# UNIVERSIDADE ESTADUAL DE CAMPINAS

## INSTITUTO DE BIOLOGIA

SECRETARIA
DE
PÓS-GRADUAÇÃO
I. B.

Mário Almeida Neto

# EFEITO DA DEGRADAÇÃO DE HABITAT SOBRE A ESTRUTURA DE INTERAÇÕES ENTRE PLANTAS E INSETOS FITÓFAGOS

Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato (a)
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e aprovada pela Comissão Julgadora.

Tese apresentada ao Instituto de Biologia para obtenção do Título de Doutor em Ecologia.

Orientador: Prof. Dr. Thomas Michael Lewinsohn

Campinas
2006

## FICHA CATALOGRÁFICA ELABORADA PELA BIBLIOTECA DO INSTITUTO DE BIOLOGIA – UNICAMP

Al64e
Almeida Neto, Mário
Efeito da degradação de habitat sobre a estrutura de interações entre plantas e insetos fitófagos / Mário Almeida Neto. -- Campinas, SP: [s.n.], 2006.

Orientador: Thomas Michael Lewinsohn.
Tese (doutorado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Interação inseto-planta. 2. Cerrado. 3. Diversidade. 4. Degradação ambiental. 5. Asteraceae. I. Lewinsohn, Thomas Michael. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

**Título em inglês:** The effect of anthropogenic disturbance on the structure of interactions between plants and phytophagous insects.
**Palavras-chave em inglês:** Plant-insect interaction; Cerrado (Brazil); Diversity; Habitat disturbance; Asteraceae.
**Área de concentração:** Ecologia.
**Titulação:** Doutor em Ecologia.
**Banca examinadora:** Thomas Michael Lewinsohn, André Victor Lucci Freitas, Carlos Roberto Sorensen Dutra da Fonseca, Glauco Machado, Sérgio Hayato Seike, Flávio Antônio Mães dos Santos, Gustavo Quevedo Romero, Paulo Inácio de Knegt López de Prado.
**Data da defesa:** 27/11/2006.
**Programa de Pós-Graduação:** Ecologia.

Campinas, 27 de novembro de 2006

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***Dedico este trabalho ao meu querido irmão
Gabriel Lucas de Almeida.***

# AGRADECIMENTOS

Agradeço inicialmente aos meus pais, Cleusa e Mário, pela educação, pelo exemplo de vida e pelos três irmãos que me deram: Léo, Nando e Bi. Agradeço também minha querida tia Irani pela sua generosidade e afeto ininterruptos.

Thomas foi orientador e incentivador. Ele teve influência direta em todas as qualidades dessa tese. Serei sempre grato pela oportunidade que ele me deu e por tudo o que me ensinou em mais de cinco anos de convivência.

Agradeço os amigos da UNICAMP, Kubota, Jiva, Paulo "Miúdo", Rafael Raimundo, Márcio Uehara-Prado e José R. Trigo, por tudo o que aprendi com eles desde que cheguei em Campinas.

Agradeço aos amigos do Laboratório de Interações Insetos-Plantas, Ricardinho, Mônica e Gui Becker, Rafa Loyola, Marina, Rosane, Paulinha, Kubota e Adrianinha, por toda ajuda e incentivo. O apoio que recebi de vocês foi fundamental!

Agradeço aos amigos da O2A na Moradia Estudantil da UNICAMP. Jiva, Marcão e Fillipão são pessoas maravilhosas. Aprendi muito com eles e sou muito grato pela convivência.

Agradeço aos "velhos e novos" amigos por todos os bons momentos que passamos juntos, principalmente à George "Porção" e Dani, Rafa e Aninha, Aluana, Juzinha, Suzana, Gabi Gaúcha e Joice.

A convivência com as seguintes pessoas foi fundamental na minha formação acadêmica: Denise C. Rossa-Feres, Reinaldo J. Fazzio Feres, Paulo G. Windisch, José R. Trigo, Carlos R. Fonseca, Paulo Inácio Prado, Paulo R. Guimarães-Jr, Gustavo Q. Romero, Thiago J. Izzo, Adriana M. Almeida, Rafael L. G. Raimundo, Glauco Machado, Umberto Kubota, Márcio Uehara-Prado, André L. Cruz e Jivanildo P. Miranda.

Agradeço aos membros da pré-banca: Glauco Machado, André V. L. Freitas e Paulo Inácio Prado. Devo agradecer especialmente ao Glauco pela leitura atenciosa de todos os detalhes da tese.

Agradeço aos membros da banca examinadora: André V. L. Freitas, Carlos R. Fonseca, Glauco Machado, Sérgio H. Seike, Gustavo Q. Romero, Paulo Inácio Prado e Flávio A. Maës dos Santos por todas as sugestões.

A ajuda de vários especialistas foi fundamental para a conclusão desta tese. Sou especialmente grato às seguintes pessoas: Valéria Cid Maia (Museu Nacional – UFRJ), Maria Virgínia Urso-Guimarães

(UFSCar), Marina Reiter Braun (UNICAMP), Paulo Inácio Prado (USP), Sérgio Vanin (USP), Ricardo Mermudes (Museu Nacional – UFRJ), Mara Magenta (Universidade Santa Cecília), João Semir (UNICAMP), Roberto Esteves (UERJ) e Ângelo P. do Prado (UNICAMP).

Por toda ajuda no campo, agradeço às seguintes pessoas: Yu Jie Ahn, Umbero Kubota, Joice M. Bariani, Rosane C. Picon, Guilherme H. Aguirre, Mário Ferreira-Neto, Martin Videla, Tehra G. Mendonça, Marília B. Santiago e Marina R. Braun.

Agradeço às seguintes pessoas pela ajuda na triagem e montagem dos insetos: Rosane C. Picon, Ricardo Fabiano, Paula Perre, Rafaela Massucato e Marília B. Santiago.

Agradeço aos funcionários do Instituto de Biologia da UNICAMP, especialmente ao pessoal da Biblioteca do IB, aos funcionários da Pós-graduação e aos funcionários do Departamento de Zoologia. Agradeço também aos motoristas Joaquim, Carlinhos, Renato e Toninho pelas viagens e pela ajuda.

Agradeço à Aninha, esposa, amiga e companheira, pelo carinho, compreensão, paciência e por este amor que nos dá cada vez mais força. Aninha compartilhou comigo cada momento de alegria e dificuldade ao longo do desenvolvimento dessa tese.

Agradeço ao Curso de Pós-graduação em Ecologia da **UNICAMP** e à **CAPES** (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) pela bolsa nos primeiros meses de meu doutorado.

Por fim, agradeço à **FAPESP** (Fundação de Amparo à Pesquisa do Estado de São Paulo) pela bolsa de doutorado (proc. FAPESP 03/02548-1) fundamental para a boa execução desse trabalho.

***"(...) interactions are the glue of biodiversity (...)"***
John N. Thompson

***"Simplicity is the ultimate sophistication"***

Leonardo da Vinci

# ÍNDICE

# Abstract

This study aimed to investigate the effects of anthropogenic disturbance on the diversity and structure of interactions between species of Asteraceae and the endophagous insects whose larvae feed inside their flower heads. Field sampling was performed in 20 remnants of cerrado vegetation in three adjacent counties in the state of São Paulo, Southeastern Brazil. The density of invasive grass cover was used as surrogate of anthropogenic disturbance level. Asteraceae richness showed a quadratic relationship with disturbance and peaked at intermediate disturbance levels. The proportion of typical Asteraceae from cerrado decreased in more disturbed sites, but the taxonomic distinctness of Asteraceae did not change consistently along the disturbance gradient. As expect, host plant richness was the major predictor of herbivore richness. Consequently, the richness of endophages also showed a quadratic variation along the disturbance gradient. However, when the effect of host plant richness on endophages is added into a multiple linear regression, the final direct effect of disturbance on insect richness is negative. Thus, the quadratic relationship between disturbance and endophage richness is explained through an indirect effect via host plant richness. The number of interactions between endophages and plants was also quadratically related to disturbance. Since connectance as a rule is negatively related to species number, those sites with intermediate disturbance levels presented lower connectance values than sites at the extremes of the gradient. After controlling for the influence of species richness on connectance values, this network property decreased at higher disturbance levels. The degree of nestedness of recorded plant-herbivore interactions was also lower in more disturbed sites. In contrast, disturbance level had no consistent effect on the level of compartmentation of the interactions. Finally, anthropogenic disturbance affected the fragility of the plant-herbivore interaction networks to secondary extinctions, but their effects were not uniform along the disturbance gradient.

# Resumo

Examinei os efeitos da degradação antrópica sobre diferentes aspectos da diversidade de espécies e interações entre plantas da família Asteraceae e os insetos herbívoros cujas larvas se alimentam no interior de seus capítulos. Toda a amostragem de campo foi realizada em vinte áreas de cerrado com diferentes níveis de degradação antrópica em três municípios vizinhos do estado de São Paulo. A densidade de gramíneas invasoras foi usada como medida indireta do nível de degradação antrópica das áreas. A riqueza de Asteraceae apresentou uma relação quadrática com a degradação, com um pico em níveis intermediários. A proporção de espécies típicas de cerrado diminuiu em áreas mais degradadas, mas a representatividade dos diferentes grupos taxonômicos não apresentou nenhuma variação consistente. Como esperado, a riqueza de plantas hospedeiras foi o principal preditor do número de herbívoros nas áreas. Conseqüentemente, a riqueza de herbívoros também apresentou uma relação quadrática com a degradação, mas pico marginalmente significativo em níveis intermediários. Quando o efeito da riqueza de hospedeiras é descontado através de uma regressão múltipla, o efeito final da degradação sobre a riqueza de herbívoros passa a ser negativo. Portanto, a relação quadrática entre degradação e riqueza de herbívoros é um efeito indireto via plantas hospedeiras. O número de interações distintas entre herbívoros e plantas também apresentou uma relação quadrática com a degradação. Visto que a conectância das redes de interações tende a diminuir com o aumento da riqueza, as áreas com níveis intermediários de degradação apresentaram valores de conectância menores que as áreas menos e mais degradadas. Quando a influência da riqueza de espécies é controlada através de uma análise alométrica, os valores de conectância mostraram uma queda em áreas onde a degradação é maior. O grau de aninhamento de interações planta-herbívoro também diminuiu significativamente nas áreas mais degradadas, enquanto que a degradação parece não afetar de forma consistente o grau de compartimentação das interações. Por fim, a degradação influenciou a resistência das redes de interações a extinções secundárias, mas seus efeitos não foram uniformes ao longo do gradiente de degradação.

# Introdução Geral

A degradação dos habitats naturais por atividades humanas é um fato evidente. Entre os ecólogos, há um consenso de que os processos de fragmentação, poluição e superexploração antrópica afetam negativamente a integridade dos habitats. Por outro lado, as conseqüências da degradação ainda são controversas e têm sido amplamente debatidas (e.g., Tilman 1999; Chapin et al. 2000; Hill & Hamer 2004). Até mesmo uma questão relativamente simples, como a relação entre degradação antrópica e diversidade de espécies, ainda não é passível de generalização (Lawton et al. 1998; Mackey & Currie 2001). A despeito desses obstáculos teóricos, o interesse por questões relacionadas à degradação antrópica dos habitats só aumenta. Esse interesse decorre, em parte, da idéia cada vez mais aceita de que a perda de espécies pode deteriorar a qualidade dos serviços da biodiversidade, os quais são direta ou indiretamente convertidos em bens de mercado (Daily 1997; Balmford et al. 2002; Dobson et al. 2006). Por essa razão, a elaboração de uma teoria robusta sobre as conseqüências da degradação dos habitats naturais é um dos principais desafios da Ecologia na atualidade.

Devido à impossibilidade prática de se realizar inventários completos da riqueza local de espécies, os estudos sobre a relação entre degradação e diversidade são realizados com subconjuntos das comunidades naturais. A escolha desses subconjuntos geralmente é baseada em algum critério taxonômico (família, classe, ordem), ecológico (guilda, habitat), morfológico (porte, hábito) ou num critério composto (e.g., aves dispersoras de sementes). Visto que as tolerâncias de diferentes grupos de espécies à degradação podem diferir bastante em função dos requisitos próprios de cada grupo, não é de se estranhar que os estudos publicados apresentem resultados tão variáveis sobre a relação entre degradação antrópica e diversidade de espécies (Lawton et al. 1998; Mackey & Currie 2001). Se por um lado a "diversidade de respostas" pode ser encarada como mais uma evidência da extraordinária variação de formas de vida, por outro ela pode significar um entrave para elaboração de uma teoria geral sobre a relação entre alterações antrópicas e diversidade biológica. Além disso, o foco sobre a diversidade de espécies em si talvez não seja o mais apropriado para a detecção de padrões relacionados aos efeitos da degradação sobre a biodiversidade.

Uma abordagem promissora e ainda pouco explorada é a investigação dos efeitos da degradação sobre a estrutura e diversidade de interações interespecíficas. Existe a expectativa de que as propriedades relacionadas à estrutura das interações possam revelar padrões não aparentes e menos dependentes da identidade das espécies envolvidas (e.g., Camacho et al. 2002; Lewinsohn et al. 2006). Esse enfoque significa não apenas uma abordagem complementar no estudo da biodiversidade, mas uma expansão teórica que pode resultar num entendimento mais refinado sobre os processos que regulam a biodiversidade. Além disso, esse enfoque nos permite explorar algumas questões ecológicas fundamentais, como a dinâmica de co-extinções (Dunne et al. 2002; Koh et al. 2004; Eklöf & Ebenman 2006) e o papel dos efeitos indiretos na fragilidade das comunidades naturais (Polis 1994; Wootton 1994; Borrvall et al. 2000). Para conduzir um estudo desse tipo é preciso selecionar um ou mais tipos de interação (ex. predação, parasitismo, mutualismo) como critério adicional de escolha dos grupos de espécies a serem investigados. Conseqüentemente, estudos focados em interações geralmente envolvem táxons bastante distintos.

Quando informações sobre as interações tróficas de uma comunidade são agrupadas, podemos representá-las no que se convencionou chamar de rede trófica (Elton 1927; Pimm 1982). Uma abordagem promissora no estudo de redes tróficas é o enfoque em determinados conjuntos de espécies de acordo com um critério mais restritivo. Enquanto uma rede trófica ideal deve mapear todas as conexões entre espécies consumidoras e espécies consumidas, a abordagem alternativa lista apenas um subconjunto dessa rede trófica definido por um critério estipulado. Um exemplo desse tipo de abordagem são as redes de interações entre plantas e insetos herbívoros (Fonseca et al. 2005; Prado & Lewinsohn 2004; Ives & Godfray 2006; Valladares et al. 2006). De modo geral, essas redes de interações apresentam maior resolução taxonômica do que as redes tróficas convencionais e costumam listar dezenas e até centenas de espécies de uma mesma localidade.

Redes de interações entre insetos fitófagos e plantas hospedeiras formam um dos subconjuntos de interações mais diversos de redes tróficas locais (Janzen 1983; Price 2002). Vários estudos têm mostrado que a maioria das espécies de insetos fitófagos apresenta alto grau de especialização alimentar (Janzen 1980; Price 1980; Ødegaard et al. 2005). Em decorrência da dependência dos insetos herbívoros em relação às suas plantas hospedeiras e das diferenças interespecíficas no grau de especialização, mudanças na riqueza e na composição das espécies de uma comunidade podem ter diversos efeitos diretos e indiretos sobre a estrutura e dinâmica de sua rede de interações. Por outro lado, a própria estrutura das interações é um aspecto fundamental das comunidades naturais porque ela pode influenciar a estabilidade das comunidades e sua dinâmica de co-extinções (Ives & Cardinale 2004; Bascompte et al. 2006; Eklöf & Ebenman 2006; Montoya et al. 2006). Além disso, os avanços recentes nas pesquisas sobre redes ecológicas (Proulx *et al.* 2005; Pascual & Dunne 2006) decorrentes da incorporação de métodos de análise de redes complexas (Albert et al. 2000; Barabási & Albert 1999), podem ajudar na elucidação de vários processos e padrões não aparentes. Nesse sentido, o presente estudo pretende contribuir para a compreensão dos efeitos da degradação antrópica sobre a estrutura e a fragilidade das interações entre plantas e insetos fitófagos.

## OBJETIVOS

O objetivo central desse estudo foi examinar os efeitos da degradação antrópica do cerrado sobre a estrutura e a integridade das interações entre plantas da família Asteraceae e os insetos fitófagos cujas larvas se desenvolvem e se alimentam no interior dos capítulos destas plantas. A tese foi dividida em cinco capítulos inter-relacionados. Como o efeito de degradação antrópica é o tópico central desta tese, sua divisão reflete os seguintes aspectos: (1) a diversidade de Asteraceae; (2) a diversidade geral de insetos fitófagos; (3) a diversidade de cada grupo taxonômico de inseto fitófago; (4) a estrutura das interações entre as espécies de Asteraceae e os insetos fitófagos; e (5) a susceptibilidade das redes de interações a extinções secundárias.

As figuras 1 e 2 ilustram as predições relacionadas aos efeitos da degradação de cerrado sobre cada aspecto da diversidade e da estrutura de interações entre Asteraceae e os insetos endófagos que consomem seus capítulos. Na figura 1 são apresentadas as predições relacionadas aos efeitos da degradação antrópica sobre a diversidade de plantas e insetos fitófagos. As relações positivas entre densidade e riqueza de espécies são baseadas no fato de que quanto mais indivíduos são amostrados, maior é a chance de se registrar uma espécie adicional (Bunge & Fitzpatrick 1993). As relações quadráticas entre o nível de degradação a densidade e riqueza de plantas são baseadas diretamente na Hipótese da Perturbação Intermediária (Grime 1973; Connell 1979). Por outro lado, minha expectativa é que o efeito da degradação sobre a densidade e riqueza de herbívoros seja, em grande parte, mediado pela riqueza e densidade de plantas hospedeiras.

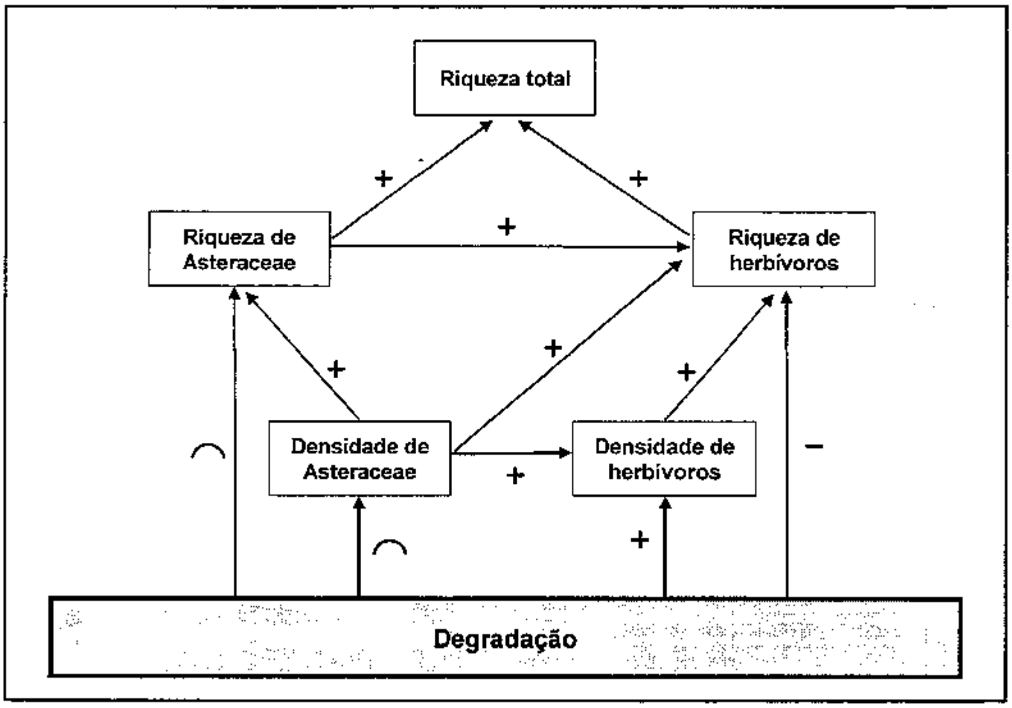

**Figura 1.** Modelo estrutural das expectativas dos efeitos da degradação antrópica sobre a abundância e diversidade de Asteraceae e seus insetos endófagos de capítulos. Os símbolos associados às setas indicam relações monotônicas, positivas (+) ou negativas (-), e relações quadráticas (⌒).

A figura 2 resume minhas expectativas em relação aos efeitos da degradação sobre as propriedades estruturais e a integridade das interações fitófago-planta. A expectativa de uma relação quadrática entre a degradação e a riqueza é uma extrapolação da Hipótese da Perturbação Intermediária para dois níveis tróficos (Grime 1973; Connell 1978). Visto que vários estudos têm estabelecido que a densidade de interações tróficas é menor em redes maiores (i.e., com maior riqueza) (Bersier et al. 1999; Montoya & Solé 2003), minha expectativa é que a conectância seja menor em níveis intermediários de degradação. Os efeitos da degradação sobre a grau de aninhamento e a compartimentação das interações são baseados no pressuposto de que tanto as espécies quanto as interações raras são mais suscetíveis à extinção ao longo do gradiente de degradação.

Estudos sobre a relação entre a degradação antrópica dos habitats naturais e a dinâmica de extinções resultantes desse processo ainda são escassos (Stork & Lyal 1993; Koh et al. 2004). O presente estudo examina os efeitos de degradação antrópica sobre a estrutura de interações tróficas e a conseqüente relação entre esta estrutura e a suscetibilidade de comunidades naturais a extinções secundárias. Na figura 2, apresento minhas expectativas sobre as relações entre as propriedades estruturais das redes de interações e a susceptibilidade das comunidades locais a extinções secundárias – ou co-extinções – de insetos herbívoros. Tendo em vista que redes de interações nas quais as espécies menos conectadas tendem a interagir com um subconjunto das espécies mais conectadas (i.e., redes mais aninhadas) são menos susceptíveis a extinções aleatórias de espécies do que redes conectadas ao acaso (Bascompte et al. 2003; Bascompte & Jordano 2006), minha expectativa é que o grau de aninhamento apresente uma relação negativa com a proporção de extinções secundárias de insetos herbívoros. Em relação à conectância, quanto maior o número médio de plantas hospedeiras alternativas menor deve ser à suscetibilidade a extinções secundárias dos fitófagos. Sobre a relação entre o grau de compartimentação e a suscetibilidade a extinções secundárias, não apresento nenhuma expectativa a priori, porque o grau de compartimentação não está diretamente associado a nenhum tipo de distribuição de freqüência do número de interações por espécie.

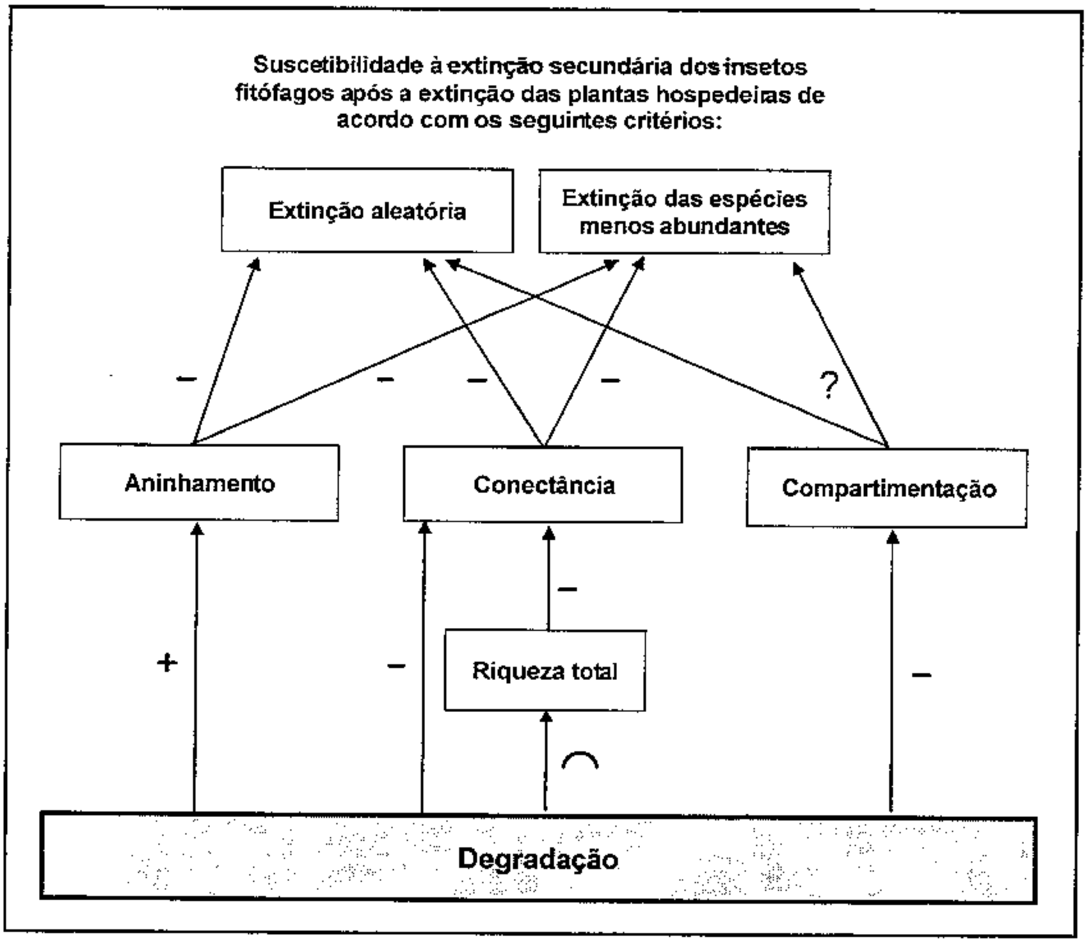

**Figura 2.** Modelo estrutural das expectativas dos efeitos da degradação antrópica sobre a estrutura das interações entre as espécies de Asteraceae e seus insetos endófagos de capítulos e sobre as relações entre estas variáveis. Os símbolos associados às setas indicam relações monotônicas, positivas (+) ou negativas (-), e relações quadráticas (⌒).

