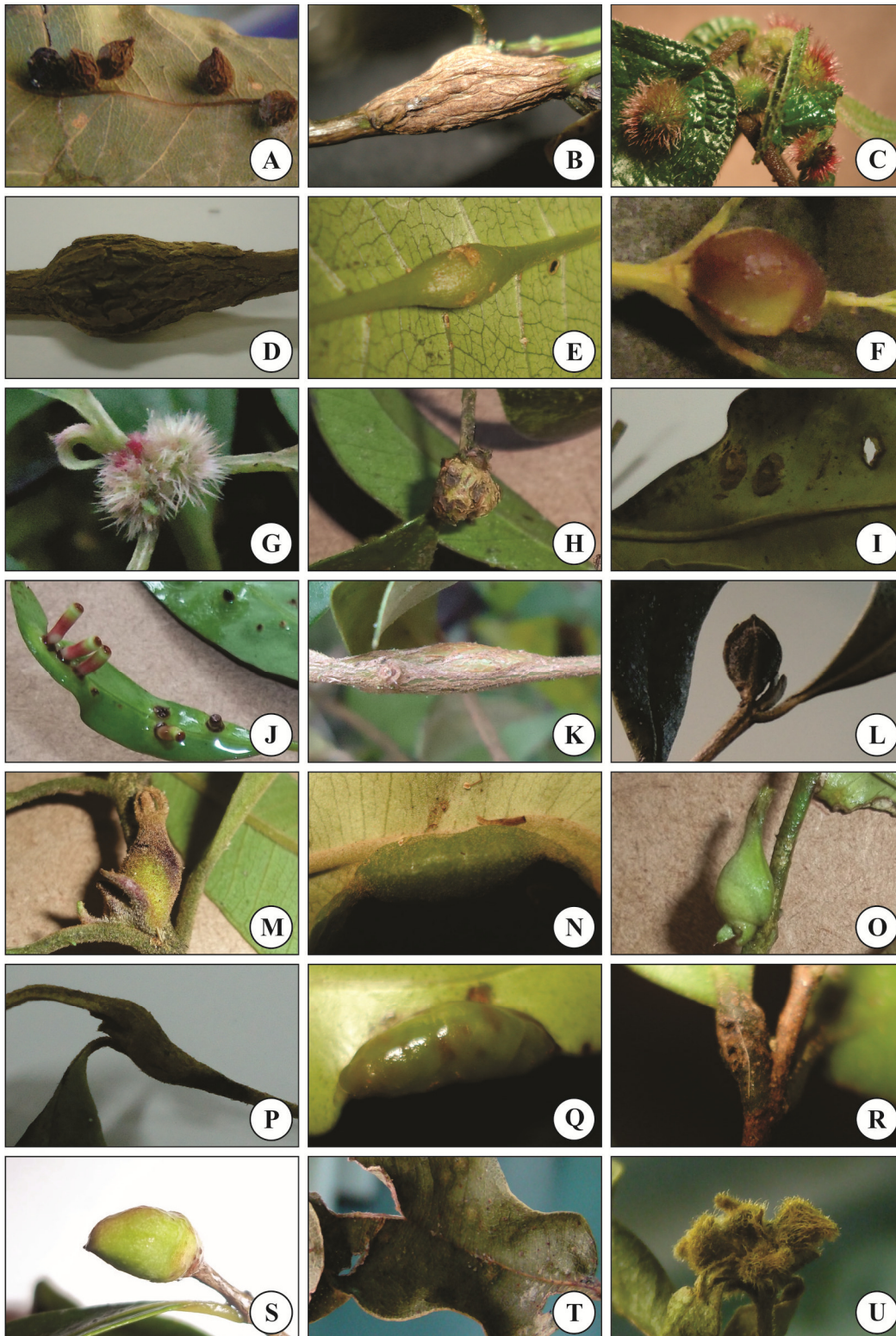
## Discussion

The total richness of galling insects found here (57) can be classified as intermediate considering the richness found by Araújo *et al.* (2011; 62 galling species) who themselves were comparing their result to other studies in terms of crude numbers. However it is important to account for differences among methods, at least in terms of time sampling effort. For instance, in a terra firme Amazon forest 309 gall morphotypes were recorded in 216 h of sampling (Almada & Fernandes 2011), and in natural forest patches of the Pantanal biome 133 gall morphotypes were recorded in 54 h of sampling (Julião *et al.* 2004). This approximates our results to the high