## MEDIDA DE DEGRADAÇÃO

Uma medida direta e precisa do nível de degradação de um habitat só é possível através de experimentos controlados, nos quais a freqüência, intensidade, área e seqüência de eventos de perturbação são conhecidas e/ou manipuladas (e.g. McCabe & Gotelli 2000). Essas condições são praticamente inexistentes em estudos sobre degradação antrópica na escala da paisagem. Por essa razão, vários estudos têm usado uma ou mais variáveis como medidas indiretas do nível de degradação antrópica, tais como tipos de uso da terra (Ribera et al. 2001), densidade de gado e/ou pastagem (e.g. Cagnolo et al. 2002), intensidade de fogo (e.g. Hoffmann 1996) e densidade de espécies invasoras ou pioneiras (De Pietri 1992; Molino & Sabatier 2001). Esta última variável é baseada no pressuposto de que degradação aumenta a susceptibilidade dos habitats à invasão por espécies que não fazem parte de sua biota original (Hobbs & Huenneke 1992; Lozon & MacIsaac 1997). Além disso, a própria densidade de espécies invasoras é um fator de degradação e de extinção local de espécies em diversos habitats (D'Antonio & Vitousek 1992). Uma vantagem do uso de espécies invasoras como medida de degradação é que essa variável pode refletir eventos de degradação passados. Medidas como área queimada ou densidade de gado refletem muito mais uma condição atual do que eventos históricos.

Neste estudo, o nível de degradação antrópica foi medido através da densidade de cinco gramíneas invasoras [*Andropogon gayanus* Kunth, *Brachiaria decumbens* Stapf, *Hyparrhenia rufa* (Ness) Stapf, *Melinis minutiflora* Beauvois, and *Panicum maximum* Jacq.]. Essas cinco gramíneas africanas figuram entre as principais espécies invasoras de cerrado no Brazil (Klink 1996; Ratter et al. 1997; Pivello et al. 1999a,b; Filgueiras 2002). Além disso, alguns estudos realizados em áreas de cerrado têm mostrado uma redução nas populações de gramíneas nativas em decorrência da entrada das invasoras (Klink 1996; Pivello et al. 1999a,b).

## SISTEMA DE ESTUDO

### *Localidades amostradas*

O cerrado é o bioma com a maior extensão de formações savânicas das Américas, abrangendo originalmente cerca de 2 milhões de km$^2$. Devido ao alto grau de endemismo e à crescente taxa de destruição de suas áreas naturais, o cerrado é considerado um *hotspot* (área prioritária) da biodiversidade mundial (Myers et al. 2000; Klink & Machado 2005). Estima-se que metade da área original do cerrado já tenha sido convertida em pastos, monoculturas e outras formas de uso antrópico (Sano et al. 2002; Klink & Machado 2005). O que denominamos cerrado é, na verdade, um mosaico de fitofisionomias, variando desde formações campestres até formações florestais. Esse complexo de fitofisionomias é o resultado de diferenças espaciais na fertilidade do solo, geomorfologia, regime de chuvas, freqüência de fogo e degradações antrópicas (Goodland & Pollard 1973; Oliveira-Filho et al. 1989; Ruggiero et al. 2002; Fonseca et al. 2005).

No estado de São Paulo, a vegetação de cerrado correspondia a cerca de 14% da vegetação original no início do século XIX. Hoje o cerrado representa menos de 1% da cobertura vegetal do estado, e sua área original tem sido continuamente convertida em paisagens antrópicas, principalmente pastagens e monoculturas (cana-de-açúcar, eucalipto, laranja) (Kronka et al. 1998; Durigan et al. 2003; Soares et al. 2003). Conseqüentemente, as áreas remanescentes de cerrado estão bastante fragmentadas e sujeitas a diversos tipos de perturbação antrópica (Brito 1997; Soares et al. 2003).

Este estudo foi realizado em 20 áreas de cerrado em três municípios vizinhos da região central do estado de São Paulo (veja figura 3). O clima da região de estudo é caracterizado por verões chuvosos e invernos secos (CWA de acordo com sistema de Köppen 1948; Embrapa-CCPSE 1999). A seleção das áreas de estudo foi realizada no sentido de maximizar o gradiente de degradação antrópica (veja figura 4).

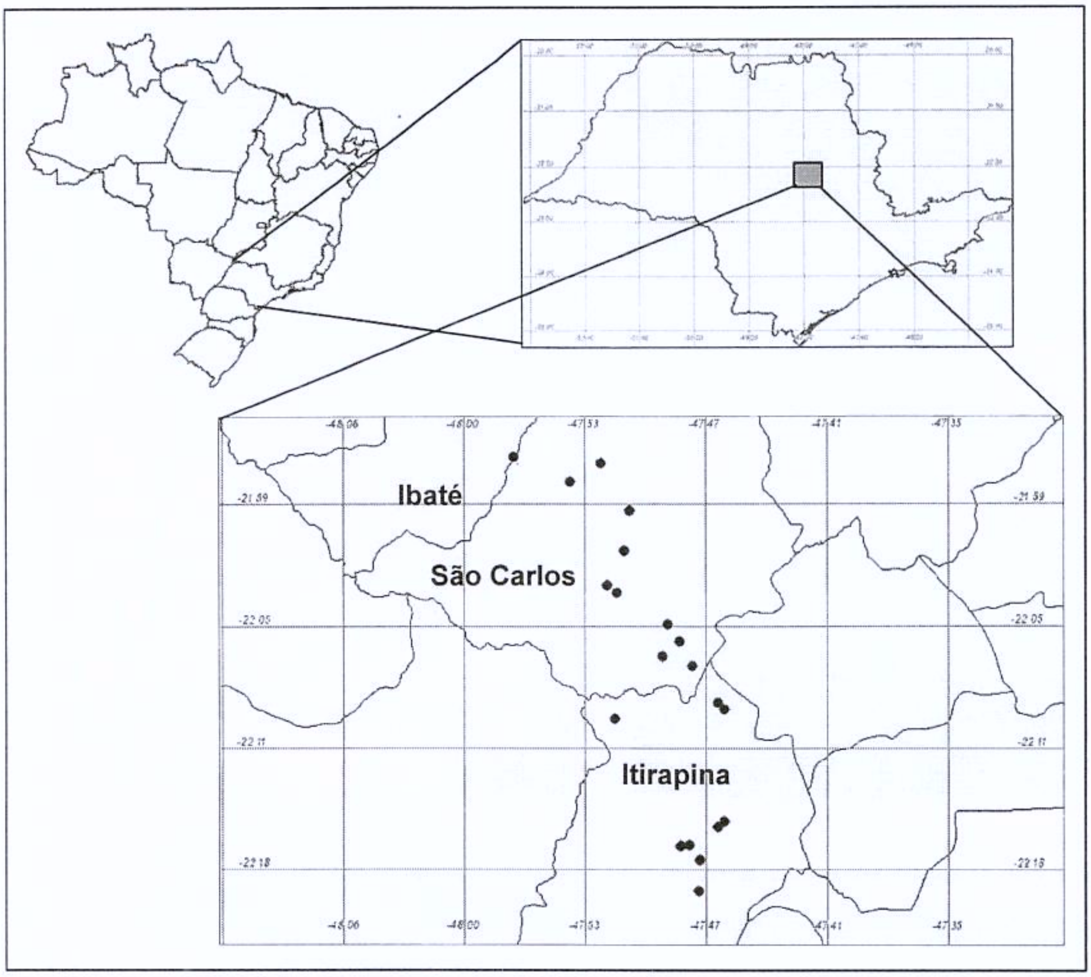

**Figura 3.** Localização geográfica da região de estudo no estado de São Paulo. Os pontos no mapa inferior (divisão municipal) mostram a localização de cada uma das vinte áreas de estudo.

### *Asteraceae*

Asteraceae é provavelmente a maior família de plantas do mundo e apresenta atualmente cerca de 23.000 espécies descritas (Bremer 1994; Stevens 2001). No Brasil existem pelo menos 1.900 espécies de Asteraceae já descritas (Barroso 1986). Dentro da flora do cerrado, a família Asteraceae é a segunda mais representativa quanto ao número de espécies (veja figura 5; Warming 1973; Mendonça et al. 1998). Por ser uma família com muitas espécies heliófilas e pioneiras, as asteráceas constituem um bom sistema para a investigação de interações entre insetos fitófagos e plantas hospedeiras em habitats com diferentes níveis de degradação.

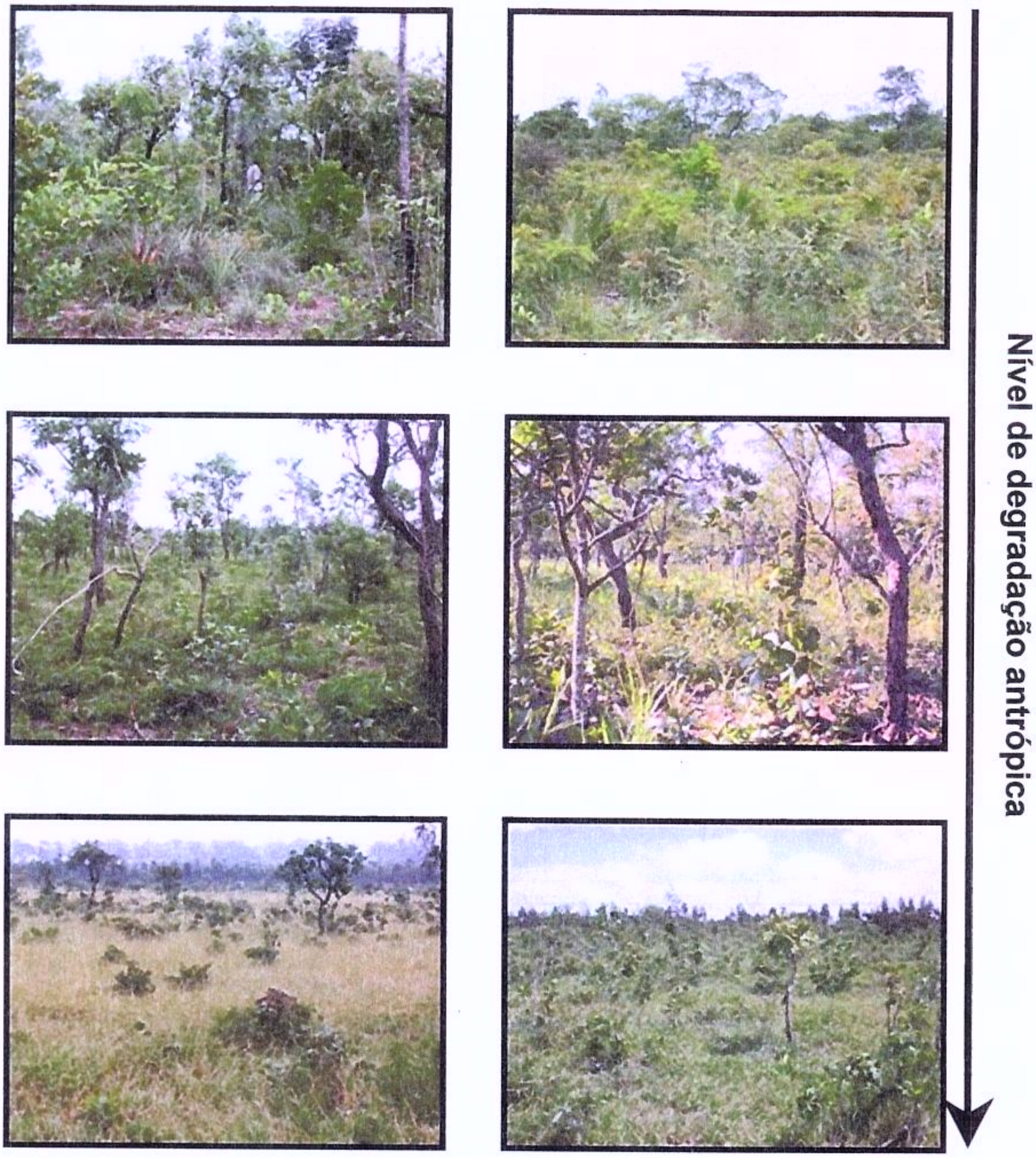

**Figura 4.** Exemplos de variação no grau de degradação antrópica das 20 áreas de estudo localizadas nos municípios de Itirapina, São Carlos e Ibaté (SP). O nível de degradação das áreas foi avaliado através da densidade de gramíneas invasoras.

**Figura 5.** Capítulos de algumas espécies de Asteraceae registradas no presente estudo. (A) *Bidens gardneri*, (B) *Calea verticillata*, (C) *Tilesia baccata*, (D) *Isostigma peucedanifolium*, (E) *Baccharis dracunculifolia*, (F) *Achyrocline satureoides*, (G) *Hoehnephytum trixoides*, (H) *Pterocaulon lanatum*, (I) *Vernonanthura ferruginea*, (J) *Vernonanthura membranacea*, (L) *Lepidaploa psilostachya*, (M) *Chrysolaena herbacea*, (N) *Lessingianthus bardanoides*, (O) *Piptocarpha rotundifolia*, (P) *Gochnatia pulchra*, (Q) *Trixis verbasciformis*, (R) *Campuloclinium chlorolepis*, (S) *Chromolaena odorata*, (T) *Chromolaena pungens* e (U) *Mikania cordifolia*.

### *Insetos endófagos de capítulos*

A estrutura floral característica da família Asteraceae é o capítulo (veja figura 5), uma inflorescência diferenciada formada por um conjunto de flores fixadas em um receptáculo e envolvido por séries de brácteas (Bremer 1994). Os capítulos são uma fonte de recursos alimentares usada por uma fauna diversificada de insetos endófagos (Figura 6; veja Zwölfer & Romstöck-Volkl 1991; Lewinsohn 1991; Prado et al. 2002). As fêmeas destes endófagos ovipõem nos capítulos, no interior dos quais as larvas se desenvolvem, consumindo seiva, flores, óvulos e frutos (veja Zwölfer & Romstöck-Volkl 1991; Gagné 1994; Headrick & Golden 1998).

Os principais grupos de insetos endófagos de capítulos de Asteraceae pertencem às três maiores ordens de insetos (Diptera, Lepidoptera e Coleoptera). As principais famílias de insetos endófagos deste estudo foram: Cecidomyiidae, Tephritidae, Agromyzidae e Tortricidae. Vale a pena mencionar que, graças à ajuda da Dra. Valéria Cid Maia (Museu Nacional - UFRJ) e da Dra. Maria Virgínia Urso Guimarães (UFSCar), os insetos endófagos da família Cecidomyiidae foram devidamente incorporados neste estudo. Apesar de toda a dificuldade associada à identificação e separação operacional dos cecidomiídeos, a inclusão deste grupo de insetos endófagos foi fundamental para que os resultados do presente estudo pudessem ser generalizados à toda fauna de insetos endófafos associados aos capítulos de Asteraceae. Os cecidomiiídeos foram o grupo mais diverso e com o maior nível de especialização no uso de plantas hospedeiras, confirmando uma suspeita já apontada em outros estudos (Möhn 1959, 1960; Gagné 1994; Lewinsohn 1988). Os tefritídeos foram identificados com a ajuda do Dr. Paulo Inácio Prado (USP) e de material previamente identificado pelo Dr. Allen Norrbom (SEL/USDA, U.S. National Museum, Washigton, DC, EUA). Os agromizídeos foram identirficados com o apoio do Dr. Ângelo Pires do Prado (UNICAMP) e Marina Reiter Brau (UNICAMP). A identificação dos coleópteros contou com o apoio dos Drs. Sérgio Vanin (USP) e Ricardo Mermudes (Museu Nacional – UFRJ). As asteráceas foram identificadas com apoio da literatura e da coleção do Herbário da UNICAMP, contando também com o apoio dos Drs. João Semir (UNICAMP) e Roberto Esteves (UERJ).

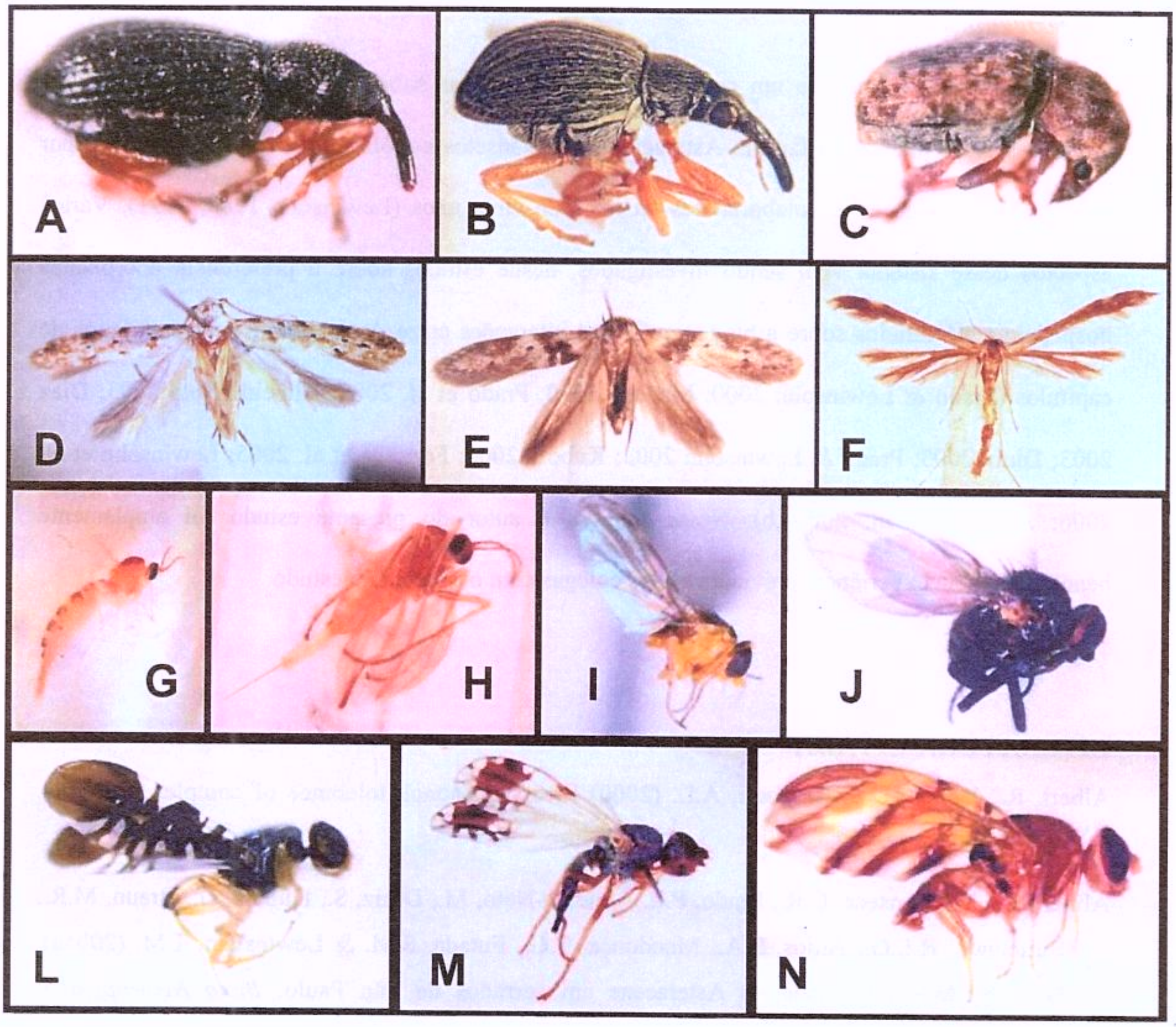

**Figura 6.** Alguns insetos endófagos de capítulos de Asteraceae representados no presente estudo. Coleoptera: (A) *Apion* sp.1, (B) *Apion* sp.4; (C) *Thrigonorrinus* sp.; Lepidoptera: (D) *Recurvaria* sp.1, (E) *Phalonidia squalida*, (F) *Lioptilodes parvus*; Diptera: (G) *Neolasioptera* sp.4, (H) *Asphondylia* sp.5, (I) *Liriomyza* sp., (J) *Melanagromyza minima*, (L) *Xanthaciura chrysura*; (M) *Trupanea* sp.6, (N) *Tomoplagia reimoseri*.

### *Contextualização*

Esta tese é parte de um conjunto maior de estudos sobre a diversidade e estrutura de interações entre plantas da família Asteraceae e seus insetos endófagos de capítulos iniciado por Thomas M. Lewinsohn e colaboradores há mais de vinte anos (Lewinsohn 1988, 1991). Vários aspectos desse sistema vêm sendo investigados, desde estudos sobre a preferência por plantas hospedeiras até estudos sobre a biogeografia das interações entre Asteraceae e seus endófagos de capítulos (Prado & Lewinsohn 2000; Macedo 2000; Prado et al. 2002; Almeida-Neto 2003; Diaz 2003; Diniz 2003; Prado & Lewinsohn 2003; Kubota 2004; Fonseca et al. 2005; Lewinsohn et al. 2006; Almeida et al. 2006a,b). Nesse sentido, o autor do presente estudo foi amplamente beneficiado pela experiência prévia de vários colegas com o sistema de estudo.

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# 1

# Does diversity peak at intermediate anthropogenic disturbance levels? A test on Asteraceae in Brazilian Cerrado

Mário Almeida-Neto, Umberto Kubota, Yu Jie Ahn, Joice M. Bariani, Rosane C. Picon, Guilherme H. Aguirre and Thomas M. Lewinsohn

## SUMMARY

The Intermediate-Disturbance Hypothesis was initially proposed to explain the mechanisms underlying variations in species richness along natural disturbed gradients. Subsequently, some studies have tested the predictions of this hypothesis on anthropogenic gradients. The aim of this study was to examine the following questions: (1) Does Asteraceae diversity peak at intermediate anthropogenic disturbance levels in remnants of Brazilian cerrados? (2) Are diversity-disturbance relationships consistent among different diversity measures? (3) What is the effect of disturbance on the proportion of invasive and typical cerrado Asteraceae species? We sampled Asteraceae from 20 cerrado sites located in three adjacent counties in Southeastern Brazil. To standardize sampling effort, we recorded all Asteraceae in 15 transects at three periods of the year in each site. We used cover of exotic grasses as a surrogate for anthropogenic disturbance level. We evaluated the effect of disturbance on Asteraceae diversity using Simpson diversity indices and three diversity measures based on taxonomic relatedness. Species density was significantly higher at intermediate disturbance levels. The expected Asteraceae richness through rarefaction showed a clear tendency to peak at intermediate disturbance levels. However, Simpson's diversity and the taxonomic diversity measures were fairly constant along the disturbance gradient. The proportion of typical cerrado Asteraceae species decreased at higher levels of disturbance, but we found no correlation between disturbance and the proportion of invasive Asteraceae. Different taxonomic groups of Asteraceae did not suffer differential species extinction or inclusion to the point of affecting taxonomic diversity measures. The strong negative effect of habitat disturbance on typical cerrado species suggests that the hump-shaped relationship between total Asteraceae richness and disturbance is due to an increase in the number of habitat-generalist species.

## INTRODUCTION

The effects of anthropogenic disturbances on biodiversity are among the most extensively investigated themes in ecology (see Kerr & Currie 1995; Rosser & Mainka 2002). Several experimental and observational studies of the effects of disturbance on species richness have shown a hump-shaped relationship between disturbance and species diversity (e.g. Armesto & Pickett 1985; Collins et al. 1995; McCabe & Gotelli 2000; but see Mackey & Currie 2001). Grime (1973a, b) and Connell (1978) proposed the hypothesis that at intermediate disturbance levels, species coexistence is maintained by a nonequilibrium state in which strong competitors cannot dominate. This hypothesis is called the Intermediate-Disturbance Hypothesis (hereafter IDH), and it predicts that diversity is higher in communities with intermediate levels of disturbance. According to the IDH, if intensity or frequency of disturbance is low, competitive dominants will eliminate other species and reduce diversity. Conversely, if disturbance intensity or frequency is high, most species will be reduced or become locally extinct, also decreasing diversity.