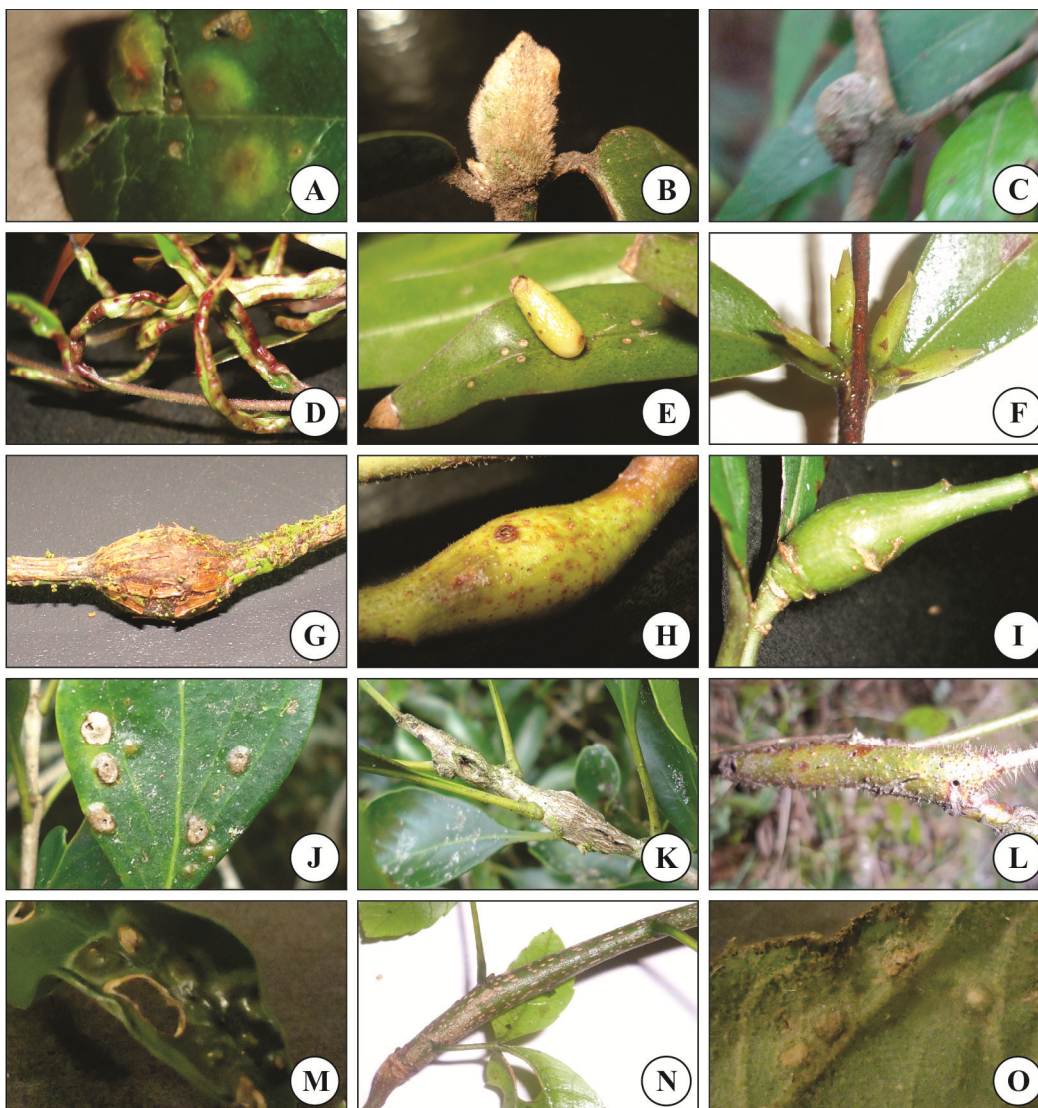


**Figure 1.** Galling insect morphotypes of an Araucaria Forest in South Brazil. A-B) *Chamissoa altissima*, C) *Lithraea brasiliensis*, D-F) *Ilex microdonta*, G) *Baccharis semiserrata*, H) *Baccharis* sp., I) *Eupatorium serratum*, J) *Mikania campanulata*, K) *Mikania paranensis*, L) *Pentacalia desiderabilis*, M) *Piptocarpha axillaris*, N) *Piptocarpha notata*, O) *Clethra uleana*, P) *Cayaponia* sp. 1, Q) *Cayaponia* sp. 2, R) *Croton* sp., S) *Sapium glandulosum*, T) *Mimosa scabrella*, U) *Nectandra grandiflora*.