Complete inventories of local floras or faunas are hard to attain, especially in highly diverse habitats such as tropical forests and savannas. Therefore, local environmental predictors of species diversity, such as disturbance and fragmentation, have been most often evaluated using a restricted taxonomic group (e.g. Scariot 1999) or through the selection of a species group on some ecological or morphological criterion, such as life-form or woodiness for plants (e.g. Burslem & Timothy 1999; Molino & Sabatier 2001; Noy-Meir & Oron 2001). However, given that distinct taxonomic groups generally present marked differences in their life history traits, in their environmental requirements, and in their susceptibility to biotic and abiotic changes, we expect the strength and shape of the disturbance-richness relationships to depend on the focused taxonomic group (see Mackey & Currie 2001, and references herein). In fact, the concept of indicator species is, in part, based on these distinct susceptibilities to habitat changes and habitat attributes (Kremen 1994). Since anthropogenic disturbance frequently increases habitat invasibility (Hobbs & Huenneke 1992;

Lozon & MacIsaac 1997) and promotes the local extinction of rare species, disturbance may often entail differential retention or extinction of higher taxa instead of simply change diversity at the species level.

In this study, we evaluated the effects of anthropogenic disturbance in cerrado (a savanna like-vegetation) on the diversity of Asteraceae. The cerrado biome in Brazil is considered a global biodiversity hotspot due to its high endemism and to the high recent rate of habitat loss (Myers et al. 2000; Klink & Machado 2005). This biome comprises an area of approximately 2 million km$^2$, of which nearly half have already been cleared or converted for human use, as pasture and cash-crop agriculture (Sano et al. 2002; Klink & Machado 2005). The term "cerrado" comprises a physiognomically complex vegetation gradient from open grasslands, called "campo limpo", to sclerophyllous dry forests, called "cerradão". These different physiognomies are the result of several combined factors, such as soil fertility, geomorphology, water regime, fire frequency, and human-induced degradation (Goodland & Pollard 1973; Oliveira-Filho et al. 1989; Ruggiero et al. 2002; Fonseca et al. 2005). Asteraceae is the second largest family within the flora of cerrado (Warming 1973; Mendonça et al. 1998), and its diversity and abundance are especially high in open physiognomies (Filgueiras 2002; Fonseca et al. 2005). Moreover, several species of Asteraceae are common in disturbed habitats and some of them rank among the most representative invasive plants in the world (Cronk & Fuller 1995; Pyšek 1998).

Our main goal was to test the prediction of the IDH that species richness peaks at intermediate disturbance levels, using Asteraceae in Brazilian cerrado remnants ranging from very slightly to extremely disturbed sites as study system. Additionally, we aim (1) to examine how consistent are the effects of disturbance on different diversity measures, and (2) to evaluate the effect of habitat disturbance on the proportion of invasive and typical Asteraceae species in cerrados.

## METHODS

### *Study area*

This study was conducted in 20 sites located in three adjacent counties in the state of São Paulo, southeastern Brazil (Table 1). Regional climate is CWA following Köppen (1948), characterized by rainy summer and dry winter (Embrapa-CCPSE 1999). The sites are spaced apart from 0.6 to 41.4 km (mean distance = 16.3 km), at elevations between 600 to 950 m a.s.l. Sites ranged from 4 to nearly 150 ha in extent.

The sites were selected a priori to maximize the length and coverage of the anthropogenic disturbance gradient. We did not include dense woodland physiognomies (cerradão) because they present a sparse herbaceous layer, where most Asteraceae species are found (Filgueiras 2002; Fonseca et al. 2005). As our aim was to investigate a disturbance gradient, we minimized the range of other additional factors, such as shade, in our analysis. Thus, major structural conversion (from forest to open field) is not a prime factor in this study.

### *Sampling procedure*

In order to minimize taxonomic sampling bias due to phenological effects we sampled each site in three periods from 2004 to 2005: April/May, August/September, and January/February. These three periods were timed to include flowering peaks of the five most representative tribes of Asteraceae in Brazilian cerrado (Astereae, Eupatorieae, Heliantheae, Mutisieae, and Vernonieae), according to records of reproductive phenology (Mantovani & Martins 1988; Batalha & Matovani 2000; Almeida et al. 2005). All sites were sampled within 35 days in each period to minimize phenological differences in species composition.

Sampling effort was standardized among sites by counting the number of flowering/fruiting individuals of Asteraceae for each recorded species in 15 transects of 30 x 5 m per period in each site. We randomised two coordinates to place transects: (1) the position along the border of the sites with a minimal spacing of 10 m between two transects, and (2) the starting position perpendicular to the border from a minimum of 5 up to 55 m. Vouchers of all plant species are deposited in the laboratory reference collection and in the Universidade Estadual de Campinas Herbarium (UEC).

**Table 1.** The geographical coordinates of 20 cerrado sites in the state of São Paulo, Brazil, and some habitat and plant community properties. Species density is total number of flowering or fruiting species of Asteraceae recorded in the sampled transects (in brackets is the total number of observed species for each site). IGC is the index of invasive grass cover.

| Site coordinates | IGC | Size (ha) | Tree density (ind.ha$^{-1}$) | Species density |
|---|---|---|---|---|
| 22°09'57"S 47°48'08"W | 1.00 | 40 | 3.20 | 13 |
| 22°07'56"S 47°48'54"W | 1.04 | 108 | 0.60 | 11 |
| 22°06'50"S 47°49'07"W | 1.62 | 28 | 1.40 | 27 |
| 22°07'04"S 47°50'46"W | 1.96 | 8 | 1.20 | 16 |
| 22°08'37"S 47°47'55"W | 2.13 | 150 | 3.00 | 21 |
| 22°16'45"S 47°48'50"W | 2.76 | 24 | 4.87 | 25 |
| 22°15'56"S 47°47'48"W | 2.80 | 60 | 2.93 | 23 |
| 22°19'02"S 47°48'22"W | 3.20 | 38 | 1.60 | 26 |
| 22°02'08"S 47°52'54"W | 3.22 | 12 | 1.40 | 23 |
| 22°05'46"S 47°49'57"W | 3.38 | 6 | 0.80 | 26 |
| 21°58'09"S 47°56'56"W | 3.78 | 10 | 4.60 | 28 |
| 22°10'03"S 47°47'16"W | 4.22 | 12 | 5.00 | 21 |
| 22°17'32"S 47°48'20"W | 4.58 | 8 | 4.67 | 27 |
| 21°57'56"S 47°53'16"W | 4.60 | 14 | 1.14 | 22 |
| 22°04'06"S 47°52'35"W | 4.67 | 5 | 0.53 | 12 |
| 22°00'21"S 47°51'48"W | 4.80 | 4 | 2.54 | 5 |
| 22°04'06"S 47°52'56"W | 4.96 | 16 | 0.00 | 8 |
| 22°15'15"S 47°45'47"W | 4.98 | 7 | 0.00 | 11 |
| 21°58'59"S 47°54'34"W | 5.00 | 75 | 0.13 | 7 |
| 22°16'49"S 47°49'16"W | 5.00 | 14 | 0.07 | 14 |

### *Disturbance level and recorded variables*

Direct measures of disturbance are only possible in controlled experiments, in which frequency, intensity, area, and sequence (history) of disturbance factors are known or, preferably, manipulated (e.g. McCabe & Gotelli 2000). Since habitat disturbance is a combination of several processes, it is rarely feasible to isolate and directly measure a single cause of natural or anthropogenic disturbance in non-experimental studies. For this reason, a common procedure for measuring disturbance levels in natural habitats or landscapes is to use one or more parameters as surrogates for disturbance, such as land use (Ribera et al. 2001), cattle load or grazing (e.g. Cagnolo et al. 2002), fire (e.g. Hoffmann 1996), or density of invasive weeds or pioneer species (De Pietri 1992; Molino & Sabatier 2001).

It has been well established that disturbance increases habitat invasibility (Fox & Fox 1996; Hobbs & Huenneke 1992; Lozon & MacIsaac 1997). Thus, we used percent cover of five African grasses, namely *Andropogon gayanus* Kunth, *Brachiaria decumbens* Stapf, *Hyparrhenia rufa* (Ness) Stapf, *Melinis minutiflora* Beauvois, and *Panicum maximum* Jacq., as a surrogate for anthropogenic disturbance level. This indirect measure of human-induced disturbance is supported by studies that have shown a displacement of native grasses by invasive ones after disturbance in South America savannas (Baruch et al. 1985; Pivello et al. 1999a,b). The five African grass species are reputedly the major invasive species in Brazilian cerrado (Klink 1996; Ratter et al. 1997; Pivello et al. 1999a,b; Filgueiras 2002; Hoffmann et al. 2004), thus we assumed that percent cover of these grasses should indicate the frequency and intensity of remote and recent history of disturbance events. The five grasses had unequal distributions and abundances in the sampled sites. *Brachiaria decumbens* was recorded in 19 of 20 sites, in which it represented more than 60% of the invasive grass cover. *Melinis minutiflora* was recorded in seven sites and it was the second most abundant invasive grass in six of them. *Panicum maximum* was recorded only in two sites, but in one of these it was the second most abundant invasive grass. *Hyparrhenia rufa* was recorded only in two sites, in which it represented less than 1% of cover. *Andropogon gayanus* was not recorded within any sample, though it was occasionally present at the border or at very low density as isolated patches in some sites. Thus, in practice, invasive grass cover here is virtually equivalent to summed percent cover of *B. decumbens* and *M. minutiflora*.

For each transect, we recorded percent invasive grass cover in five classes: 1) 0%, 2) 1 to 25%; 3) 26 to 50%; 4) 51 to 75%, and 5) 76 to 100%. As an index of invasive grass cover (IGC) we used the mean value for all 45 transects pooled over the three sampling periods in each site. Although some distributions of IGC values did not show a symmetrical distribution, we used the mean because there is no extreme value that would distort the mean as a measure of central tendency. On the other hand, both the median and mode produce discrete values which do not show small differences in degradation level among the sites.

We also recorded the following habitat characteristics to examine their effects on Asteraceae diversity: mean tree density per transect, mean canopy cover (%), and size of the sites (ha). In each transect, we counted the number of trees with diameter at breast height larger than 10 cm. Hemispherical photographs of the canopy above the centre of the transects were taken with a digital camera equipped with a fisheye lens. We used the software Gap Light Analyzer version 2.0 (Frazer et al. 1999) to calculate canopy cover.

We considered as invasive species of Asteraceae all exotic ones, as well as non-natives from cerrado flora with a wide geographical distribution. Typical cerrado Asteraceae species are those whose known distribution is restricted to savannas of South-America. Species were classed as weeds or invasive according to Leitão-Filho et al. (1975), Lorenzi (2000), 'The PLANTS Database' website (http://plants.usda.gov), and 'The Global Compendium of Weeds' website (http://www.hear. org/gcw). As our classification of species as typical of cerrado may have some margin of uncertainty, we tested the relationships between invasive grass cover and percentage of typical Asteraceae species using more or less restrictive criteria for cerrado Asteraceae species, and these alternative analyses did not affect the results at a significance level of 5%.

### *Data analysis*

According to Gotelli & Colwell (2001), standardizing the data sets either by area or by sampling units may produce very different results compared to standardizing by number of collected individuals. Thus, in order to examine the effect of anthropogenic disturbance per unit of sampling effort, we compared species richness and species density between sites using both individual- and sample-based rarefaction standardizations. The sample-based rarefaction curve was generated by Monte Carlo resampling in the software EstimateS (Colwell 2004). For the individual-based rarefaction approach, we used Hurlbert's (1971) rarefaction method to calculate the expected number of Asteraceae species for each site based on the recorded number of individuals in the smallest sample.

We examined the effect of IGC on abundance, species density, proportion of typical and invasive species on the following four diversity measures for Asteraceae species: Simpson complement ($1 - \lambda$), and three diversity measures based on taxonomic relatedness among species proposed by Warwick & Clarke (1995) and Clarke & Warwick (1998, 1999), namely taxonomic diversity ($\Delta$), taxonomic distinctness ($\Delta^*$), and average taxonomic distinctness ($\Delta^+$). The taxonomic based indices were chosen to provide information on a third important component of biological diversity, taxonomic diversity above the species level (Warwick & Clarke 1998; Clarke & Warwick 1998; Magurran 2004). Taxonomic diversity ($\Delta$) estimates the average taxonomic path length within a classification tree between any pair of individuals in the sample; it is similar to Simpson's diversity, weighted by the taxonomic relatedness among species. Taxonomic distinctness ($\Delta^*$) is calculated as taxonomic diversity, but excludes conspecific pairs. The same measure with presence/absence data produces average taxonomic distinctness ($\Delta^+$), which is the expected average path length between any pair of species, regardless of their abundances. We determined the taxonomical relationships among Asteraceae species based on the classification of genera, subtribes, and tribes according to Bremer (1994) with additional information for Vernonieae based on Robinson (1999).

We employed both linear and quadratic regressions to examine the effects of disturbance (as the IGC), total abundance (log transformed), species density, diversity measures, and proportion of cerrado species. Models were chosen through comparison of the sum of squares for the quadratic and linear models following Zar (1999). We used Murtaugh's test for monotonicity (Murtaugh 2003) in each quadratic regression to evaluate whether the relationships between disturbance and the response variables show an intermediate maximum, that is, unimodality against the null hypothesis of monotonicity. As the proportion of invasive species did not fulfil the requirements to perform a regression analysis, we evaluated its relationship with habitat disturbance through a Spearman rank correlation. This correlation analysis was also used to explore the relationships of disturbance variables and habitat characteristics with Asteraceae abundance and species density.

## RESULTS

We recorded 66 species of Asteraceae within the sampled transects, representing 37 genera, 21 subtribes, and 9 tribes in the 20 cerrado sites (Appendix). The three most representative tribes, respectively Vernonieae, Eupatorieae, and Heliantheae, comprised 71% of all Asteraceae species and to 81% of the 7,072 recorded individuals. The proportion of species per tribe was highly unequal among sites, and did not show any clear tendency along the disturbance gradient (Fig. 1).

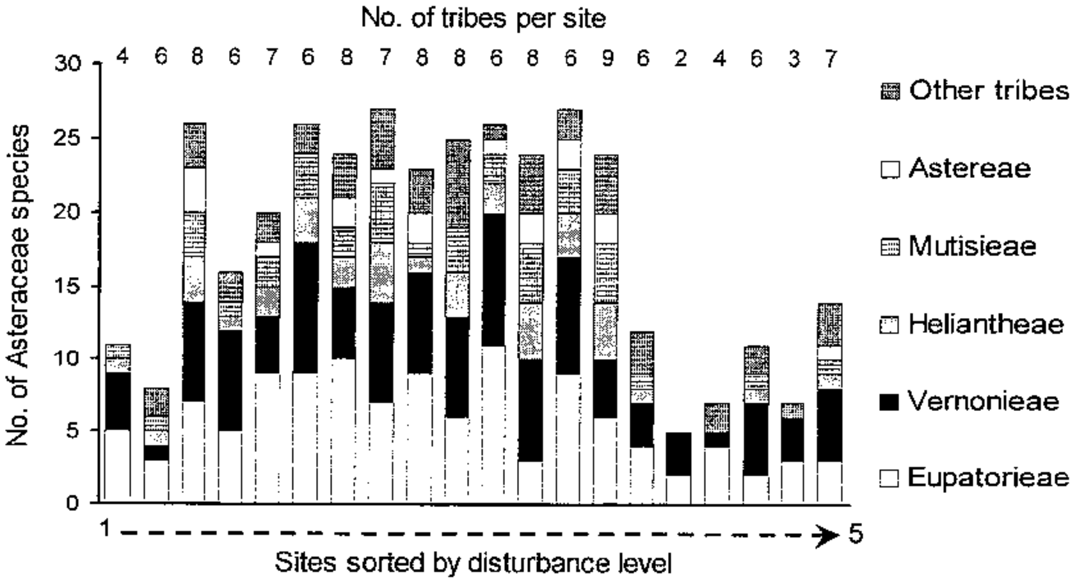

**Figure 1.** Number of Asteraceae tribes along 20 cerrado sites ordered from lower to higher disturbance levels (see table 1). Other tribes are Plucheeae, Senecioneae, Helenieae, and Gnaphalieae. The numbers of tribes in each site are presented above the bars.

The expected species number per sampled area (species density) tended to be consistently higher at intermediate disturbance levels (Fig. 2). This result is supported by the quadratic relationships of disturbance with total individual density, total species density, and expected species richness (Fig. 3). According to Murtaugh's test for monotonicity, total species density showed a significant peak at intermediate disturbance levels (*P* = 0.003), while total individual density (*P* = 0.069) and expected species richness (*P* = 0.08) presented marginally significant peaks at intermediate levels. Since expected species richness showed both a quadratic relationship with disturbance (Fig. 3c) and a marginally significant peak at intermediate disturbance levels, the observed richness-disturbance relationship is not merely a by-product of sampling effect.

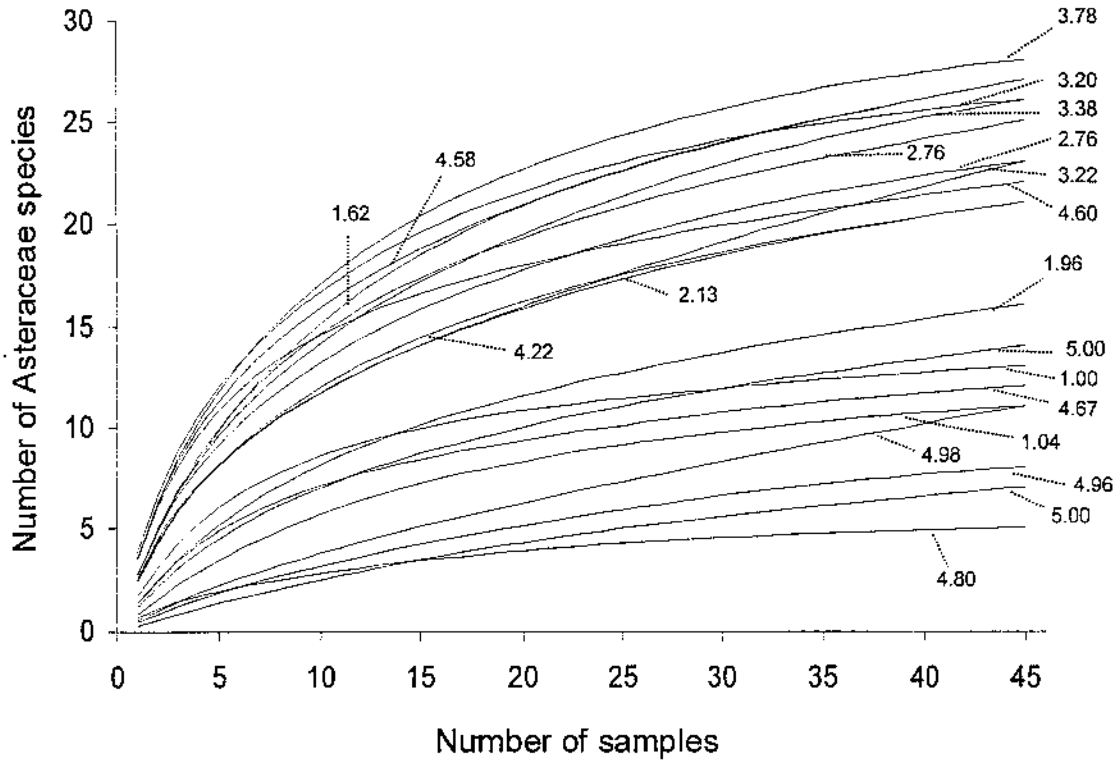

**Figure 2.** Sample-based rarefaction curves of Asteraceae for 20 cerrado sites with several levels of anthropogenic disturbance. The disturbance levels are the values of index of invasive grass cover shown as curve labels. This index varies from 1 (low disturbance; i.e. 0% IGC) to 5 (high disturbance; i.e. > 75% IGC).

Simpson's diversity showed a marginally significant quadratic relationship with disturbance level (Fig. 4a) and peaked at intermediate levels (*P* = 0.037). The taxonomic diversity measures showed no clear tendency of change, but instead they appear fairly constant along the disturbance gradient (Figs. 4b, c, d).

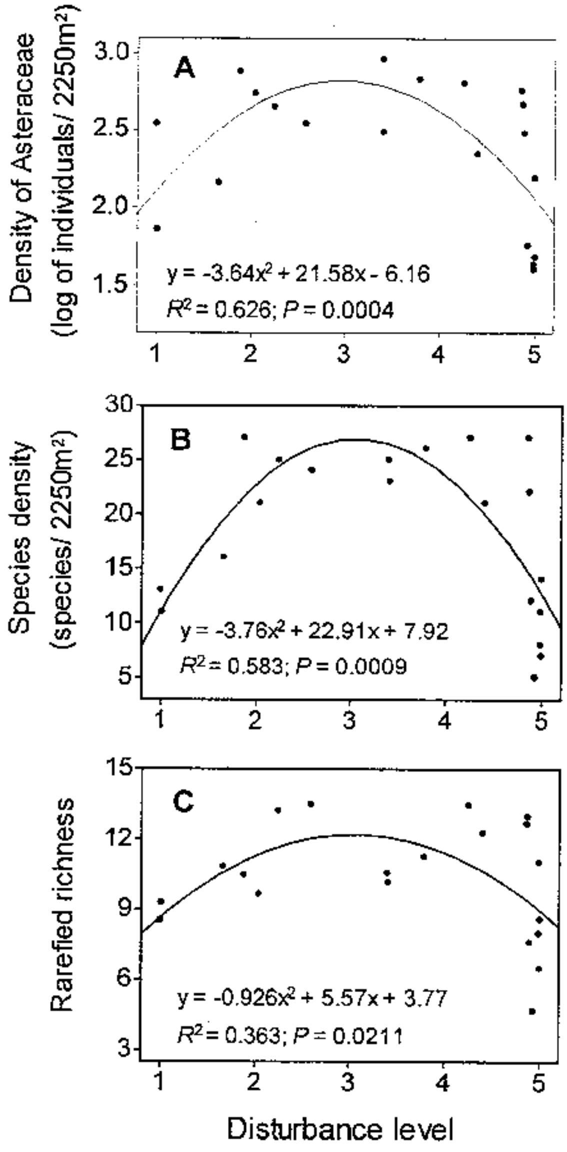

**Figure 3.** (A) Number of Asteraceae individuals, (B) number of species recorded in the sampled transects, and (C) expected Asteraceae species richness standardized to 40 sampled individuals, in 20 cerrado sites along a gradient of anthropogenic disturbance. The x-axis represents a gradient of disturbance based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance). See text for details and scales of the five measures

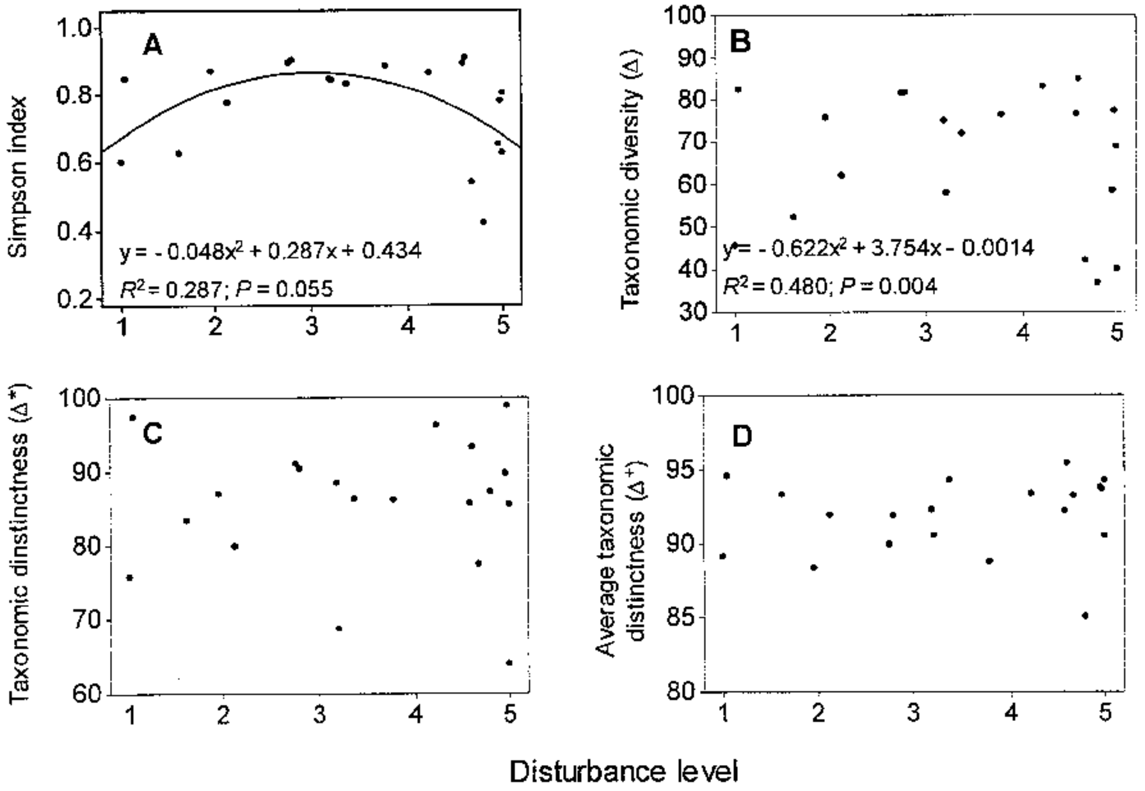

**Figure 4.** Diversity measures of 20 cerrado sites with several levels of anthropogenic disturbance. The x-axis represents a gradient of disturbance based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance). Only statistically significant regression lines are depicted. See text for details and scales of the five measures.