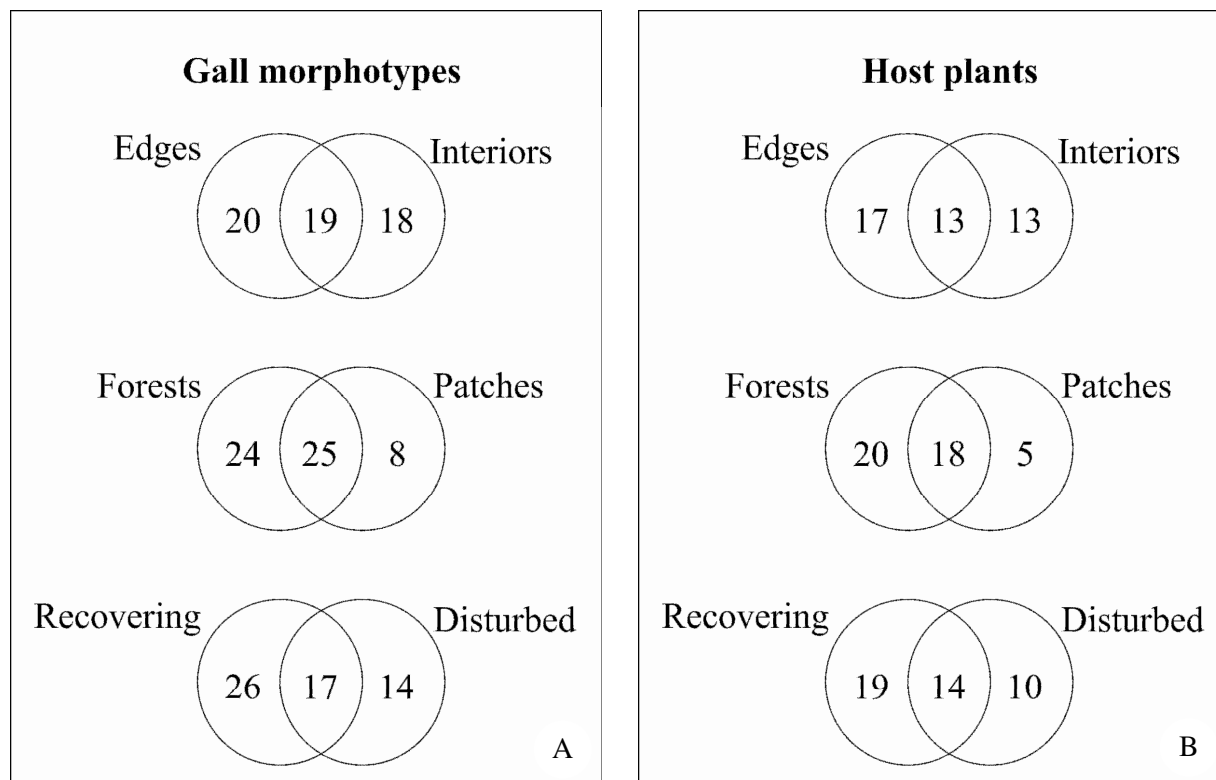
**Figure 2.** Galling insect morphotypes of an Araucaria Forest in South Brazil. A-B) *Ocotea corymbosa*, C) *Leandra* sp., D) *Miconia hyemalis*, E) *Miconia pusilliflora*, F-G) *Tibouchina sellowiana*, H-I) *Calyptanthes concinna*, J) *Eugenia pluriflora*, K) *Myrceugenia euosma*, L) *Myrceugenia mesomischa*, M) *Myrceugenia miersiana*, N-O) *Myrceugenia myrcioides*, P) *Myrceugenia oxyspala*, Q-S) *Myrcia guianensis*, T-U) *Myrcia hartwegiana*.