Eighteen species were classed as typical from cerrados while only four were confidently named invasive (Appendix). The proportion of typical cerrado Asteraceae species decreased significantly in more disturbed sites (Fig. 5a; $F_{1,18} = 25.76$; $R^2 = 0.589$; $P = 0.0002$), whereas the proportion of invasive Asteraceae species did not show any clear change along the disturbance gradient (Fig. 5b; $rs = -0.17$; $P = 0.473$). One of the least disturbed and some of the most disturbed sites had no invasive Asteraceae species at all.

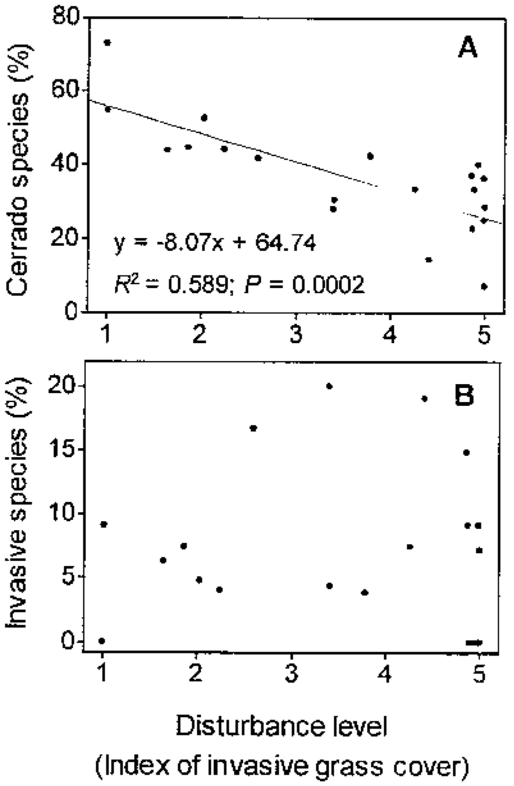

**Fig. 5.** Proportion of core (A) and invasive (B) species of Asteraceae from cerrados for 20 sites with several levels of anthropogenic disturbance. The x-axis represents a gradient of disturbance level based on the proportion of invasive grass-cover, varying from 1 (low disturbance) to 5 (high disturbance).

As expected, canopy cover and tree density showed a strong positive correlation (Table 2). However, this was the only significant correlation among the independent variables. The IGC presented marginally significant correlations with tree density and size of the sites. Both Asteraceae abundance and species density presented significant, and positive, correlations only with canopy cover and tree density (Table 2).

**Table 2.** Spearman rank correlation matrix between disturbance, canopy cover, tree density, Asteraceae species density and abundance in an anthropogenic disturbance gradient of 20 Brazilian cerrado remnants. CV is the coefficient of variation and ES (40) is the expected species richness for a sample of 40 individuals.

| | Site size | Canopy cover | Mean tree density |
|---|---|---|---|
| Canopy cover | -0.065 | | |
| Mean tree density | -0.019 | 0.858*** | |
| Invasive grass cover | -0.426$^{+}$ | -0.366 | -0.431$^{+}$ |
| Species density | -0.037 | 0.643** | 0.524** |
| Asteraceae abundance | 0.076 | 0.550* | 0.518* |
| ES (40) | -0.050 | 0.572** | 0.486* |

$^{+}P = 0.06$; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

# DISCUSSION

### *Asteraceae species density and richness*

Our results showed that the density of plants of the family Asteraceae tended to be higher at intermediate levels of anthropogenic disturbance in Brazilian cerrados. This could in principle provide the simplest proximal reason for the observed hump-shaped relationship of Asteraceae species density with disturbance. However, the standardized expected species richness showed a clear tendency to peak at intermediate disturbance levels. Thus, even after accounting for the higher density of individual plants, the richness-disturbance relationships of Asteraceae in cerrados was consistent with the predicted effects of disturbance on individual and species density.

McCabe & Gotelli (2000) and Gotelli & Colwell (2001) argued the importance of individual-based rarefaction curves to explore hypotheses related to species richness. According to them, the majority of studies on the relationships between disturbance effects and diversity have used species density instead of species richness for rarefaction. Given that species density is strongly related to total abundance, the effects of disturbance on species diversity in sample-based studies should be interpreted with caution, because abundant samples tend to have more species

(McCabe & Gotelli 2000).

The peak of species richness at intermediate levels of disturbance observed in this study is in accord with the prediction of the IDH, and with the results reported by many studies on the effects of disturbance on species richness (e.g. Molino & Sabatier 2001; but see Mackey & Currie 2001). Differences among taxa in the observed effects of a disturbance gradient are well documented, for instance, in the study carried out in Cameroon forests by Lawton et al. (1998). In that study, birds, butterflies, flying and canopy beetles, canopy and ground ants, termites and soil nematodes presented very different responses to habitat disturbance. Presumably, the relationship between anthropogenic disturbance and Asteraceae richness in cerrado would be different if angiosperm families less tolerant of disturbances had been studied. Nonetheless, we argue that Asteraceae are useful as focal group for disturbance evaluation in open habitats, precisely because of the gamut of responses shown by different species and lower taxa within this family.

### *Relationships between disturbance and diversity indices*

To evaluate the effects of disturbance on species diversity, some studies have used species richness (e.g. Lawton et al. 1998), others have used species density (McCabe & Gotelli 2000), and yet others have used several measures of diversity (Kocher 2000; Vujnovic et al. 2002). As each of these distinct diversity measures capture different components of diversity, further comparison of disturbance effects on species diversity is hindered. We believe that the best alternative for the plethora of possible indices is to use the simplest effective measures. This can be achieved through the combined use of an evenness-based diversity index, a richness-based diversity measure, and a third index based on the taxonomic relatedness among species. Regardless of which or how diversity indices are used, it is important to ascertain whether their relationships with the disturbance variables are consistent. Accordingly, we chose the widely applied Simpson's index and explored three recently proposed diversity indices that are weighted by taxonomic distances among individuals or species (Warwick & Clarke 1998; Clarke & Warwick 1998).

Several authors have argued that phylogenetic or taxonomic relationships among species are important components of biodiversity and should be used for conservation purposes or to assess the effects of disturbance on species assemblages (Warwick & Clarke 1998; Rogers et al. 1999). However, few studies till now have investigated the relationships between habitat disturbance and taxonomic, rather than species, diversity in terrestrial environments. Clarke & Warwick (2001) propose that, under disturbance, species from relatively species-poor higher taxa tend to disappear first, so that the remaining species will belong to a smaller number of groups that tend to be relatively speciose. Contrary to some studies in soft-bottom marine assemblages in which assemblages of disturbed sites showed smaller taxonomic diversity (Warwick & Clarke 1995; Clarke & Warwick 1998), in the present study no taxonomic based diversity measure presented any clear change along the disturbance gradient (Figs. 4c-e); thus, diversity above the species level is essentially conserved along the gradient. This means that the different taxonomic groups of Asteraceae did not suffer differential species extinction or recruitment to the point of affecting the taxonomic diversity measures, as expected according to Warwick and Clarke. Somerfield et al. (1997) also found no consistent pattern of decreasing taxonomic diversity of marine macrofaunal assemblages with increasing environmental impact. Although the taxonomic diversity of Asteraceae did not decrease along our anthropogenic disturbance gradient, we still do expect a correlation between the taxonomic diversity of the entire flora and the disturbance gradient, because many poorly represented plant groups are less tolerant to disturbance. This hypothesis is supported by the study of Durigan et al. (1994), which suggests that a frequently burned cerrado area has fewer plant families than cerrados protected from fire in neighbouring areas.

### *Disturbance effects on core and invasive species*

Many studies have found positive correlations between disturbance and susceptibility to invasion (e.g. Hobbs & Huenneke 1992; Lozon & MacIsaac 1997). Although a number of

Asteraceae species have been classified as invasive in degraded and human-dominated ecosystems (Cronk & Fuller 1995; Pyšek 1998), we did not find any correlation between habitat disturbance and the proportion of Asteraceae species known to be extraneous to cerrado communities. We suppose this can be ascribed to some cerrado features, such as its soil of low fertility and high acidity. In fact, we recorded few invasive species in all the sites, and this may help to explain why we did not find a simple correlation between the proportion of invasive Asteraceae and the level of anthropogenic disturbance.

Contrary to the invasive species, the proportion of typical/core cerrado Asteraceae species decreases clearly along the anthropogenic disturbance gradient (Fig. 5). The strong effect of habitat disturbance on these "core" cerrado species showed that the hump-shaped relationships between the number of species of Asteraceae and the disturbance is due to an unimodal increase in the number of habitat generalist species. The reduction in the number of habitat-specialists followed by an increase in the number of habitat-generalists in more degraded sites has been shown for other taxonomic groups, as butterflies (Swengel 1996) and birds (Tubelis & Cavalcanti 2000). Thus, at the landscape and regional scales, cerrado disturbance should lead to a higher homogenisation of species composition, and consequently to a reduction in beta diversity between different habitats, though average alpha diversity may even increase (Rosenzweig 2001).

### *Relationship between disturbance and tree density*

The marginally significant negative correlation of invasive grass cover with tree density and with size of the sites is to be expected, because invasive grasses have their growth optimum in sunny habitats and usually encroach on cerrado areas inwards from the borders (Pivello et al. 1999a,b). Although most Asteraceae are heliophilous, tree density and canopy shading may still foster Asteraceae abundance and diversity in two ways: (1) moderate tree density and shading may increase heterogeneity, and benefit species with distinct microhabitat requirements; (2) canopy shading also helps to inhibit encroachment by invasive grasses, whose negative effect on cerrado Asteraceae species is clearly seem in our results, indirectly promoting Asteraceae abundance and diversity. These effects can explain why our results showed a positive correlation of tree density and canopy cover with total abundance and species density of Asteraceae, apparently contrary to initial expectation based on previous studies (e.g. Fonseca et al. 2005).

## CONCLUSIONS

Our study shows that Asteraceae, the second largest plant family in the Cerrado Biome, presents higher species richness at intermediate levels of human-caused disturbance. We found that this hump-shaped relationship between Asteraceae species richness and disturbance is due to an increase in the number of habitat-generalist species, whereas the proportion of typical cerrado species decreases along the anthropogenic disturbance gradient. Additionally, we noted that the ascertained effect of disturbance on species diversity is dependent on the diversity index used. None of the taxonomical diversity indices varied with disturbance, hence the number of higher taxa (genera to tribe) per species or individuals of Asteraceae is not substantially affected by disturbance.

## ACKNOWLEDGEMENTS

We are grateful to Martin Videla, Marina R. Braun, Mário Ferreira-Neto, Tehra G. Mendonça and Marília B. Santiago, for helping us with fieldwork, and to João Semir, Roberto L. Esteves and Mara Magenta for providing or confirming identification of Asteraceae. This manuscript was improved by comments by Vânia R. Pivello, Paulo Inácio Prado, Glauco Machado and André V.L. Freitas. This study was supported by FAPESP grants #98/05085-2 to TML within the BIOTA-FAPESP Program, #04/15482-1 to TML, #03/02541-0 to MAN, and CNPq grant # 306049/2004 to TML.

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**Appendix.** Tribes, subtribes and species of Asteraceae recorded in the sampled transects in an anthropogenic disturbance gradient of 20 cerrado sites in three adjacent counties in the state of São Paulo, Brazil. "C" represents core cerrado Asteraceae species, "I" represents invasive Asteraceae species, and * represents habitat-generalist species.

| **Tribe** | **Subtribe** | **Species** | **C or I** |
|---|---|---|---|
| Astereae | Asterinae | *Baccharis coridifolia* DC. | * |
| | | *Baccharis dracunculifolia* DC. | * |
| | | *Baccharis punctulata* DC. | * |
| | | *Baccharis subdentata* DC. | * |
| | | *Conyza canadensis* (L.) Cronquist | I |
| Eupatorieae | Ageratinae | *Ageratum fastigiatum* (Gard.) R.M. King., H. Rob. | * |
| | | *Stevia commixta* B. Robinson | * |
| | Ayapaninae | *Ayapana amygdalina* (Lam.) R.M. King., H. Rob. | * |
| | | *Heterocondylus alatus* (Vell.) R.M. King., H. Rob. | * |
| | Gyptidinae | *Campuloclinium chlorolepis* (Baker) R.M. King., H. Rob. | C |
| | | *Campuloclinium hirsutum* Gardner | C |
| | | *Trichogonia salviaefolia* Gardner | * |
| | Mikaniinae | *Mikania cordifolia* (L. f.) Willd | * |
| | | *Mikania hirsutissima* DC. | * |
| | | *Mikania micrantha* Kunth | * |
| | | *Mikania* aff. *nummularia* | * |
| | | *Mikania oblongifolia* DC. | * |
| | Praxelinae | *Chromolaena chaseae* (B.L. Robins) R.M. King., H. Rob. | C |
| | | *Chromolaena laevigata* (Lam.) R.M. King., H. Rob. | * |
| | | *Chromolaena odorata* (L.) R.M. King., H. Rob. | * |
| | | *Chromolaena pedunculosa* (Hook., Arn.) R.M. King., H. Rob. | * |
| | | *Chromolaena pungens* (Gardner) R.M. King., H. Rob. | C |
| | | *Chromolaena squalida* (DC.) R.M. King., H. Rob. | * |
| | | *Praxelis clematidea* (Griseb.) R.M. King., H. Rob. | * |
| Gnaphalieae | Gnaphaliinae | *Achyrocline satureioides* (Lam.) DC. | * |
| Helenieae | Pectidinae | *Porophyllum angustissimum* Gardner | C |
| | | *Porophyllum ruderale* (Jacq.) Cass. | * |
| Heliantheae | Coreopsidinae | *Bidens gardneri* Baker | * |
| | | *Isostigma peucedanifolium* Less. | C |
| | Eclipdinae | *Aspilia reflexa* Baker | C |
| | Helianthinae | *Viguiera arenaria* Baker | C |
| | | *Viguiera robusta* Gardner | * |
| | Melamponiinae | *Calea verticillata* (Klatt) Pruski | C |
| | Verbesininae | *Dimerostemma rotundifolium* (Baker) Blake | C |
| | | *Tilesia baccata* (L.f.) Pruski | * |
| Mutisieae | Mutisiinae | *Chaptalia integerrima* (Vell.) Burkart | * |
| | | *Gochnatia barrosii* Cabrera | C |
| | | *Gochnatia polymorpha* (Less.) Cabrera | * |
| | | *Gochnatia pulchra* Cabrera | C |
| | Naussauviinae | *Trixis verbasciformis* Less. | * |
| Plucheeae* | | *Pluchea sagittalis* (Lam.) Cabrera | I |
| | | *Pterocaulon alopecuroides* (Lam.) DC. | * |

| Tribe | Subtribe | Species | C or I |
|---|---|---|---|
| Plucheeae* | | *Pterocaulon lanatum* Kuntze | * |
| | | *Pterocaulon rugosum* (Vahl.) Malme | * |
| Senecioneae | Senecioninae | *Emilia sonchifolia* (L.) DC. | I |
| | | *Erechtites hieracifolius* (L.) Raf. ex DC. | I |
| | | *Hoehnephytum trixoides* (Gardner) Cabrera | * |
| Vernonieae | Chrestinae | *Chresta sphaerocephala* DC. | C |
| | Elephantopodinae | *Elephantopus biflorus* (Less.) Sch. Bip. | C |
| | | *Elephantopus mollis* Kunth | * |
| | | *Orthopappus angustifolius* (Sw.) Gleason | * |
| | Piptocarphinae | *Piptocarpha rotundifolia* (Less.) Baker | C |
| | Vernoniinae | *Chrysolaena herbacea* (Vell.) Rob. | * |
| | | *Lepidaploa canescens* (Kunth) H. Rob. | * |
| | | *Lepidaploa psilostachya* (DC.) H. Rob. | * |
| | | *Lepidaploa remotiflora* (L.C. Rich.) H. Rob. | * |
| | | *Lessingianthus bardanoides* (Less.) H. Rob. | C |
| | | *Lessingianthus brevifolius* (Less.) H. Rob. | * |
| | | *Lessingianthus grandifolius* (Less.) H. Rob. | C |
| | | *Lessingianthus laevigatus* (Mart. ex DC.) Robins. | * |
| | | *Stenocephalum apiculatum* (Mart. ex DC.) Sch. Bip. | C |
| | | *Vernonanthura brasiliana* (L.) H. Rob. | * |
| | | *Vernonanthura ferruginea* (Less.) H. Rob. | * |
| | | *Vernonanthura membranacea* (Gardner) H. Rob. | * |
| | | *Vernonanthura mucronulata* (Less.) H. Rob. | * |
| | | *Vernonanthura phosphorica* (Vell.) H. Rob. | * |

# 2

# Does herbivore diversity respond to human-induced disturbance as well as host-plant does?

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## SUMMARY

The high dependence of insect herbivores on their host plants means that they can respond both directly and indirectly to disturbance, via habitat requirements and host-plant availability, respectively. In this study, we evaluated the effects of anthropogenic disturbance in remnants of cerrado vegetation on the diversity of endophagous insects of Asteraceae flowerheads. Specifically, we aimed to investigate: (1) if herbivore diversity peaks at intermediate disturbance levels as their host-plants; (2) if there is a disturbance effect on herbivore richness independently of host-plant richness, and (3) if the ratio of herbivore to host-plant richness changes in a consistent way along the disturbance gradient. We sampled Asteraceae flowerheads in 20 remnants of Brazilian cerrado varying from slightly to extremely disturbed sites. The number of sampled host-plant species had a strong positive effect on total herbivore richness. The observed herbivore richness showed a significant quadratic relationship with disturbance, whereas the rarefied richness decreased at more disturbed sites. Simpson's diversity did not present any clear tendency along the gradient. After take into account the number of sampled-plant species through a linear multiple regression, disturbance had a significant negative effect on herbivore richness. The ratio of herbivore to host-plant richness decreased significantly along the gradient. Although it seems obvious at a first glance that plant diversity begets herbivore diversity, it is not clear whether other factors affect this relationship. Our results indicate that anthropogenic habitat disturbance should mediate the effect of plant diversity on herbivore due to differential responses of these two trophic levels to disturbance magnitudes. Herbivore diversity did not increase substantially from low to intermediate disturbance levels, but their host-plants did.

# INTRODUCTION

Herbivore insects constitute a large proportion of global biodiversity, comprising at least one-quarter of all described species (Strong et al. 1984; May 2000). However, the huge diversity of tropical herbivore insects, particularly of endemic and rare ones, has been continually impoverished at larger spatial scales due to the high rates of habitat loss and human-induced disturbances (Brooks et al. 2002). Although several studies have addressed the effects of human-caused disturbances on different insect groups (e.g. Holloway et al. 1992; Lawton et al. 1998), the current information on the ecological mechanisms and consequences of insect diversity losses are incipient, taxonomically biased, and very disproportional both to numerical diversity and ecological importance of this animal group.

It is well known that most herbivore insects feed on phylogenetically close plants and on specific plant organs or tissues (Price 1980; Janzen 1988; Novotny et al. 2002; Novotny & Basset 2005; Ødeggard et al. 2005; Novotny et al. 2006). Thus, all else being equal, we can expect a positive correlation between plant richness and insect herbivore richness. In fact, this assertion is part of a larger ecological hypothesis which states that a greater variety of resources support a greater diversity of consumers (Hutchinson 1959; Hunter & Price 1992). For herbivore insects and plants, this prediction has been confirmed by experimental and correlative studies at several spatial scales (Murdoch et al. 1972; Southwood et al. 1979; Prendergast et al. 1993; Siemann et al. 1998; Symstad et al. 2000; Haddad et al. 2001; but see Hawkins & Porter 2003).

The high dependence of insect herbivores on their host plants means that they can respond both directly and indirectly to disturbance, via habitat requirements and host-plant availability, respectively. Therefore, an important question to be addressed is whether disturbance effects on host plants mediate variations in herbivore diversity along disturbance gradients. Furthermore, it remains unclear if species highly connected by trophic interactions, such as herbivore insects and their host plants, respond similarly to anthropogenic disturbance. According to the Intermediate-

Disturbance Hypothesis (IDH; Grime 1973a,b; Connell 1978), at low disturbance levels, species diversity is reduced due to exclusion promoted by few competitive dominant species. At intermediate disturbance levels species coexistence is maintained by a nonequilibrium state in which strong competitors cannot dominate. Finally, at high disturbance levels most populations are reduced or extinct, decreasing total diversity. Thus, IDH predicts a hump-backed variation in diversity along a disturbance gradient. Although this prediction has been confirmed by many studies (e.g. Molino & Sebatier 2001; Almeida-Neto et al. chapter 1), several other ones have refuted it by showing positive, negative and no-effect of disturbance on diversity (see Mackey & Currie 2001; Hill & Hamer 2004, and references in both studies). Mackey & Currie (2001) reviewed the literature on the disturbance-diversity relationship and concluded that this relationship is neither consistently strong nor consistently higher at intermediate levels. In fact, there is a consensus that the disturbance-diversity relationship is dependent on several factors such as spatial scale, target taxa and habitat (Lawton et al. 1998; Hamer & Hill 2001; Mackey & Currie 2001; Hill & Hamer 2004).

In this study, we evaluated the effects of anthropogenic disturbance in remnants of cerrado vegetation on the diversity of a set of herbivorous insects defined by a similar resource rather than by a purely taxonomic criterion: the endophagous fauna of Asteraceae flowerheads. Asteraceae is the second largest plant family in Brazilian cerrados (Warming 1973; Mendonça et al. 1998) and their flowerheads are food resources of a speciose endophytic insect fauna in many habitats of the world (Zwölfer 1988; Zwölfer & Romstöck-Volkl 1991; Lewinsohn 1991; Prado et al. 2002; Almeida et al. 2006). Based on a parallel study on Asteraceae diversity (Almeida-Neto et al. chapter 1), which shown that plant richness tends to peak at intermediate disturbance levels, we expect a similar disturbance-diversity relationship for the endophagous fauna of Asteraceae flowerheads. More specifically, we aimed to investigate three major questions: (1) do abundance and diversity of herbivores follow the same response to anthropogenic disturbance of their host-plants, i.e. a peak at intermediate disturbance levels?; (2) is there a disturbance effect on herbivore richness independently of host-plant richness? (3) does the ratio of endophagous insects to host-plant richness change in a consistent way along the disturbance gradient? To explore possible mechanisms underlying the disturbance-diversity relationship, we investigated the effect of host-plant identity by contrasting the potential herbivore richness of each site according to host plant composition along the disturbance gradient.

## METHODS

### *Study sites and habitat characterisation*

This study was conducted from April 2004 to February 2005 in 20 cerrado sites located in three adjacent counties in the state of São Paulo, Southeastern Brazil (see details about the sites in the chapter 1). The regional climate is classified as Cwa by the Köppen system, being characterized by two well-defined seasons: dry winters and rainy summers (Embrapa-CCPSE 1999). Original landscape of the region was composed mainly by cerrado, semideciduous and riparian forests (Soares et al. 2003). Currently, the original vegetation comprises less than 10% of the studied region and has been replaced by pastures, monocultures, silvicultures and urbanized areas (Soares et al. 2003). The sites are spaced apart from 0.6 to 41.4 km, at elevations between 600 to 950 m a.s.l.

The cerrado biome is the largest savanna vegetation in South America, comprising approximately 2 million km$^2$. This biome is considered a global biodiversity hotspot (Myers et al. 2000) and has been greatly converted for human use, as pasture and cash-crop agriculture (Klink & Machado 2005). The cerrado biome is constituted by a mosaic of physiognomies, ranging from open grasslands to sclerophyllous dry forests. These different physiognomies result from variations in soil fertility, geomorphology, rainfall regime and fire frequency (Goodland & Pollard 1973; Oliveira-Filho et al. 1989; Fonseca et al. 2005). Thus, to minimize the influence of additional factors in our analysis, such as shade and humidity, we did not include woodland physiognomies, because they present a sparse herbaceous layer, and, consequently, low density and diversity of

Asteraceae (Filgueiras 2002; Fonseca et al. 2005). Moreover, the sites were selected *a priori* to maximize the length and coverage of the human disturbance gradient.

### *Sampling methods*

Due to phenological differences among Asteraceae species, the availability of flowerheads varies in abundance and composition along the year. Thus, we adopted two strategies to minimize taxonomic bias of host-plant sampling: (1) we sampled each site in three periods (April/May, August/September, and January/February), and (2) we sampled all sites within an interval of 35 days in each period. The sampling periods include the flowering peaks of the most speciose tribes of Asteraceae in Brazilian cerrados (Mantovani & Martins 1988; Batalha & Matovani 2000).

We extrapolated total density of flowerheads per site by estimating the modal flowerhead display for each species, and counting the number of flowering/fruiting individuals of each Asteraceae species in 15 randomly placed transects of 30 x 5 m per period. In order to perform a random sampling of host plant density, we randomised two coordinates to place the transects using the edges of sites as references: (1) the position along the edge of the sites with a minimal spacing of 10 m between two transects, and (2) the starting position perpendicular to the edge from a minimum of 5 up to 55 m. The modal number of flowerheads per individual plant for each species was classified into the following classes: 1) 1–3; 2) 4–10; 3) 11–30; 4) 31–100; 5) 101–300; 6) 300–1000; 7) 1000–3000, and 8) 3000–10000. Flowerhead density per site was estimated as the sum across species of the product of the plant population density and the modal flowerhead display.

In order to spread our sampling, we collect roughly 80 ml of flowerheads (or less, if not available) per individual plant and make an effort to sample 20 sub-samples (if available) per Asteraceae species. Moreover, we spent more-or-less four person hours collecting flowerheads in each sampling period and site. Consequently, those rare Asteraceae species and/or those with few flowerheads per plant were proportionally over-sampled. In fact, both total sampled weight and number of sampled plant individuals were highly correlated to our estimates of average plant and average flowerhead density per transect (Pearson correlation coefficients > 0.85 and $P < 0.0001$ for all correlations).

In the laboratory, the flowerhead samples were kept in plastic containers covered with a mesh lid, where adult herbivore emergency were weekly checked out for a period of two months. The insects were identified to the loweest taxonomic category. Several undescribed species and poorly known insect groups, mainly cecidomyiids and microlepidoptera, were analysed using a morphospecies approach.

### *Disturbance measurement*

Since habitat disturbance is a combination of several factors, it is rarely feasible to isolate and measure a single cause of human disturbance in non-experimental studies at the landscape or regional scales. For this reason, a common procedure for measuring the magnitude of disturbance is to use one or more easily measurable variables as surrogates for disturbance, such as land use (Ribera et al. 2001), cattle load or grazing (Cagnolo et al. 2002), and density of invasive weeds or pioneer species (De Pietri 1992; Molino & Sabatier 2001). This last surrogate is justified because it has been well established that disturbance increases habitat invasibility (Hobbs & Huenneke 1992; Lozon & MacIsaac 1997). Moreover, invasive species *per se* can be a factor of disturbance (D'Antonio & Vitousek 1992).

Here, we used the cover of five African grasses, namely *Andropogon gayanus* Kunth, *Brachiaria decumbens* Stapf, *Hyparrhenia rufa* (Ness) Stapf, *Melinis minutiflora* Beauvois, and *Panicum maximum* Jacq., as a surrogate for human disturbance level. This indirect measure of human-induced disturbance is supported by studies that have shown a displacement of native grasses by invasive ones after disturbance in South America savannas (Baruch et al. 1985; Klink 1996; Pivello et al. 1999a,b). The five African grass species are reputedly the major invasive species in Brazilian cerrado (Klink 1996; Ratter et al. 1997; Pivello et al. 1999a,b; Filgueiras 2002), thus, we assumed that percent cover of them should indicate the frequency and intensity of remote and recent history of human-induced disturbances. For each transect, we recorded invasive grass cover in five classes: 1) 0%, 2) 1 to 25%; 3) 25 to 50%; 4) 50 to 75%, and 5) 75 to 100%. As an index of invasive grass cover we used the average value for all 45 transects pooled over three sampling periods in each site.

### *Data analysis*

We employed both linear and quadratic regressions to examine the effects of disturbance on all response variables related to herbivores and their host-plants. Residual normality was checked for all regression analyses. Models were chosen through comparison of the sum of squares for the quadratic and linear models following Zar (1999). We used Murtaugh's test for monotonicity (Murtaugh 2003) on each quadratic regression to evaluate whether the relationships between disturbance level and the response variables display an intermediate maximum, that is, unimodality against the null hypothesis of monotonicity.

Initially, we examined the effect of disturbance on herbivore abundance. As we can assume a linear relationship between sampling effort and sampled individuals, we standardize our comparisons by dividing the number of herbivores by the dry weight of sampled flowerheads in each site. In order to avoid biased estimations of abundance per sampling effort we did not include samples of host-plant species without any herbivore record. We then examined the effect of disturbance on herbivore diversity using species richness, and Simpson's complement index ($1 - \lambda$). These two diversity indices are in wide use and, furthermore, they respond differently to two important components of diversity, number of species and evenness (Magurran 2004). Additionally, we adjusted herbivore richness in each site to a common standard, the lowest herbivore abundance found in a site (82 individuals), through Hurlbert's (1971) rarefaction method. We used an individual, rather than sample-based rarefaction (see Gotelli & Colwell 2001), because most herbivore species are monophages, and, consequently, most host-plant species are used by a small fraction of the herbivore species. Sample-based rarefaction assumes that species can occur at random among samples.

In order to examine the effect of disturbance on herbivore richness taking host-plant richness into account, we performed a multiple linear regression with disturbance level and plant richness as independent variables. We compared the effects of both independent variables by contrasting their standardized coefficients of regression and their partial coefficients of determination. Furthermore, we investigated the effect of host-plant composition in our analysis using the potential herbivore richness along the disturbance gradient. The potential herbivore richness was estimated by assuming that all host-plants in a specific site are used by their regional pool of endophagous insects instead of by only those insects recorded in that site. Finally, we investigated another important attribute of communities, the ratio between trophic levels (Cohen 1977; Martinez & Lawton 1995). The herbivore/plant ratio was regressed on disturbance levels to assess whether it changes systematically with disturbance.

## RESULTS

Altogether, we sampled flowerheads from 5655 plant individuals and 71 species of Asteraceae in the 20 study sites. From these flowerhead samples, 14512 endophagous individuals, representing 138 insect species of 10 families and three orders, were collected (Table 1; see Appendix). Sixty six percent of the herbivore species were recorded exclusively on one host-plant species, and only 12.3% were sampled in two or more plant species of different tribes (Fig. 1). The number of sampled herbivores per site ranged from 82 to 1431 individuals, and their abundances per unit weight of sampled flowerheads did not change consistently along the disturbance gradient ($F_{1,18} = 2.84$; $P = 0.106$; Fig. 2).

The richness of sampled host plants showed a quadratic relationship with the magnitude of disturbance and a significant peak at intermediate disturbance levels (Fig. 3; Murtaugh's test, $P$ = 0.025). As expected, endophage richness was highly correlated with sampled host plant richness (Fig. 4; $F_{1,18}$ = 54; $R^2$ = 0.750). Hence, total endophage richness per site also showed a significant quadratic relationship with disturbance level (Fig. 5A), but did not show a significant peak at intermediate disturbance levels (Murtaugh's test, $P$ = 0.175). The quadratic relationship between herbivore richness and disturbance did not change for potential herbivore richness (see Methods) compared with observed richness (Fig. 5B). By contrast, the endophage richness standardized by rarefaction showed an inverse linear relationship with disturbance level (Fig. 5C), and Simpson's diversity did not present any clear tendency along the gradient (Fig. 5D).

**Table 1.** Composition of herbivore insects feeding on asteracean flowerheads in 20 Brazilian cerrado sites varying from slightly to highly human disturbed.

| Order | Family | Number of species and morphospecies | Number of individuals |
|---|---|---|---|
| Diptera | Agromyzidae | 14 | 468 |
| | Cecidomyiidae | 49 | 2866 |
| | Tephritidae | 39 | 7572 |
| Coleoptera | Anthribidae | 1 | 111 |
| | Apionidae | 8 | 3046 |
| Lepidoptera | Blastobasidae | 1 | 2 |
| | Gelechiidae | 4 | 107 |
| | Pterophoridae | 5 | 142 |
| | Pyralidae | 3 | 95 |
| | Tortricidae | 14 | 102 |

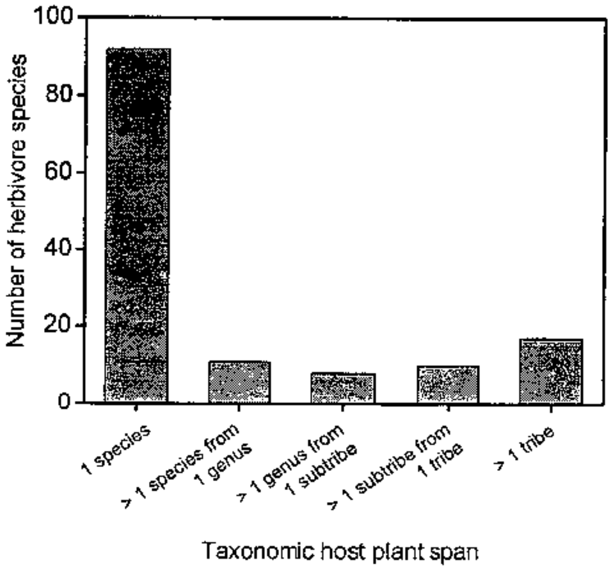

**Figure 1.** Pooled host taxonomic span of flowerhead feeding insects on Asteraceae species from 20 Brazilian cerrado sites.

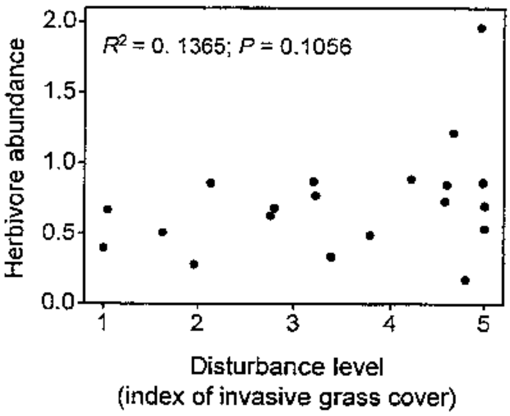

**Figure 2.** Number of flowerhead feeding insects per gram of dry weight of Asteraceae flowerheads (pooled from all host plants and sampling periods for each site) along a gradient of anthropogenic disturbance comprised by 20 sites. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

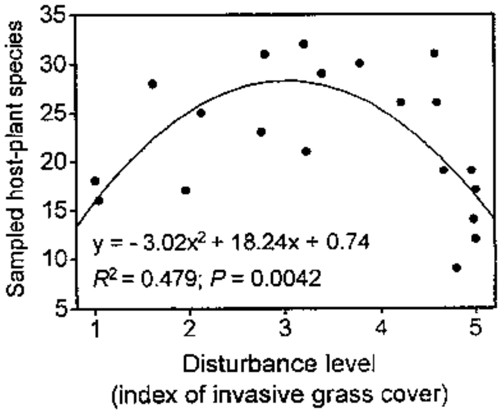

**Figure 3.** Number of sampled host plants along a gradient of anthropogenic disturbance along the disturbance gradient, in 20 Brazilian cerrado sites. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

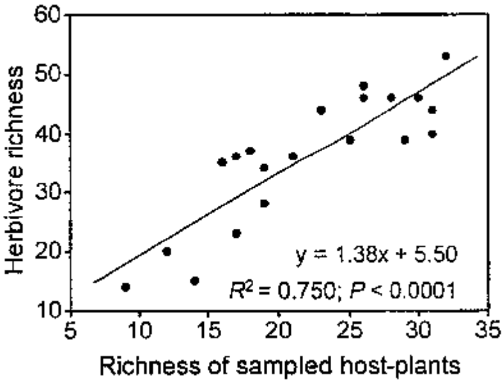

**Figure 4.** Relationship between the number of sampled host species of Asteraceae and the number of species of flowerhead feeding insects in 20 Brazilian cerrado sites.

The level of disturbance had a weak, but significant, negative effect on herbivore richness when we taken into account the number of sampled-plant species through a linear multiple regression (Table 2; Full model: $R^2 = 0.822$; $F_{2,17} = 39.3$; $P < 0.0001$; *HERBIVORE RICHNESS* = 1.304 *HOST-PLANT RICHNESS* – 2.183 *DISTURBANCE LEVEL* + 14.89). Thus, the initial quadratic relationship between disturbance level and herbivore richness can be explained as an indirect effect via host-plant richness.

The ratio of herbivore to host plant richness decreased significantly along the gradient (Fig. 6). This result cannot be ascribed to changing plant composition because the potential herbivore richness did not decrease monotonically along the disturbance gradient (Fig. 5B).

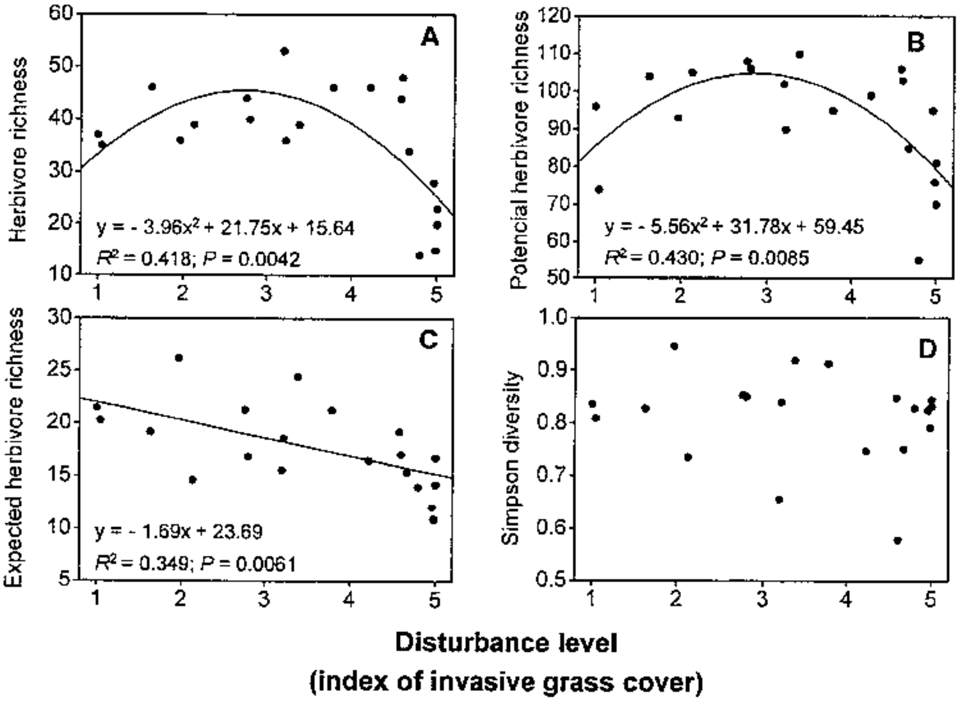

**Figure 5.** Effect of disturbance level on (A) total herbivore richness, (B) potential herbivore richness according to regional herbivore pool for each host-plant, (C) standardized herbivore richness rarefied according to the smallest sample, and (D) Simpson (1 - λ) diversity of herbivores. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

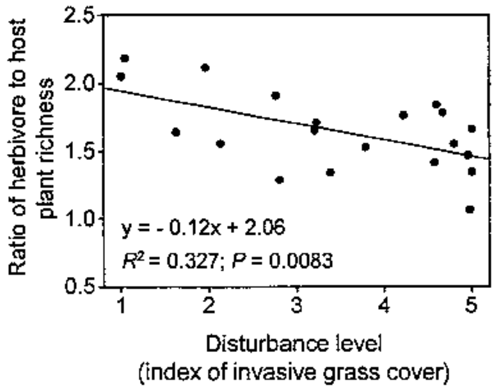

**Figure 6**. Effect of anthropogenic disturbance on the ratio of herbivore to host plant richness in 20 Brazilian cerrado sites. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

**Table 2.** Multiple linear regression between herbivore richness and two independent variables: richness of host-plants and disturbance level. $r^2$ is the coefficient of determination, $r^2_{adj}$ in is the adjusted coefficient of determination for the other independent variable, $b$ is the regression coefficient, $b'$ is the standardized regression coefficient, and $P$ is the probability for the associated $t$-value.

| **Independent variable** | $r^2$ | $r^2_{adj}$ | $b$ | $b'$ | **$t$-value** | $P$ |
|---|---|---|---|---|---|---|
| Host-plant richness | 0.643 | 0.783 | 1.304 | 0.816 | 7.837 | <0.0001 |
| Disturbance level | 0.072 | 0.288 | -2.183 | -0.273 | -2.621 | 0.0179 |

## DISCUSSION

To our knowledge, this is the first study to use a clearly circumscribed system of endophagous insects to investigate disturbance effects on herbivore diversity taking diversity of their hosts into account as well. Infested and non-infested plant parts by most endophagous insect herbivores, except for leaf-miners and gall-makers, cannot be easily recognized. Thus, sampling assemblages of concealed endophagous insects demands to collect and process a great amount of indiscriminate host plants. This difficulty may account for the scarceness of studies on endophagous insect faunas, compared to studies on externally feeding herbivores, mainly leaf-chewers and sap-suckers (e.g. Janzen 1988; Novotny et al. 2002). However, studies on endophytic insect faunas can reveal important aspects of plant-animal interactions because endophagous herbivores tend to be more specialized on their host plants (Janzen 1980; Gaston et al. 1992) and, thus, they may be more affected by variations in host-plant abundance and composition than external feeders.

In this study, the pattern of flowerhead endophage richness along the anthropogenic disturbance gradient is similar to the pattern shown by their host plants (Almeida-Neto et al. chapter 1). Since host plant richness is known to be a strong predictor of herbivore richness (e.g., Murdoch et al. 1972; Janz et al. 2006), the similarity in both responses to habitat disturbance was expected. However, differently from their hosts, herbivore richness does not show a significant peak at intermediate disturbance levels. Moreover, after adjusting for the influence of herbivore abundance on herbivore richness by a rarefaction procedure, the number of herbivore species decreased significantly as the disturbance level increased. This result contrasts with the quadratic relationship between disturbance and rarefied host-plants (Almeida-Neto et al. chapter 1). Fuentes & Jaksic (1988) proposed that the hump-backed relationship between diversity and disturbance should be more frequent in land plants than among land animals due to three conditions more likely to be met among the formers: (1) significant reduction in the number of users of an area or resource patch after a disturbance event; (2) availability of a more diverse pool of species capable of occupying released resources, and (3) stronger competitive effects leading to exclusion of most colonizers. In their review, Mackey & Currie (2001) reinforced this prediction by reporting that significant intermediate peaks of diversity are most frequent in plants than in animals. Our results illustrate this difference for an interactive system formed by herbivore insects and their host plants in a human disturbance gradient.

Differently from the patterns shown by herbivore richness and diversity, herbivore abundance per unit weight did not vary consistently along the disturbance gradient. This indicates that disturbance does not promote generalized population declines of herbivores and contradicts, in part, the results of other studies that have shown lowered insect herbivore abundances, mainly of specialist insect pests, in richer plant communities (Root 1973; Strong et al. 1984). This apparent contradiction could result from a more efficient herbivore control by their predators, mainly parasitoids, in less disturbed sites. Marino & Landis (1996) suggested that diversity of parasitoids, and hence intensity of parasitism, may be greater in later successional habitats, due to more abundant and diverse food resources, such as plant nectar and homopteran honeydew, for adult parasitoids. Further studies are necessary to test this hypothesis.

The ratio between trophic levels is an important community attribute related to food web structure (Cohen 1977; Briand & Cohen 1984), but it has been rarely investigated in studies on plant-herbivore interactions (but see Dixon et al. 1987; Gaston 1992; Fonseca et al. 2005). Our results showed that disturbance may lead to a decrease in the herbivore to plant richness ratio. This decrease seems to result of the negative effect of disturbance on herbivore richness, as evidenced by the multiple regression with host-plant richness and disturbance level as independent variables. An important implication of this result is that both local and regional comparisons of trophic ratios, such as herbivore to plant richness, can be affected by differences in disturbance levels across sites or regions.

Although it seems obvious at first that plant diversity should beget herbivore diversity, it is not self-evident whether, and how, other factors such as disturbance, productivity and temperature, affect this relationship. Our results indicate that anthropogenic habitat disturbance mediates the effect of plant diversity on herbivore diversity due to differential responses of these two trophic levels to disturbance magnitude.

## ACKNOWLEDGEMENTS

We are grateful to various colleagues for their valuable help with fieldwork, and to Marina R. Braun, Valéria C. Maia, Maria V. Urso-Guimarães, Sérgio Vanin, José R. Mermudes, João Semir, Roberto L. Esteves and Mara Magenta for providing or confirming identification of insects and plants. This manuscript was improved by comments by Glauco Machado, Carlos R. Fonseca, André V.L. Freitas, and Gustavo Q. Romero. This study was supported by FAPESP grants # 98/05085-2 to TML within the BIOTA-FAPESP Program, # 04/15482-1 to TML, # 03/02541-0 to MAN, and CNPq grant # 306049/2004 to TML.

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**Appendix.** Orders, families and species of endophagous insects reared from asteracean flowerheads sampled in 20 cerrado remnants in three adjacent counties in the State of São Paulo, Brazil.

| **Order** | **Family** | **Species/morphospecies** |
|---|---|---|
| Coleoptera | Anthribidae | *Trigonorhinus* sp. |
| | Apionidae | *Apion* sp.1 |
| | | *Apion* sp.2 |
| | | *Apion* sp.4 |
| | | *Apion* sp.5 |
| | | *Apion* sp.6 |
| | | *Apion* sp.9 |
| | | *Apion* sp.10 |
| | | *Apion* sp.11 |
| Diptera | Agromyzidae | *Liriomyza* sp. |
| | | *Melanagromyza bidentis* Spencer |
| | | *Melanagromyza chaptaliae* Spencer |
| | | *Melanagromyza erechtitidis* Spencer |
| | | *Melanagromyza floris* Spencer |
| | | *Melanagromyza minima* Malloch |
| | | *Melanagromyza minimoides* Spencer |
| | | *Melanagromyza neotropica* Spencer |
| | | *Melanagromyza* sp. 1 |
| | | *Melanagromyza* sp. 2 |
| | | *Melanagromyza* sp. 3 |
| | | *Melanagromyza* sp. 4 |
| | | *Melanagromyza* sp. 5 |
| | | *Melanagromyza* sp. 6 |
| | Cecidomyiidae | *Asphondylia* sp.1 |
| | | *Asphondylia* sp.2 |
| | | *Asphondylia* sp.3 |
| | | *Asphondylia* sp.4 |
| | | *Asphondylia* sp.5 |
| | | *Asphondylia* sp.6 |
| | | *Asphondylia* sp.7 |
| | | *Asphondylia* sp.8 |
| | | *Asphondylia* sp.9 |
| | | *Asphondylia* sp.11 |
| | | *Asphondylia* sp.12 |
| | | *Asphondylia* sp.13 |
| | | *Asphondylia* sp.14 |
| | | *Asphondylia* sp.15 |
| | | *Asphondylia* sp.16 |
| | | *Asphondylia* sp.17 |
| | | *Asphondylia* sp.18 |
| | | *Asphondylia* sp.19 |
| | | *Asphondylia* sp.20 |
| | | *Asphondylia* sp.21 |

| Order | Family | Species/morphospecies |
|---|---|---|
| Diptera | Cecidomyiidae | *Asphondylia* sp.23 |
| | | *Asphondylia* sp.23 |
| | | *Asphondylia* sp.24 |
| | | *Clinodiplosis* sp.1 |
| | | *Clinodiplosis* sp.2 |
| | | *Clinodiplosis* sp.3 |
| | | *Clinodiplosis* sp.4 |
| | | *Clinodiplosis* sp.5 |
| | | *Clinodiplosis* sp.6 |
| | | *Contarinia* sp.1 |
| | | *Contarinia* sp.2 |
| | | *Dasineura* sp.1 |
| | | *Dasineura* sp.2 |
| | | *Dasineura* sp.3 |
| | | *Dasineura* sp.4 |
| | | *Dasineura* sp.5 |
| | | *Dasineura* sp.6 |
| | | *Dasineura* sp.7 |
| | | *Dasineura* sp.8 |
| | | *Dasineura* sp.9 |
| | | *Dasineura* sp.10 |
| | | *Dasineura* sp.11 |
| | | *Neolasioptera* sp.1 |
| | | *Neolasioptera* sp.2 |
| | | *Neolasioptera* sp.3 |
| | | *Neolasioptera* sp.4 |
| | | *Neolasioptera* sp.5 |
| | | *Schizomya* sp.1 |
| | | *Trotteria* sp. |
| | Tephritidae | *Baryplegma* sp. |
| | | *Caenoriata pertinax* Bates |
| | | *Cecidochares connexa* Macquart |
| | | *Cecidochares fluminensis* Lima |
| | | *Cecidochares* sp.E |
| | | *Dictyotrypeta* sp.6 |
| | | *Dictyotrypeta* sp.A |
| | | *Dioxyna chilensis* Macquart |
| | | *Dioxyna thomae* Curran |
| | | *Dyseuaresta* sp.B |
| | | *Euarestoides* sp.5 |
| | | *Neomyopites paulensis* Steyskal |
| | | *Paroxyna* sp. |
| | | *Tetreuaresta* sp.1 |
| | | *Tetreuaresta* sp.2 |
| | | *Tomoplagia achromoptera* Prado, Norrbom & Lewinsohn |

| Order | Family | Species/morphospecies |
|---|---|---|
| Diptera | Tephritidae | *Tomoplagia costalimae* Aczel |
| | | *Tomoplagia heringi* Aczel |
| | | *Tomoplagia formosa* Aczel |
| | | *Tomoplagia incompleta* Williston |
| | | *Tomoplagia* sp. "incompletissima" |
| | | *Tomoplagia minuta* Hering |
| | | *Tomoplagia reimoseri* Hendel |
| | | *Tomoplagia* sp.1 |
| | | *Tomoplagia* sp.3 |
| | | *Tomoplagia* sp.5 |
| | | *Tomoplagia* sp.6 |
| | | *Tomoplagia trivittata* Lutz & Lima |
| | | *Trupanea* sp.A |
| | | *Trupanea* sp.B |
| | | *Trupanea* sp.C |
| | | *Trupanea* sp.D |
| | | *Trupanea* sp.E |
| | | *Trupanea* sp.5 |
| | | *Xanthaciura biocellata* Thomson |
| | | *Xanthaciura chrysura* Thomson |
| | | *Xanthaciura insecta* Loew |
| | | *Xanthaciura* sp. "itirapinensis" |
| | | *Xanthaciura mallochi* Aczel |
| Lepidoptera | Blastobasidae | Blastobasidae sp.A |
| | Gelechiidae | Gelechiinae sp.A |
| | | Gelechiinae sp.B |
| | | *Recurvaria* sp.1 |
| | | *Recurvaria* sp.3 |
| | | *Recurvaria* sp.A |
| | Geometridae | *Eupithecia* sp.A |
| | | *Eupithecia* sp.B |
| | | *Eupithecia* sp.C |
| | | *Eupithecia* sp.D |
| | | *Pleuroprucha* sp.A |
| | | *Synchlora* sp. |
| | Pterophoridae | *Adaina bipunctata* Möschler |
| | | *Adaina fuscohodias* Möschler |
| | | *Lioptilodes parvus* Walsingham |
| | | *Lioptilodes* sp. |
| | | *Oidematophorus* cf. *angulofuscus* |
| | Pyralidae | Phycitinae sp.A |
| | | *Rotruda* sp. |
| | | *Unadilla* cf. *erronela* |
| | Tortricidae | *Argyrotaenia* sp.A |
| | | *Argyrotaenia* sp.B |
| | | Cochylini sp.9 |

| Order | Family | Species/morphospecies |
|---|---|---|
| Lepidoptera | Tortricidae | Cochylini sp.A |
| | | Cochylini sp.B |
| | | Cochylini sp.C |
| | | Cochylini sp.C12 |
| | | Cochylini sp.D |
| | | Cochylini sp.E |
| | | Cochylini sp.F |
| | | Cochylini sp.G |
| | | *Cochylis* cf. *sagitifera* |
| | | *Phalonidia squalida* Raz. & Becker |
| | | *Phalonidia unguifera* Raz. & Becker |