**Figure 3.** Galling insect morphotypes of an Araucaria Forest in South Brazil. A) *Myrcia palustris*, B) *Myrcia retorta*, C-F) *Siphoneugena reitzii*, G) *Podocarpus lambertii*, H) *Myrsine coriacea*, I) *Myrsine lorentziana*, J-K) *Roupala montana*, L) *Rubus erythrocladus*, M) *Rudgea parquioides*, N) *Allophylus edulis* (photography by Cristina R. Wenzel), O) *Solanum* sp.

richness found in the Amazon given that we recorded 1.42 galls/hour and Almada & Fernandes (2011) recorded 1.43 galls/hour. On the other hand, Julião *et al.* (2004) recorded 2.46 galls/hour. We hypothesize that this could be due to a larger area sampled in the latter study, together with longer distances among sampling sites, which would result in more chances of finding species restricted in range. Our samples, alternatively, were performed in a more restricted area with the galling fauna of patches representing either subsets of the continuous forest or being very similar to them (Chapter 1). Other issues may also interfere and direct comparisons are certainly tentative, but scale is a likely factor influencing richness in gall surveys.





**Figure 4.** Total numbers of gall morphotypes and host plants occurrence by habitat (edge and interior), forest type (continuous forests and patches) and type of disturbance (recovering and disturbed). A) Venn diagrams of the gall morphotypes, B) Venn diagrams of the host plants.

The most representative taxon of gall inducers was the dipteran family Cecidomyiidae, as is found for other ecosystems worldwide (Espírito-Santo & Fernandes 2007). This might be expected given that the family Cecidomyiidae is the most speciose group of gall-inducing insects (Gagné 2010). The other taxa also appear in many studies, but with clear differences between regions (Mani 1964; Espírito-Santo & Fernandes 2007). However, our study is most likely the single one to present detailed identification of Thysanoptera gall inducers, which are probably new species. It is important to stress that unidentified gallers were mostly from rare plants with few galls, which in turn were either open or attacked by parasitoids.

Galled organs did not show a strong predominance for leaves, with galls evenly distributed among plant organs. This trend is uncommon for insect galls, which are usually reported to occur predominantly on leaves (Mani 1964; Dreger-Jauffret & Shorthouse 1992). Only a few studies report more galls on stems (african savanna; Veldtman & McGeoch 2003) or stems and buds (rupestrian fields; Carneiro *et al.* 2009b). Interestingly, these studies were performed on areas geographically related to the ones of our study, either in terms of altitude

(Carneiro *et al.* 2009b) or southern location (Veldtman & McGeoch 2003). However, their explanations, despite being valuable, did not account for this geographic trend and its ecological and evolutionary implications, which we consider worthy of further studies.

The predominance of glabrous galls is widely reported, for instance, glabrous plants of the species *Arbutus xalapensis* (Ericaceae) had higher density of galls compared to the hairy conspecifics (Ezcurra *et al.* 1987). Considering gall occurrence, isolated galls were more frequent, as reported by other studies. Fernandes *et al.* (1988) hypothesized that galls which occur isolated would be favored because parasitoid pressure would be diminished due to the greater searching time implied by isolation.