# 3

# Contrasting responses of herbivore insects of the same guild to anthropogenic disturbance

Mário Almeida-Neto, Paulo I. Prado, Marina R. Braun, Valéria C. Maia, Maria V. Urso-Guimarães and Thomas M. Lewinsohn

## SUMMARY

Studies on disturbance have shown disparate results, varying from positive to negative effects on species diversity. One possible explanation for contrasting results derives from life history traits of species, generally expressed as taxonomically related differences. Consequently, studies focusing on lower taxonomic levels are more likely to detect circumstantial effects of disturbance on diversity than studies on more inclusive taxa. Here, we examined how different taxonomical groups of the flower head feeding insect guild of Asteraceae respond to anthropogenic disturbance in remnants of Brazilian cerrados. We aimed to investigate if specialization level differs among distinct herbivore taxa and, if so, whether more specialised insect groups are more sensitive to disturbance. Moreover, we evaluated whether the response of one taxonomic group reflects those of other taxonomic groups and could thus serve as a surrogate for estimating other taxa diversity. Overall, we recorded 9 species of Coleoptera, 102 of Diptera and 27 of Lepidoptera. Among the dipterans, 14 species of Agromyzidae, 49 of Cecidomyiidae, and 39 of Tephritidae were found. The coleopterans seem to be more specialized than dipterans and lepidopterans. Among the dipterans, cecidomyiids were more specialized than both agromyzids and tephritids. The observed richness of most insect groups showed a quadratic variation with disturbance level. However, apart from a clear decline of rarefied coleopteran richness, the expected richness adjusted by rarefaction did not show any consistent variation along the disturbance gradient. Although no taxonomic group had a strong relationship with complementary richness, all groups were positively and significantly related to the complementary richness of herbivore insects. This study reveals that even insect taxa from the same guild can respond distinctly to disturbance.

## INTRODUCTION

The search for patterns related to species distribution along environmental gradients has been, and still is, one of the major goals of ecology (MacArthur 1972; Rosenzweig 1995). A few decades ago, the majority of studies concerning patterns of species distribution were focused only on natural gradients, whereas the effects of human-induced disturbances were practically ignored in the ecological literature. Similarly, studies on the disturbance-diversity relationship investigated mostly those due to natural disturbance events (e.g., Connell 1978; Armesto & Pickett 1985). Currently, the alarming rates of habitat degradation have promoted a widespread interest in the effects of anthropogenic disturbance on species diversity (Pimm et al. 2006).

Theory predicts (Grime 1973; Horn 1975; Connell 1978; Huston 1979) and several empirical studies have shown a hump-backed relationship between disturbance and diversity (e.g., Aronson & William 1995; Molino & Sabatier 2001). However, the review of Mackey & Currie (2001) suggests that the diversity-disturbance relationship is not always strong, nor does it consistently peak at intermediate levels. In fact, studies on disturbance have shown disparate results, varying from positive to negative effects on species diversity (see Mackey & Currie 2001, and references therein). There are several possible explanations for these contrasting results, which can be grouped in three major classes according to their major cause: (1) environmentally-driven effects, such as productivity (Grime 1973; Huston 1979; Kondoh 2001) and soil fertility (Givnish 1999); (2) sampling-related effects, such as the spatial scale at which communities are studied (Hamer & Hill 2000; Hill & Hamer 2004), the intensity range of the disturbance gradient (Li et al. 2004), and differences in the detection of rare species (Mackey & Currie 2000), and finally (3) those variations related to the life history traits of species (Fuentes & Jaksic 1988; Ribera et al. 2001), generally expressed as taxonomically related differences (Lawton et al. 1998; Schulze et al. 2004), trophic level (Wootton 1998), dispersal ability (Fuentes & Jaksic 1988; Thomas 2000), and the level of specialization on food resources (Lawton 1995). On this last attribute, it has been suggested that higher levels of specialization increase the susceptibility to disturbance (Den Boer 1968; Kitahara et al. 2000; but see Vázquez & Simberloff 2002). Obviously, studies focusing on lower taxonomic levels are more prone to evince circumstantial effects of disturbance on diversity than studies on more inclusive taxa, because a group composed of phylogenetically close species tends to respond in a similar way to the same environmental factors, due to niche conservatism (Peterson et al. 1999).

Complete surveys of insect diversity are unfeasible in species-rich habitats, such as tropical forests and savannas, due to the huge number of unknown and rare species. For this reason, the majority of studies regarding the effects of human-induced disturbances on insect diversity has focused on taxonomically well-resolved insect groups, such as butterflies (Hamer & Hill 2000; Uehara-Prado et al. 2006), ants (Andersen 1997), bees (Liow et al. 2001), and some groups of beetles (Davis et al. 2001; McGeoch et al. 2002). Given that both habitat requirements and ecophysiological traits differ considerably among distinct insect groups, it is not surprising that studies on different taxa have shown disparate relationships between disturbance and diversity (e.g., Basset et al. 1998; Lawton et al. 1998; Hamer & Hill 2000; see Mackey and Currie 2001 and references therein). Another common procedure in studies on disturbance-diversity relationship has been to use some species group as indicator or surrogate of biodiversity. According to McGeoch (1998), a biodiversity indicator is a taxonomic or functionally defined species group whose diversity reflects some measure of the diversity (richness, endemism) of other higher taxa in a habitat or set of habitats. Several insects groups, such as butterflies, moths, some beetles families, and ants have been proposed as efficient indicators of biodiversity in terrestrial ecosystems (Pearson & Cassola 1992; Andersen 1997; Alonso 2000; Brown & Freitas 2000). Another approach is to use certain habitat features as surrogates for estimating insect richness. This could be done in cases where species-level conservation is impractical due to huge system diversity, in which case habitat-conservation may be used as a surrogate (Loyola & Martins, in press). However, despite widespread use of the bioindicators in the ecological literature, there is little consensus on the applicability of this approach (Schulze et al. 2004).

Since the responses of different insect taxa to disturbance can be ascribed to trophic level or, more specifically, to the way in which a given species explores its resources, an alternative way to test the taxonomic consistency of the disturbance-diversity relationship is to focus on insect taxa of the same guild. In this study, we seek to examine how different taxonomical groups of the phytophagous insect fauna of Asteraceae flower heads respond to anthropogenic disturbance. This fauna can be considered as a guild and, in fact, it fit quite well the original concept of Root (1967). Flower heads of Asteraceae are formed by a group of florets on a common receptacle surrounded by involucral bracts and it constitutes the functional unit which serves as the flower (Bremer 1994). This floral structure constitutes a food resource for larval stages of a speciose fauna of insects composed mainly by dipterans, microlepidopterans and curculionoid beetles (Lewinsonh 1991; Gagné 1994; Redfern 1983; Headrick & Goeden 1998; Prado & Lewinsohn 2004; Almeida 2006). Besides investigating the effect of disturbance on the diversity of distinct taxonomical groups, we asked the following questions: (1) does specialization level of the herbivores differ among distinct taxa?; (2) if so, are those more specialised insect groups more sensitive to disturbance?; (3) does richness of the distinct taxonomic groups of herbivores predict the richness of other groups, i.e. whether the response of one taxonomic group reflects those of other taxonomic groups and could thus serve as a surrogate for estimating other taxa diversity?; (4) do different taxonomic groups of endophagous insects suffer differential extinction or inclusion in a disturbance gradient, to the point of affecting taxonomic-based diversity measures?

## METHODS

### *Study area*

This study was conducted in 20 remnants of cerrado vegetation forming a gradient from slightly to highly anthropogenically disturbed sites, spaced apart from 0.6 to 41.4 km in three adjacent counties of São Paulo state, Southeastern Brazil. The regional climate is characterized by two well-defined seasons, dry winters and rainy summers (Embrapa-CCPSE 1999), and the altitude of the sites varies from 600 to 950 m a.s.l.

The cerrado is a savanna-like vegetation and comprises a mosaic of physiognomies varying from open grasslands to dense woodlands (see Goodland & Pollard 1973; Oliveira & Marquis 2002 for further details). To minimize the range of additional factors, such as shade and humidity, in our analysis, we did not include dense woodland physiognomies, called cerradão, because they present a sparse herbaceous layer, in which most Asteraceae species are to be found (Filgueiras 2002; Fonseca et al. 2005). Moreover, the sites were selected a priori to maximize the range of the anthropogenic disturbance gradient.

### *Sampling procedures*

Flower head samples were collected in three periods (April/May, August/September, and January/February) from 2004 to 2005. These sampling periods include the flowering peaks of the five most speciose tribes of Asteraceae in Brazilian cerrado (Mantovani & Martins 1988; Batalha & Matovani 2000; Almeida et al. 2005). In order to reduce phenological variations, all sites were sampled within an interval of 35 days in each period.

Insects were recorded only through rearing from flower head samples. Since often there are no external marks to spit concealed endophagous insects, we collected and processed a great amount of host plants and flower heads. In order to spread our sampling among and within the sites, we collected roughly 80 ml of flower heads (or less, if not available) per individual plant and we endeavoured to sample 20 individual plants per Asteraceae population. Circa four person hours were spent collecting flower heads in each period and site. Both total sampled weight of flower heads and number of sampled host-plant individuals were highly correlated with our estimates of plant and flower head density per site (Pearson correlation coefficients > 0.85 and $P < 0.0001$ for all correlations). In the laboratory, the flower head samples were kept in plastic containers covered with a mesh lid, where adult herbivore emergence were weekly checked for a period of two months. The insects were identified to the lowest taxonomic category, based on the literature and reference collection. Several undescribed or poorly known taxa were sorted and analyzed as morphospecies.

### ***Disturbance measurement and additional variables***

The level of anthropogenic disturbance in any habitat is a combination of several processes, and, thus, it is rarely feasible to isolate and directly measure a single cause of disturbance in non-experimental studies. A common solution adopted in studies on anthropogenic disturbance is to measure one or more variables as surrogates for disturbance level, such as land use (Ribera et al. 2001), cattle load or grazing (Cagnolo et al. 2002), fire (Hoffmann 1996), or density of invasive weeds or pioneer species (De Pietri 1992; Molino & Sabatier 2001). Here, we used the cover of five African grasses, namely *Andropogon gayanus* Kunth, *Brachiaria decumbens* Stapf, *Hyparrhenia rufa* (Ness) Stapf, *Melinis minutiflora* Beauvois, and *Panicum maximum* Jacq., as a surrogate for anthropogenic disturbance level. These five African grass species are reputedly the major invasive species in Brazilian cerrado (Klink 1996; Ratter et al. 1997; Pivello et al. 1999a,b; Filgueiras 2002; Hoffmann et al. 2004). This indirect measure of human-induced disturbance is supported by studies that have shown a displacement of native grasses by invasive ones after disturbance in South American Savannas (Baruch et al. 1985; Pivello et al. 1999a,b).

For each transect, we recorded invasive grass cover in five classes: 1) 0%, 2) 1 to 25%; 3) 25 to 50%; 4) 50 to 75%, and 5) 75 to 100%. As an index of invasive grass cover (IGC) we used the mean value for all 45 transects in each site. Although the IGC values did not conform to a normal distribution in some sites, the use of mean, instead of median or mode, as a measure of central tendency is justified because there is no extreme value (range = 1 to 5). Furthermore, these three measures of central tendency are highly correlated (Pearson's correlation coefficients > 0.94).

***Data analysis***

We measured the level of specialization of herbivores through (1) the number of host plant species consumed by each herbivore and (2) through an approach based on the taxonomic inclusiveness of the host plants consumed. For this second measure, we establish the following values for specialization level: 1 = one host species; 2 = more than one host species from one genus; 3 = more than one genus from one subtribe; 4 = more than one subtribe from one tribe; 5 = more than one tribe. To test for differences in specialization level among the insect groups, we applied the nonparametric Kruskal-Wallis test. Paired differences between taxa were compared through a Tukey-type nonparametric test (Zar 1999). Singleton herbivore species were excluded from these analyses in order to avoid biased calculations of specialization level. We evaluated the effects of disturbance on the relative number of species of each herbivore taxonomic group by testing the correlation between the proportion of species from each group and disturbance level through a Spearman rank correlation test.

We employed both linear and quadratic regressions to examine the effects of disturbance on species richness of each taxonomic group. Models were chosen through comparison of the sum of squares for the quadratic and linear models following Zar (1999). We examined the effect of disturbance on both raw and adjusted species richness through Hurlbert's (1971) rarefaction method. This individual-based rarefaction standardizes comparisons by correcting for the differences in total abundance among samples. For each taxonomic group, we used the smallest number of individuals sampled in one locality as reference for rarefactions. Only sites with at least 15 individuals were included in the individual based-rarefactions. We used Murtaugh's test for monotonicity in each quadratic regression to evaluate whether the relationships between disturbance and richness showed an intermediate maximum, that is, unimodality against the null hypothesis of monotonicity (Murtaugh 2003).

Linear least-squares regression was applied to examine whether different taxonomic groups can be used as surrogates of other taxa in evaluating the overall effects of disturbance. In order to avoid non-independence in these regressions, we used complementary herbivore richness by subtracting the richness of the predictor taxonomic group from the total herbivore richness. Additionally, we evaluated the correlation between each pair of observed as well as the rarefied species richness of each taxonomic group through Pearson correlation coefficients.

To evaluate whether there is a consistent taxonomic inflation of some herbivore taxa along the disturbance gradient, we applied three diversity measures based on taxonomic relatedness among species proposed by Warwick & Clarke (1995) and Clarke & Warwick (1998, 1999), namely taxonomic distinctness ($\Delta^*$), average taxonomic distinctness ($\Delta^+$), and variation in taxonomic distinctness ($\Lambda^+$). Taxonomic distinctness estimates the average taxonomic path length within a classification tree between any pair of non-conspecific individuals in the sample. The same measure with presence/absence data produces average taxonomic distinctness, which is the expected average path length between any pair of species, regardless of their abundances. Variation in taxonomic distinctness measures whether certain taxa are over or under- represented. To estimate the relatedness of individual species, we used four taxonomic levels (species, genus, family and order). All diversity indices were calculated using PRIMER 5 (Clarke & Gorley 2001).

## RESULTS

We sampled flower heads from 5655 plant individuals and 71 species of Asteraceae in the 20 sites. From these samples, we recorded nine species of Coleoptera (3157 individuals), 102 of

Diptera (10906 individuals) and 27 of Lepidoptera (489 individuals). Among the dipterans, we found 14 species of Agromyzidae (468 individuals), 49 species of Cecidomyiidae (2866 individuals), and 39 species of Tephritidae (7572 individuals).

Specialization level did not differ among the three orders of herbivores when measured as number of host species (Fig. 1 insets; Kruskal-Wallis $H = 3.62$; $P = 0.164$), but showed a significant difference when we used the level of taxonomic inclusiveness of their hosts as proxy for level of specialization (Fig. 1; Kruskal-Wallis $H = 8.29$; $P = 0.016$). Nonetheless, paired nonparametric Tukey-type tests for this last measure of specialization did not detect significant differences between the three insect orders. The herbivore species of the three families of Diptera differed in their level of specialization both when measured as number of hosts (Fig. 2 insets; Kruskal-Wallis $H = 21.19$; $P < 0.0001$) and in the taxonomic span of their host species (Fig. 2; Kruskal-Wallis $H = 27.59$; $P < 0.0001$). Nonparametric Tukey-type multiple comparisons showed that the Cecidomyiidae species were significantly more specialized than either Agromyzidae or Tephritidae, but these two families did not differ in their specialization levels.

The observed richness of coleopterans did not show any clear tendency along the disturbance gradient (Fig. 3A), but both dipteran and lepidopteran richness varied quadratically with disturbance (Fig. 3D, E). On the other hand, only for coleopterans, did the rarefied richness show a significant negative relationship with disturbance level (Fig. 3B). All three dipteran families showed quadratic relationships with disturbance level (Fig. 4), but their shapes (i.e. parameters) were clearly different among the families. None of these relationships between richness and disturbance for the taxonomic groups showed a significant peak at intermediate levels of disturbance ($P > 0.10$) according to Murtaugh's test.

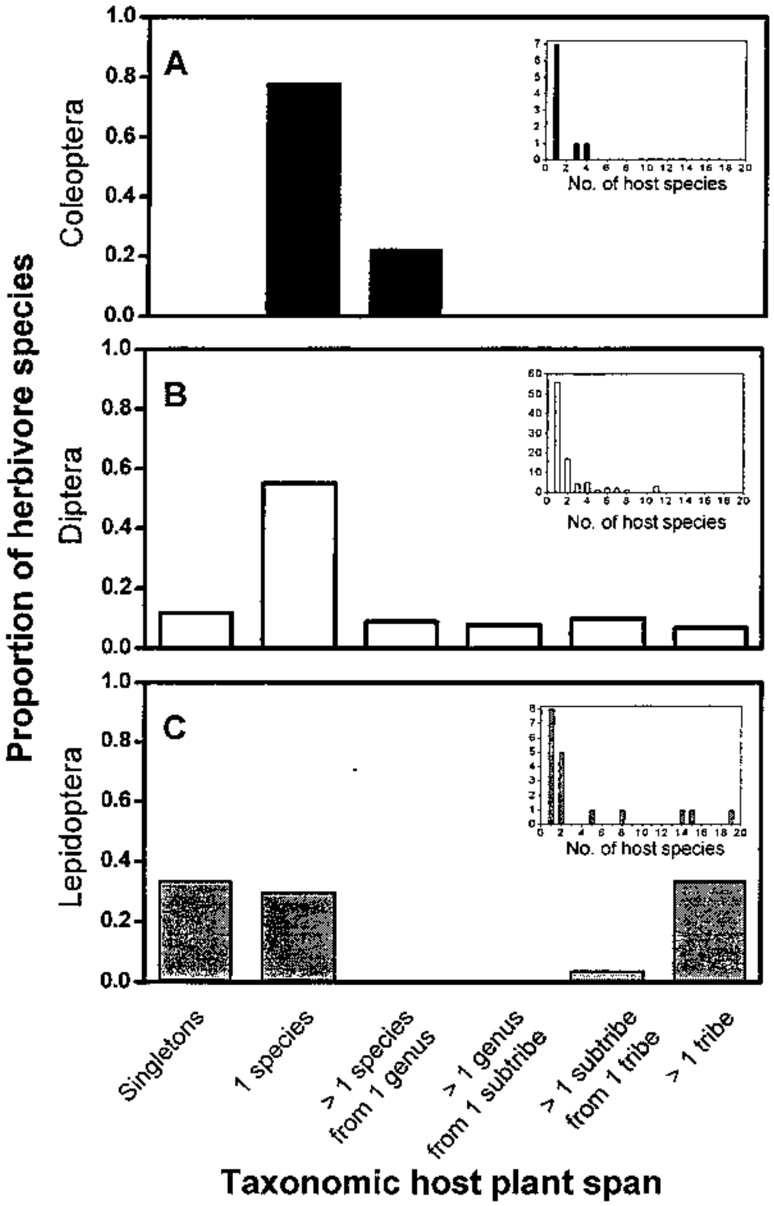

**Figure 1**. Pooled host taxonomic span of three orders of flower head feeding insects on Asteraceae species from 20 Brazilian cerrado sites. Insets show the number of host species used by the herbivores.

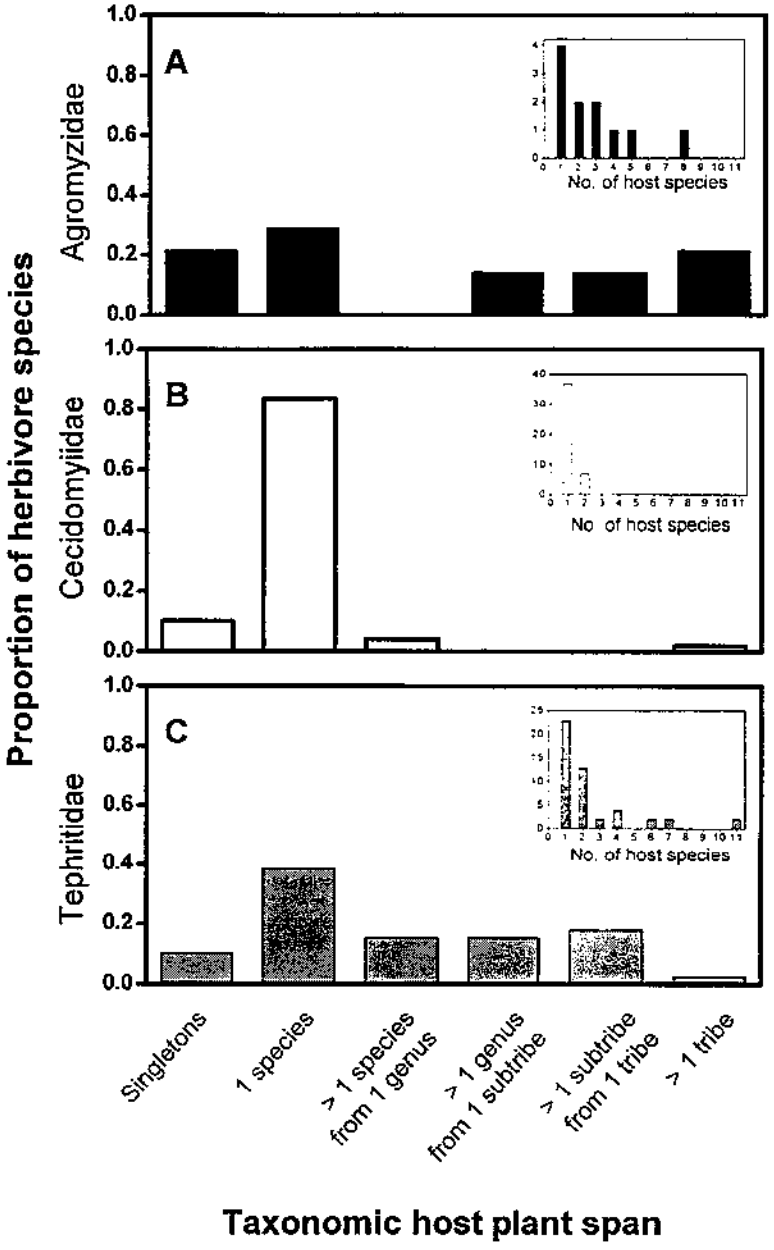

**Figure 2.** Pooled host taxonomic span of three dipteran families of flower head feeding insects on Asteraceae species from 20 Brazilian cerrado sites. Insets show the number of host species used by the herbivores.

Every each taxonomic group was positively and significantly related to the summed richness of all the other herbivore groups (Fig. 5). The explained variation in complementary herbivore richness varied from 38.6% for Lepidoptera to 58.8% for Tephritidae, and the other groups explained approximately 50% of variation of complementary species richness of all other insects (Fig. 5). Correlations between observed richness of insect groups varied from 0.81 for tephritids with agromyzids to 0.49 for cecidomyiids with agromyzids. Moreover, correlations of observed richness were always higher than for their rarefied richness (Tables 1 and 2).

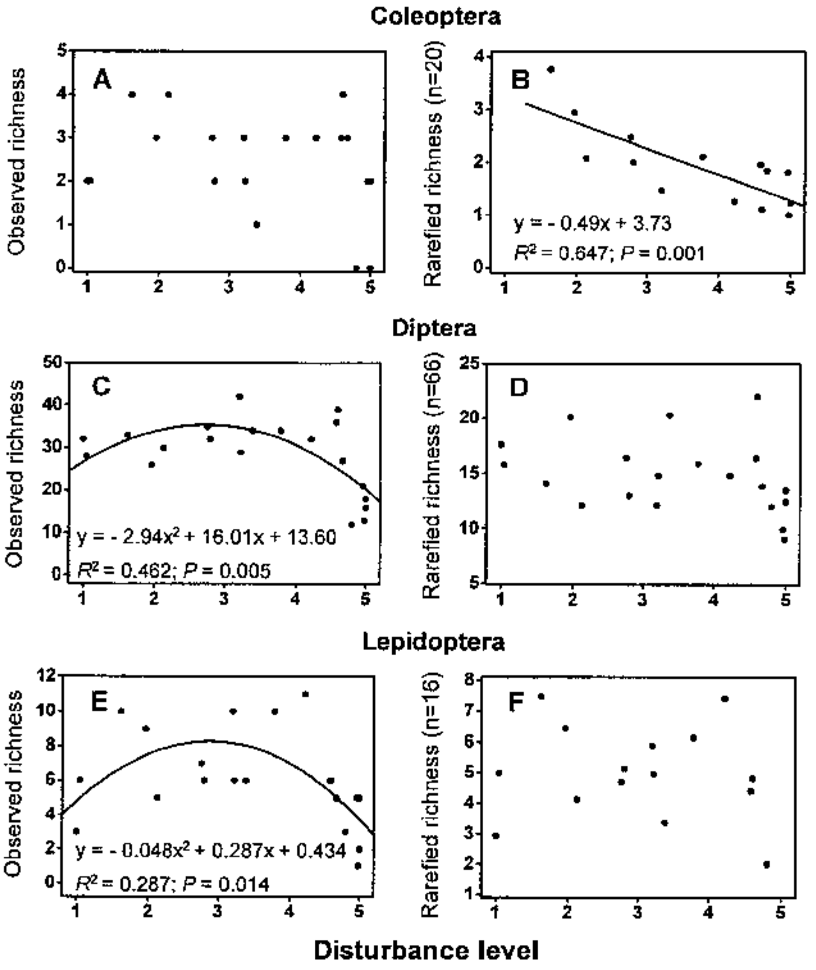

**Figure 3.** Effect of disturbance level on observed and rarefied richness of the three orders of flower head feeding insects sampled from Asteraceae species in 20 Brazilian cerrado sites. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

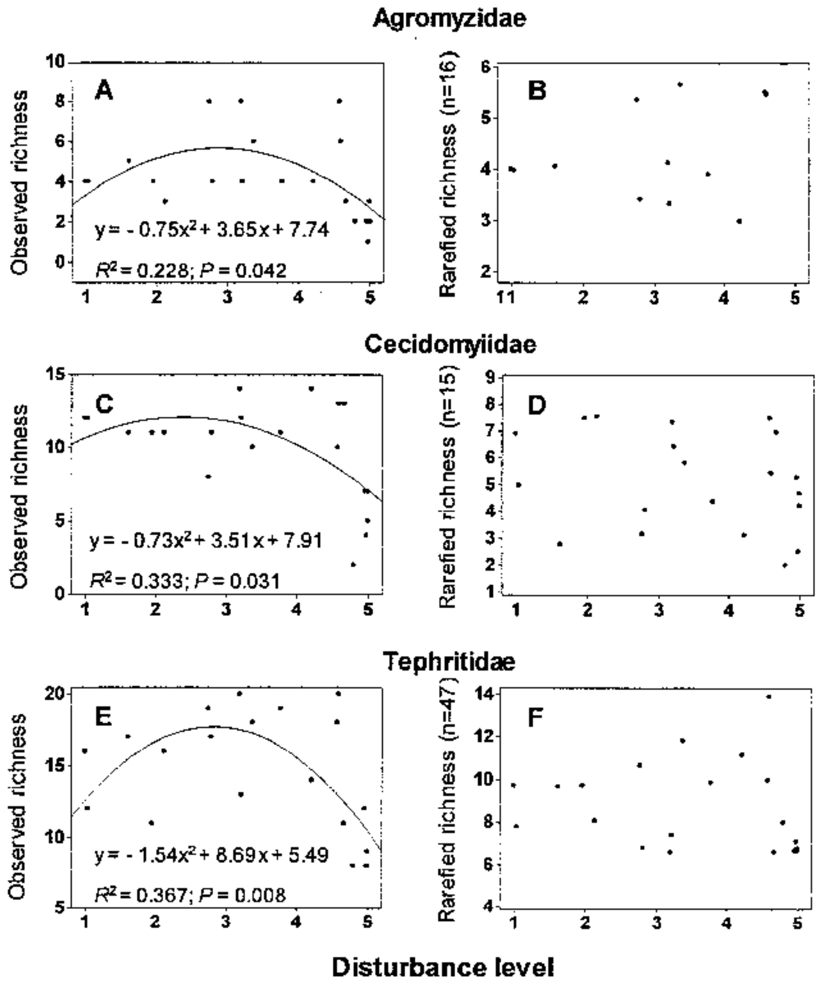

**Figure 4.** Effect of disturbance level on observed and rarefied richness of the three dipteran families of flower head feeding insects sampled from Asteraceae species in 20 Brazilian cerrado sites. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

No trend of change in the proportion of species of any order, or of any dipteran family, is apparent along the disturbance gradient, and the corresponding Spearman rank coefficients were lower than 0.32 ($P > 0.17$) in all cases (Fig. 6). We found no significant effect of disturbance level on the diversity indices based on taxonomic distinctness and disturbance level (Fig. 7).

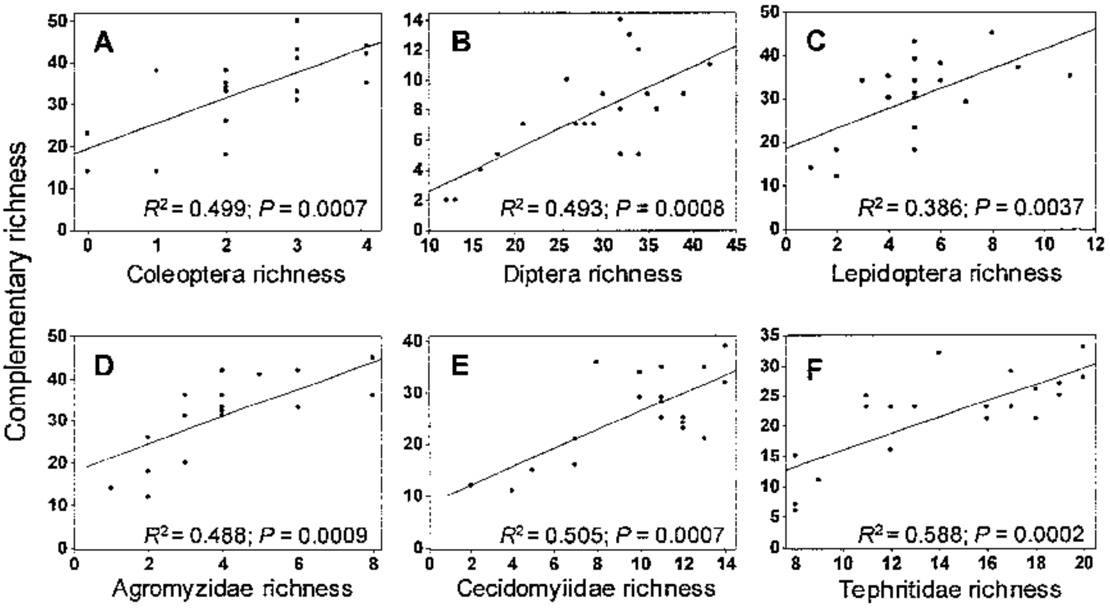

**Figure 5.** Relationship of the three orders of flower head feeding insects and the three dipteran families with the complementary herbivore richness (i.e., total richness of all other insect taxa). All insects were sampled from Asteraceae species in 20 Brazilian cerrado sites.

**Table 1.** Pearson correlation coefficients of species richness among three herbivore orders. The upper right part of the table shows correlations of observed species richness; the lower left portion of the table (below the diagonal) presents correlations of expected species richness through rarefaction. Values in the diagonal represent correlations between observed and rarefied species richness. Degrees of freedom vary with the number of sites in which each taxon was found.

| | **Coleoptera** | **Diptera** | **Lepidoptera** |
|---|---|---|---|
| **Coleoptera** | 0.443NS<br>(df = 11) | 0.685***<br>(df = 18) | 0.558*<br>(df = 18) |
| **Diptera** | 0.221NS<br>(df = 12) | 0.549*<br>(df = 18) | 0.606**<br>(df = 18) |
| **Lepidoptera** | 0.322NS<br>(df = 9) | -0.030NS<br>(df = 13) | 0.943***<br>(df = 13) |

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

**Table 2.** Pearson correlation coefficients of species richness among three families of dipteran herbivores. The upper right part of the table shows correlations of observed species richness; the lower left portion of the table (below the diagonal) presents correlations of expected species richness through rarefaction. Values in the diagonal represent correlations between observed and rarefied species richness. Degrees of freedom vary with the number of sites in which each taxon was found.

| | **Agromyzidae** | **Cecidomyiidae** | **Tephritidae** |
|---|---|---|---|
| **Agromyzidae** | 0.722**<br>(df = 10) | 0.494*<br>(df = 18) | 0.807***<br>(df = 18) |
| **Cecidomyiidae** | 0.253NS<br>(df = 10) | 0.547*<br>(df = 18) | 0.612**<br>(df = 18) |
| **Tephritidae** | 0.584*<br>(df = 10) | -0.024NS<br>(df = 18) | 0.570**<br>(df = 18) |

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

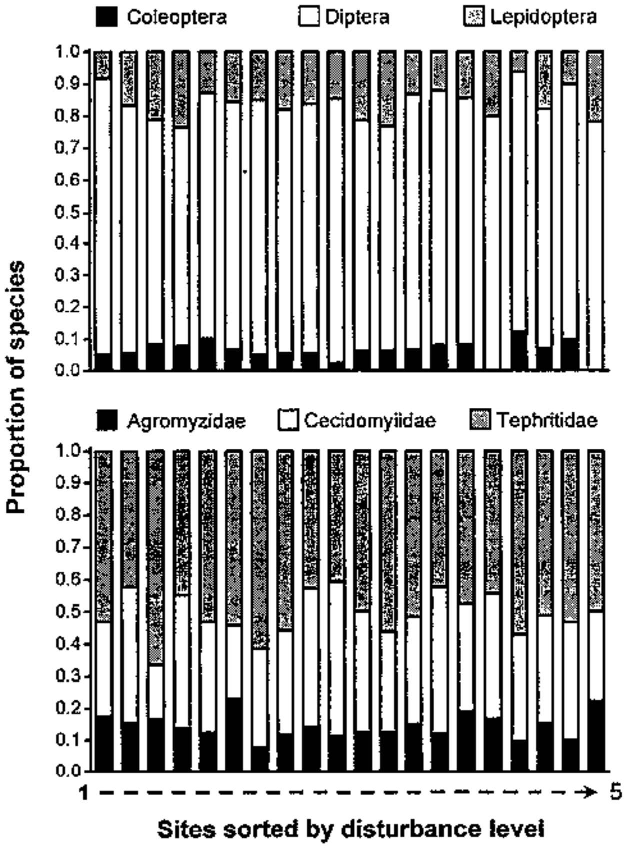

**Figure 6.** Proportions of the three orders of flower head feeding insects and the three dipteran families sampled from Asteraceae species in 20 Brazilian cerrado sites.

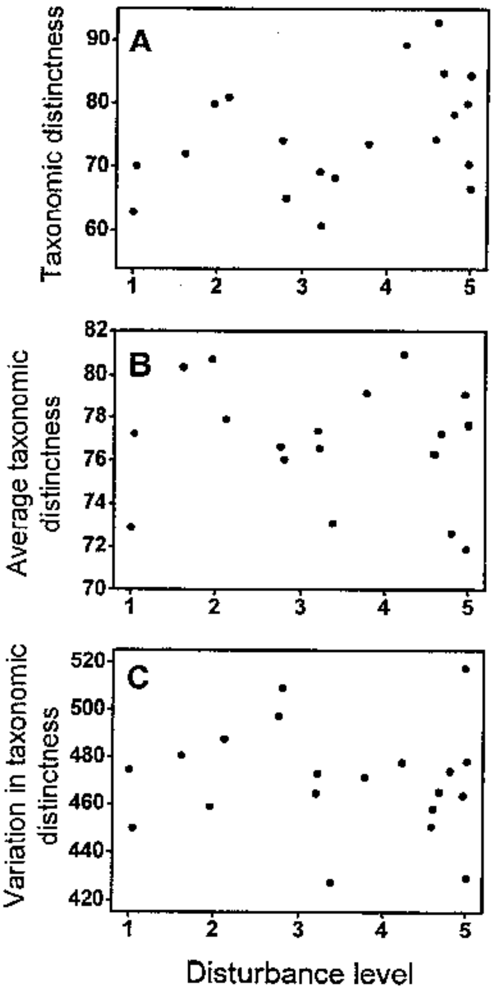

**Figure 7.** Effect of disturbance level on three measures of diversity based on the taxonomic distinctness of species, namely (A) taxonomic distinctness, (B) average taxonomic distinctness, and (C) variation in taxonomic distinctness of flower head feeding insects sampled from Asteraceae in 20 sites of Brazilian cerrados. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

## DISCUSSION

The first aim of this paper was to examine whether herbivore taxa within the same guild show similar or discrepant responses to anthropogenic disturbance. In a previous study (chapter 2 of this thesis), we showed that the observed richness of flower head feeding insects varies quadratically with disturbance, whereas the rarefied expected richness decreased in more disturbed sites. In the present study, we found that the general relationship between endophage richness and disturbance cannot be generalized among distinct taxonomic groups that constitute the fauna of flower head feeding insects. The observed richness of two orders (Diptera and Lepidoptera) and of three dipteran families showed quadratic relationships with disturbance. However, after species richness was adjusted for sample size through rarefaction, except for coleopterans, the richness of flower head feeding taxa showed no significant trend with disturbance level.

Several studies have shown differences in the responses of arthropod taxa to habitat disturbance. In a study carried out in Cameroon forests, Lawton et al. (1998) found that butterflies, flying and canopy beetles, canopy and ground ants, and termites presented very different responses to change in habitat disturbance. In two studies in Borneo, Beck et al. (2002) and Fiedler & Schulze (2004) showed that moth diversity generally declined with forest disturbance, but different moth taxa did not respond in the same manner. The list of studies reporting positive, negative, quadratic and neutral effects of disturbance on the diversity of determined insect taxa is extensive (e.g. Mackey & Currie 2001; Hill & Hamer 2004; Schulze et al. 2004; Moretti et al. 2006). In our judgment, a large part of these discrepancies arises from studies focusing on excessively restricted taxonomic levels. Moreover, at smaller spatial scales, habitat disturbance frequently increases diversity (Hamer & Hill 2000; Hill & Hamer 2004). Therefore, generalizations on the effect of disturbance on insect diversity based on local studies focusing on a restricted taxonomic group should be conservatively viewed as circumstantial findings. On the other hand, the response of higher taxa to disturbance does not obligatory carry through to each of its constituent lower taxa, as shown here.

Given the hypothesis that more specialized species tend to be more susceptible to disturbance (Den Boer 1968; Lawton 1995; Kitahara et al. 2000), we expected that those insect groups more specialized on their host plants should be more susceptible to disturbance than the more generalist ones. Our findings provide partial support for this hypothesis. The rarefied richness of the seemingly most specialized insect order, Coleoptera, showed a significant decrease in higher disturbed sites. However, neither the observed nor the rarefied richness of the most specialized dipteran family, Cecidomyiidae, presented negative relationships with disturbance. Vázquez & Simberloff (2002) also found no relationship effect of degree of specialization in a plant-pollinator system in sites grazed by cattle in southern Argentina. According to them, failure to assess crucial resources, substantial direct effects of disturbance, inaccurate measures of specialization, difficulty to detect nonlinear relationships, and limitations of a nonexperimental approach are possible reasons for not findings a positive relationship between specialization and disturbance. Our herbivore-plant system did not suffer from the first, and maybe the principal, problem listed by Vázquez & Simberloff (2002) because asteracean flower heads are themselves the critical resource to the herbivore fauna studied here.

We also found no relationship between disturbance and the proportion of species from each insect group. In a study on arctiid moths along a successional gradient in Ecuadorian rain forest, Hilt & Fiedler (2006) found that the proportions of subfamilies varied distinctly along the gradient. They hypothesized that both larval specialization and change in host plant composition can account for the differences along the gradient. Their study illustrates a common approach in studies on disturbance-diversity relationship: to focus on a given well-delimited taxonomic group. Our approach was to delimit the taxa studied by focusing on a similar resource, asteracean flower heads. In this sense, we first delimit a guild instead of a taxonomic group. For this reason, further comparisons of our findings on proportions of insect groups with other studies should be caution evaluated because other studies frequently focused on very distinct guilds and at some instances on distinct trophic levels.

A fundamental question in conservation biology is whether diversity is related among different taxonomic groups and whether any group can be used as a surrogate of the effects of disturbance on the remaining groups. In our study, Tephritidae is the most effective candidate insect group to serve as a surrogate for the entire guild of flower head feeding insects. However, no insect group explained more than 60% of the variation in complementary richness of all other insects. A possible explanation for this result is that the distribution of specialization levels within Tephritidae is the most similar to that for all insect species (see Chapter 2 of this thesis). Interestingly, although all coleopterans consumed only 20% of all host-plants, their observed richness explain practically 50% of the variation in species richness of all other insects. Additionally, all relationships were positive, indicating that all herbivore groups respond in the same direction to disturbance.

Our findings on diversity measures based on taxonomic distinctness did not support the statement of Clarke & Warwick (2001) that under disturbance, species from relatively species-poor higher taxa tend to disappear first, so that the remaining species will belong to a smaller number of groups that tend to be relatively speciose. In the present study no taxonomic based diversity measure showed a monotonic change along the disturbance gradient. This means that the different taxonomic groups of endophagous insects did not suffer differential species extinction or recruitment to the point of affecting taxonomic diversity measures. In a recent study performed in inland waters in the Iberian Peninsula, Abellán et al. (2006) found that taxonomic distinctness measures were not able to identify human disturbance effects. According to them, taxonomic distinctness measures were apparently less sensitive to the effects of anthropogenic impact than other diversity measures, such as species richness and rarity.

In summary, our study shows that, excluding the coleopterans, the richness of the other major taxa of flower head feeding insects varies quadratically with disturbance. As showed for total endophagous richness, no insect order or family peaked at intermediate levels of disturbance. Moreover, the proportions of species from the distinct insect taxa showed no consistent change with disturbance and nor any taxonomic distinctness measure decrease along the disturbance gradient. This study reveals that even insect taxa from the same guild can respond distinctly to disturbance and that a response to higher taxonomic levels cannot correspond to the responses to their component taxa.

## ACKNOWLEDGEMENTS

We are grateful to various colleagues for their valuable help with fieldwork. We also thank S. Vanin and J.R. Mermudes for taxonomical assistance with coleopterans. This manuscript was improved by comments by Rafael D. Loyola, Umberto Kubota, and Glauco Machado. This study was supported by FAPESP grants # 98/05085-2 to TML within the BIOTA-FAPESP Program, # 04/15482-1 to TML, # 03/02541-0 to MAN, and CNPq grant # 306049/2004 to TML.

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# 4

# The structure of plant-herbivore interactions along a human disturbance gradient

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## SUMMARY

A primary question related to ecological networks is how environmental factors affect their structure. We evaluated the effects of anthropogenic disturbance on the structure of a plant-herbivore system formed by Asteraceae species and their flower head feeding insects. In order to explore the effects of disturbance on interaction structure, we used four network-related properties, namely the number of interactions, connectance, nestedness and compartmentation. We sampled Asteraceae flower heads in 20 remnants of Brazilian cerrado varying from very slightly to extremely disturbed. The number of interactions varied quadratically with disturbance level. Connectance showed a marginally significant U-shaped relationship with anthropogenic disturbance. However, after controlling for the influence of species richness on connectance values, connectance was lower at higher disturbance levels. The degree of nestedness decreased significantly from least- to most- disturbed sites. Species richness was significantly correlated with all measures of degree of compartmentation, but the number of sub-networks was not related to disturbance level. We found evidence of non-random structures in most of the 20 plant-herbivore local networks. Although this result is not unexpected, our findings provide the first evidence of significant and consistent effects of anthropogenic disturbance on the structure of plant-herbivore networks.

# INTRODUCTION

Trophic interactions are not randomly established among species in ecological communities. Several processes and constraints, from simple physical boundaries to complex coevolutionary histories, determine both the number and identity of species that consume or that are consumed by one another (Pimm 1982; Cattin et al. 2004). Therefore, the set of trophic linkages among species constitutes a distinguishing feature of communities beyond their species richness and composition. When species interactions are organized into a network, such as food webs, we can look for several collective properties to describe the topological, dynamical or energetic aspects of interactions at the community level (see Cohen 1978; Pimm 1982; Dunne 2006). Two fundamental questions related to ecological networks are (1) how environmental factors affect their structure and, consequently, (2) whether we can predict the structure of ecological networks at different spatial scales (Briand 1983; Jenkins et al. 1992; Bengtsson 1994; Townsend et al. 1998).

Currently, human-caused disturbances are a prime factor of interest in ecological studies due to high rates of habitat loss and intense modifications of natural landscapes by human activities (Vitousek et al. 1997). Although there is a consensus that disturbance can have major effects on species diversity from local to regional scales (Whittaker et al. 2001), there is little agreement on how diversity is affected by distinct disturbance factors and magnitudes (Mackey & Currie 2001). In fact, the disturbance-diversity relationship seems to be highly sensitive to particular factors and contingencies of local communities, such as productivity (Kondoh 2001), choice of studied taxa (Fuentes & Jaksic 1988), and the spatial scale at which communities are examined (Hamer & Hill 2001). These discrepancies of the disturbance-diversity relationship may be a signal that diversity per se is not a general descriptor of disturbance effects on natural communities. Thus, it is imperative to expand our comprehension of the effects of anthropogenic disturbances on other biodiversity attributes, such as the structure of interactions (Memmott et al. 2006; Solé & Montoya 2006). One might surmise that other community attributes, such as interactive properties within food webs, can be more consistently related to environmental gradients and less sensitive to biotic and abiotic contingencies than species count or composition. To date however, few empirical studies have examined the relationships between disturbance and topological food-web properties (Jenkins et al. 1992; Townsend et al. 1998).