The two host plant families with more gall morphotypes, Myrtaceae and Asteraceae, figure as important taxa in other vegetation types in South Brazil (Mendonça 2007; Mendonça *et al.* 2010), and even in other ecosystems throughout Brazil, as the cerrado (Gonçalves-Alvim & Fernandes 2001), rupestrian fields (Maia & Fernandes 2004) and restinga coastal forests (Maia *et al.* 2008). The importance of Melastomataceae, ranked as the third most representative host family, is not widespread, being more rarely found in Atlantic forest remnants (Fernandes *et al.* 2002) and in an Amazon forest (Almada & Fernandes 2011), despite being for a long time ranked as one of the richest in zoocecidea, along with the other two families (Houard 1933). Fabaceae hosted only one gall species in our study; it usually ranks high in most of the above cited gall inventories. This has been already pointed out by Mendonça (2007) based on another study conducted in South Brazil, a pattern derived perhaps from a lack of legumes in Araucaria forest relative to other Atlantic forest formations (Jarenkow & Waechter 2001).

At the genus level, *Myrcia* also appeared in another study as the most representative genus (Maia *et al.* 2008), but not *Myrceugenia* or *Siphoneugena*. The genera *Mikania* and *Eugenia*, accounting respectively for only two and a single gall species, were the genera with highest number of galls in another study in an Atlantic forest relatively close to the area sampled in this study, while *Myrcia* had only three galls and *Myrceugenia* and *Siphoneugena* did not have any (Mendonça 2007). This difference might reflect the absence of host species but also differences in these genera contribution to the flora of the region. The presence of “super-hosts” belonging to the most representative family and genera was expected (Mendonça 2007) but even Myrtaceae with *Siphoneugena reitzii* and *Myrcia guianensis* had relatively low numbers of gall species.

Total numbers of galling insect species occurrence by sites considering factors and habitats gives an idea of species distribution for Araucaria forests. Forest edges and interiors had similar richness, while disturbance seemed to negatively affect insect galls. As expected, continuous forests represent the species pool for forest patches given the higher species richness and similarity. Further analysis of these factors effects on the galling insects fauna are presented in Chapter 1.

This first report on the diversity of gall inducing insects from Araucaria forests constitutes an important contribution to the taxonomic knowledge of this group in the Neotropics. In general, gall characteristics follow trends already reported for the Neotropics and worldwide, sometimes more similar to studies performed in nearby ecosystems, probably reflecting a spatial correlation in a larger, biogeographical scale. We encourage more studies of gall-inducing insects in Araucaria forests in order to provide us with a clearer view of its biodiversity.

## Acknowledgements

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## Considerações Finais

A fauna de insetos galhadores em transições floresta-campo responde a alterações na vegetação, conforme esperado para esta guilda de insetos herbívoros parasitas altamente dependentes dos seus hospedeiros. Embora a resposta dos galhadores em número de espécies não tenha demonstrado a preferência destes organismos pelos ambientes de borda, conforme o esperado, esta reflete alterações na vegetação decorrentes de distúrbios antrópicos. Além disso, diferenças na composição de espécies considerando os ambientes de borda e interior de florestas e diferentes intensidades de distúrbios atuando sobre eles demonstram a importância da estrutura das comunidades na análise de padrões ecológicos.

Algumas similaridades encontradas nos padrões gerais das características morfológicas das galhas provavelmente resultam de correlação espacial em uma escala maior, devido a processos ecológicos e evolutivos, e deveriam ser mais estudadas. Além disso, a identificação dos insetos galhadores nos diversos ambientes, aliada aos estudos ecológicos, permite o estabelecimento de relações mais específicas, que explicam melhor os padrões encontrados, assim como contribuem para a ampliação do conhecimento sobre a diversidade destes organismos.

Em suma, a conservação dos insetos indutores de galhas em transições floresta-campo parece depender da existência de áreas com regeneração natural que possibilitem o estabelecimento e manutenção de suas populações, além de esforços direcionados ao conhecimento da sua diversidade que permitam idealizar o desenvolvimento de ações mais claras visando sua preservação.

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