In this study, we evaluated the effects of anthropogenic disturbance on the structure of plant-herbivore interactions. A central characteristic of this trophic system is the high average level of feeding specialization of insects on phylogenetically close plants (Ehrlich & Raven 1964; Novotny & Basset 2005; Ødegaard et al. 2005). We focused on the endophytic fauna of Asteraceae flower heads. This herbivore-plant system is particularly interesting because Asteraceae is the largest plant family in the world (Bremer 1994) and their flower heads are food resources of a speciose endophytic insect fauna in many habitats (Zwölfer 1988; Lewinsohn 1991; Gagné 1994; Almeida et al. 2006), allowing further comparisons among geographical regions. In order to explore the effects of disturbance on interaction structure, we used four network-related properties: (1) number of interactions, which together with web size (i.e., species richness) is one of the simplest properties of ecological networks; (2) connectance, which is a scaled measure of the density of interactions into ecological networks; (3) nestedness, which is a kind of interaction asymmetry in which more specialized species interact with a proper subset of those species connected with the most generalist ones (Bascompte et al. 2003; Dupont et al. 2003; Lewinsohn et al. 2006); and (4) compartmentation, which can be broadly defined as sets of species that interact more strongly among themselves than with the rest of the network. Regarding this last property, it is important to stress that in plant-herbivore system, compartments can result both from proximal ecological factors, as habitat subdivision, and from specialized herbivores consuming phylogenetically related host plant species (Pimm 1982; Prado & Lewinsohn 2004; Lewinsohn et al. 2006).

In two previous studies we found that species richness of both endophagous insects and of their host plants varied quadratically with disturbance (see chapters 1 and 2). Thus, we predict a similar hump-backed relationship between the number of interactions and the disturbance level.

Since connectance tends to be smaller in larger networks (Bersier et al. 1999; Montoya & Solé 2003), we expect a U-shaped relationship between this property and the degree of anthropogenic disturbance, i.e. an inverse pattern from that shown by endophage and host plant richness with disturbance. However, after adjusting for the effect of species richness on connectance, we predict a decrease in connectance in more disturbed sites, based on a previous result that showed an inverse relationship between the ratio of endophage to host plant richness with disturbance level (see chapter 2). Based on the assumption that both rare species and rare interactions are prone to disappear before more common ones along the disturbance gradient, we expect a higher degree of nestedness in more disturbed sites. Finally, as we had found that the proportion of typical host plant species from our study habitat (cerrado) decreased in more disturbed sites (see chapter 1), we expect a decrease in compartmentation, based on the hypothesis that disturbance promotes the decrease of typical and specialist species compared to opportunistic and generalist ones, either by selective loss of the former, or by their replacement by the latter.

## METHODS

### *Study sites and habitat characterisation*

We conducted field sampling of flower heads in 20 remnants of cerrado vegetation located in three adjacent counties in the state of São Paulo, Southeastern Brazil, at elevations between 600 to 950 m a.s.l. (see Table 1). We selected the sites a priori to maximize the span and coverage of the human disturbance gradient and to minimize other potentially confounding factors, such as shading, soil moisture, and topography (see chapter 1). The original regional landscape was composed mainly by cerrado, semideciduous and riparian forests (Soares et al. 2003). The cerrado is the largest savanna vegetation in South America, comprising an area of approximately 2 million km$^2$. This biome is considered a global biodiversity hotspot (Myers et al. 2000) and has been largely converted for human use, as pasture and cash-crop agriculture (Sano et al. 2002; Klink & Machado 2005).

### *Flower head sampling and insect rearing*

Asteraceae is the second largest plant family in Brazilian cerrados (Mendonça et al. 1998), and they are very abundant and diverse as herbs and shrubs in physiognomies with open canopies and high light incidence (Filgueiras 2002; Fonseca et al. 2005). Flower head sampling of Asteraceae species was performed from April 2004 to February 2005. Since both abundance and composition of flower heads vary along the year, we used two strategies to minimize sampling bias: (1) each site was sampled in three periods (April/May, August/September, and January/February), and (2) all sites were sampled within 35 days in each sampling period (see details in chapter 1).

We estimated the density of host plant species by counting the number of flowering/fruiting individuals of each Asteraceae species in 15 randomly placed transects of 30 x 5 m per period. In order to perform a random sampling of host plant density, we randomised two coordinates to place the transects using the edges of sites as references: (1) the position along the edge of the sites with a minimal spacing of 10 m between two transects, and (2) the starting position perpendicular to the edge from a minimum of 5 up to 55 m. In order to spread our sampling into sites, we collected roughly 80 ml of flower heads (or less, if not available) per individual plant and we endeavoured to sample 20 individual plants per Asteraceae population. We spent circa four person hours collecting flower heads in each period and site. Both total sampled weight of flower heads and number of sampled host plant individuals were highly correlated with our estimates of average plant and average flower head density per transect (Pearson correlation coefficients > 0.85 and $P < 0.0001$ for all correlations).

In the laboratory, flower head samples were kept in plastic containers covered with fine mesh lids, where adult herbivore emergence was checked once or twice weekly for a period of two months. The insects were identified to the lower taxonomic category (see chapter 2). Several undescribed species and poorly known insect groups, mainly cecidomyiids and microlepidoptera, were sorted and analysed as morphospecies.

### *Anthropogenic disturbance*

Disturbance level is a consequence of several current and historical factors, and, for this reason, it is rarely feasible to isolate and measure a single cause of human disturbance in non-experimental studies. A common procedure to overcome this practical problem is to use one or more easily measurable variables as surrogates for disturbance, such as density of invasive weeds or pioneer species (De Pietri 1992; Molino & Sabatier 2001). This surrogate is justified because disturbance increases habitat invasibility (Hobbs & Huenneke 1992; Lozon & MacIsaac 1997), and invasive species are itself a factor of disturbance (D'Antonio & Vitousek 1992).

We used the aggregate density of five African grasses that are the major invasive species in Brazilian cerrados (see details in chapter 1) as surrogate for human disturbance level. This indirect measure of human-induced disturbance is supported by studies that have shown a displacement of native grasses by invasive ones after disturbance in Brazilian cerrados (Pivello et al. 1999a,b). We assumed that percent cover of these African grasses should reflect the frequency and intensity of remote and recent disturbance events. For each transect, we recorded invasive grass cover in five classes: 1) 0%, 2) 1 to 25%; 3) 25 to 50%; 4) 50 to 75%, and 5) 75 to 100%. As an index of invasive grass cover (IGC) per site we used the mean value for all 45 transects. Although the IGC values did not conform to a normal distribution in some sites, the use of mean, instead of median or mode, as a measure of central tendency is justified because there is no extreme value (range = 1 to 5). Furthermore, these three measures of central tendency are highly correlated (Pearson's correlation coefficients > 0.94).

***Structure of interactions***

The numbers of interactions are direct counts of the number trophic links recorded between herbivores and plants. Obviously, as more species are sampled more interactions can be recorded. Thus, it is conventionally applied a scaling, the so-called connectance, by dividing the number of observed by the number of possible interactions. In a herbivore-plant system, the number of possible interactions is given by $P \times H$, where $P$ is plant richness and $H$ is herbivore richness. Although some authors have proposed that connectance should be a constant property (Sugihara et al. 1989; Martinez 1992), currently, there is little doubt that connectance tends to be smaller in larger networks (Bersier et al. 1999; Montoya & Solé 2003). In order to evaluate if connectance is related to species richness, in this study we follow the community allometry approach proposed by Fonseca & John (1996; see also Fonseca et al. 2005). First, we performed a linear regression between the number of possible and the number of observed interactions (both variables $\log_{10}$ transformed). Then, we used the residuals of this regression as a connectance measure independent of community matrix size, or in other terms, of plant and herbivore species richness.

The degree of nestedness usually has been measured through two metrics, either the matrix temperature of Atmar & Patterson (1993), or Wright & Reeves's (1992) standardized metric of the total number of species shared across all sites. However, the presence of non-nested endemics (i.e., singular interactions) biases the values of these two metrics (Greve & Chown 2006). For this reason, we calculated nestedness degree through a modification of Brualdi & Sanderson's (1999) discrepancy metric ($d$) proposed by Greve et al. (2005). The discrepancy metric uses the number of interactions ("ones") that need to be changed to create a perfectly nested matrix from the observed matrix. The modification proposed by Greve et al. (2005), called $d1$, standardizes $d$ by calculating $d/n$, where $n$ is the number of presences (interactions) in the matrix. The value of $d1$ goes from zero, for a perfectly nested matrix, asymptotically up to one as nestedness declines. Therefore, we show nestedness degree as 1- *d1*. We calculated *d1* through the *Nestedness Programme* (see Greve et al. 2005; Greve & Chown 2006).

Several concepts and metrics have been applied in studies on compartmentation (Pimm & Lawton 1980; Raffaelli & Hall 1992; Krause et al. 2003; Prado & Lewinsohn 2004), and here, we used two complementary approaches. First, we simply count the number of disconnected sub-networks (i.e. a herbivore-plant link not connected to any other), but it is important to stress that this procedure is very sensitive to the number of singular interactions (i.e. a plant consumed uniquely by a monophagous insect). The second approach is based on the measurement of clumping boundaries proposed by Leibold & Mikkelson (2002) to explore metacommunity structure. They used Morisita's Index of aggregation (Morisita 1971) to quantify clumping into a matrix with columns and rows sorted according to the scores of the first axis of a Correspondence Analysis (Pielou 1984; Lewinsohn et al. 2006). Through Leibold & Mikkelson's approach, we can evaluate both the boundary clumping of host plant species among herbivores and that of herbivore species among plants. Values of Morisita's index greater than 1.0 mean that boundaries are more clumped than expected, while values less than 1.0 indicate over-dispersed boundaries. This analysis and the chi-squared to test its significance were performed with an Excel® Macro developed by Gregory M. Mikkelson (see Leibold & Mikkelson 2002).

### *Statistical analysis*

In order to examine the effects of disturbance on the response variables related to interaction structure, we initially performed both linear and quadratic least-squares regressions. Residual normality and homoscedasticity were checked for all regression analyses. When both models were significantly fitted, we used their sum of squares to choose between them, following Zar (1999). In the cases where regression residuals were not normalised nor showed homogeneity of variances after usual transformations, we tested the effect of disturbance on network properties through a Spearman's rank correlation. We also used this correlation analysis to evaluate if the response variables were related to species richness. For those response variables significantly related with species richness, we performed a multiple linear regression with disturbance level and species richness as independent variables.

## RESULTS

Summed species richness of herbivores and host plants per site ranged from 23 to 85 species (mean = 58.3 ± 17.4) and showed a quadratic relationship to disturbance ($F_{1,18} = 8.28$; $P = 0.003$; Fig. 1a), with a marginally significant peak at intermediate levels of disturbance (Murtaugh's test, $P = 0.066$). The number of distinct interactions between plants and herbivores, whose maximum depends on species richness, also varied quadratically with disturbance level (Fig. 1b; $F_{1,18} = 9.4$, $P = 0.002$), but no intermediate maximum was apparent or statistically significant (Murtaugh's test, $P >> 0.05$).

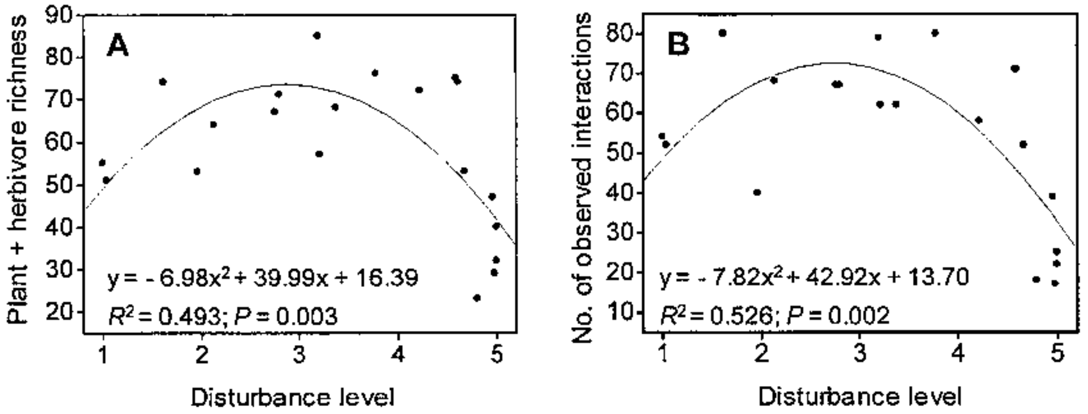

**Figure 1.** Effect of disturbance level on (A) summed species richness and (B) number of observed interactions between Asteraceae and their flower head feeding endophagous insects in remnants of Brazilian cerrados. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

Connectance ranged from 4.8 to 14.3% (mean = 7.1 ± 2.2%) and showed a non-significant quadratic U-shaped relationship with disturbance level ($F_{1,18} = 2.7$; $P = 0.090$). The outlier of this quadratic relationship is the site with lowest host plant richness (see Table 1). If we remove this site from the analysis, then the quadratic relationship turns out to be significant (Fig. 2; $F_{1,16} = 5.5$; $P = 0.015$).

The number of observed interactions was positively related to the number of possible interactions, and showed a regression coefficient of 0.68, significantly lower than 1 ($P < 0.001$; both variables log-transformed; Fig. 3). The community allometry approach revealed that residuals of connectance decrease linearly and significantly from least- to most-disturbed sites (Fig. 4; $F_{1,18} = 5.16$; $P = 0.028$). This means that, after controlling for the influence of species richness on connectance values, connectance is lower at higher disturbance levels.

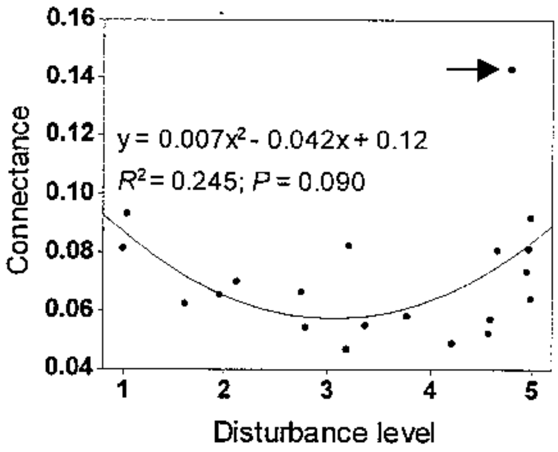

**Figure 2**. Effect of disturbance level on the connectance between Asteraceae and their flower head endophagous insects in remnants of Brazilian cerrados. When the outlier indicated by the row is removed, the regression turns to be significant ($P = 0.015$). The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

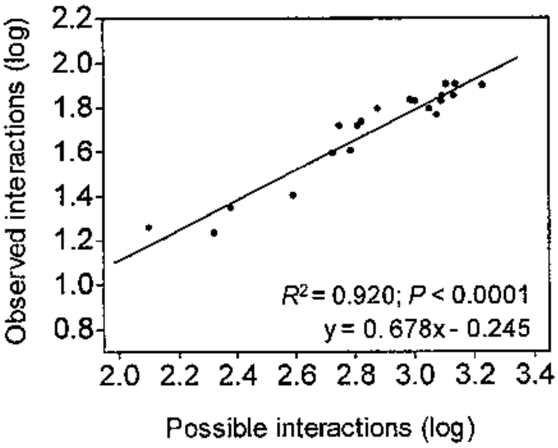

**Figure 3**. Relationship between the number of possible interactions and the number of observed interactions between Asteraceae and their flower head feeding endophagous insects in 20 sites of Brazilian cerrados.

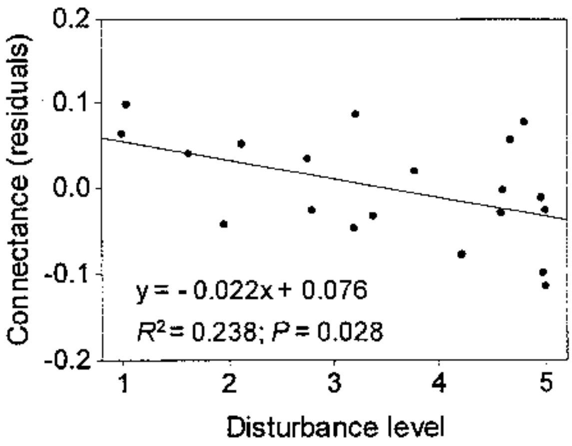

**Figure 4**. Effect of disturbance level on connectance of the trophic interactions between Asteraceae and their flower head endophagous insects in remnants of Brazilian cerrados. Connectance was measured by the residuals of the regression between the number of observed and possible interactions. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

**Table 1**. Sites coordinates, values of the disturbance level based on the proportion of invasive grass cover (IGC), species richness and network properties of interactions between Asteraceae and their flower head feeding insects in 20 remnants of Brazilian cerrados. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance). The arrow in the table is the outlier site in figure 2.

| | | Species richness | | | | | | Degree of compartmentation | |
|---|---|---|---|---|---|---|---|---|---|
| Site coordinates | IGC | Plants | Herbivores | No. of interactions | Connectance (%) | Degree of nestedness (1-*dI*) | No. of sub-networks | Herbivores on plants | Herbivore composition |
| 22°09'57"S 47°48'08"W | 1.00 | 18 | 37 | 54 | 8.0 | 0.48** | 10 | 1.79* | 1.15* |
| 22°07'56"S 47°48'54"W | 1.04 | 16 | 35 | 52 | 9.3 | 0.40 | 4 | 1.91* | 1.12 |
| 22°06'50"S 47°49'07"W | 1.62 | 28 | 46 | 80 | 6.2 | 0.49** | 8 | 1.31 | 1.22* |
| 22°07'04"S 47°50'46"W | 1.96 | 17 | 36 | 40 | 6.5 | 0.15 | 11 | 0.54 | 1.30* |
| 22°08'37"S 47°47'55"W | 2.13 | 25 | 39 | 68 | 7.0 | 0.44* | 6 | 1.19 | 1.34** |
| 22°16'45"S 47°48'50"W | 2.76 | 23 | 44 | 67 | 6.6 | 0.40* | 7 | 1.96** | 1.59*** |
| 22°15'56"S 47°47'48"W | 2.80 | 31 | 40 | 67 | 5.4 | 0.37 | 5 | 2.53*** | 1.59*** |
| 22°19'02"S 47°48'22"W | 3.20 | 32 | 53 | 79 | 4.5 | 0.30 | 8 | 1.31 | 1.56*** |
| 22°02'08"S 47°52'54"W | 3.22 | 21 | 36 | 62 | 8.2 | 0.50 | 5 | 4.12*** | 1.18* |
| 22°05'46"S 47°49'57"W | 3.38 | 29 | 39 | 62 | 5.4 | 0.40** | 11 | 1.31 | 1.47*** |
| 21°58'09"S 47°56'56"W | 3.78 | 30 | 46 | 80 | 5.7 | 0.35 | 6 | 1.85** | 1.14* |
| 22°10'03"S 47°47'16"W | 4.22 | 26 | 46 | 58 | 4.8 | 0.28 | 11 | 1.04 | 1.33*** |
| 22°17'32"S 47°48'20"W | 4.58 | 31 | 44 | 71 | 5.2 | 0.34* | 9 | 1.49* | 1.41*** |
| 21°57'56"S 47°53'16"W | 4.60 | 26 | 48 | 71 | 5.6 | 0.33* | 12 | 1.29 | 1.47*** |
| 22°04'06"S 47°52'35"W | 4.67 | 19 | 34 | 52 | 8.0 | 0.40 | 6 | 2.35*** | 1.41*** |
| 22°00'21"S 47°51'48"W → | 4.80 | 9 | 14 | 18 | 14.3 | 0.33 | 4 | 1.31 | 1.03 |
| 22°04'06"S 47°52'56"W | 4.96 | 19 | 28 | 39 | 7.3 | 0.36 | 8 | 1.85* | 1.54** |
| 22°15'15"S 47°45'47"W | 4.98 | 14 | 15 | 17 | 8.0 | 0.12 | 9 | 0.91 | 1.17 |
| 21°58'59"S 47°54'34"W | 5.00 | 12 | 20 | 22 | 9.2 | 0.23 | 7 | 0.59 | 1.03 |
| 22°16'49"S 47°49'16"W | 5.00 | 17 | 23 | 25 | 6.4 | 0.20 | 8 | 0.68 | 1.28* |

* $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$

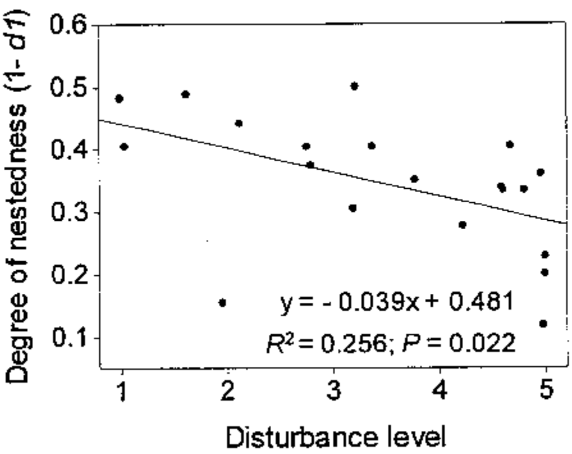

**Figure 5**. Effect of disturbance level on degree of nestedness of the trophic networks formed by Asteraceae and their flower head endophagous insects in 20 sites of Brazilian cerrados. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

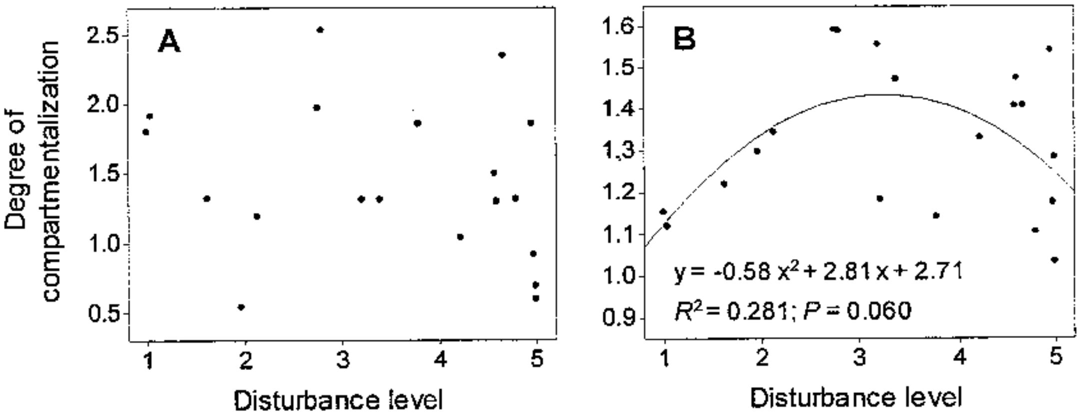

**Figure 6**. Effect of disturbance level on the degree of compartmentation (A) of host plant species used by herbivores, and (B) of herbivore assemblages among plants. All plant species belong to Asteraceae and all herbivore insects are flower head feeding endophages. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

Degree of nestedness ranged from 0.12 to 0.48 (mean = 0.34 ± 1.1) and decreased significantly in more disturbed sites (Fig. 5; $F_{1,19} = 6.20$, $P = 0.022$). Significant nestedness was found in seven plant-herbivore networks (Table 1). Species richness was not significantly correlated with degree of nestedness ($r_s = -0.221$; $P = 0.481$).

The number of totally disconnected sub-networks ranged from four to twelve (Table 1) and it was not related to disturbance level ($r_s = 0.061$; $P = 0.797$). We also did not find any significant correlation between species richness and number of sub-networks ($r_s = 0.255$; $P = 0.277$). Degree of compartmentation of host plant species used by herbivores showed no clear relationship with disturbance level (Fig. 6a), whereas compartmentation of herbivore assemblages among plants showed a marginally significant quadratic relationship with disturbance level (Fig. 6b). Species richness had no correlation with the host compartmentation measure ($r_s = 0.204$; $P = 0.389$), but was significantly correlated with the second one ($r_s = 0.482$; $P = 0.031$). For this reason, we performed a multiple linear regression with both disturbance level and species richness as explanatory variables and degree of compartmentation of herbivore composition among plants as the dependent one. Even so, disturbance level did not showed significant effect on degree of compartmentation (Table 2). Species richness showed a significant and positive effect on the degree of compartmentation of herbivore assemblages among plants (Table 2).

**Table 2.** Linear multiple regressions between the degree of compartmentation of herbivore composition by plant and two explanatory variables: disturbance level and summed richness of herbivores and host plants. $r^2$ is the coefficient of determination, $r^2$ in brackets is the coefficient of determination adjusted for the other independent variable, *b* is the regression coefficient, *b* in brackets is the standardized regression coefficient, and *P* is the probability for the associated *t*-value.

| **Explanatory variables** | $r^2$ | *b* | *t*-**value** | *P* |
|---|---|---|---|---|
| Disturbance level | 0.076 (0.110) | 0.0377 (0.294) | 1.45 | 0.165 |
| Log of species richness | 0.379 (0.381) | 0.0067 (0.655) | 3.24 | 0.005 |

# DISCUSSION

Interactions between herbivore insects and their host plants constitute a major structural and dynamic part of most terrestrial food webs (Schoenly et al. 1991; Price 2002). Although several studies have focused on network-related properties of plant-herbivore systems, few till now have investigated whether these properties are affected by environmental factors (but see Fonseca et al. 2005). In this study, we found evidence for certain consistent effects of anthropogenic disturbance on the structure of plant-herbivore interactions. To our knowledge, this is the first observational study showing how anthropogenic disturbance affects several network properties of a plant-herbivore system.

### *Web size and number of interactions*

In our plant-herbivore, web size varies quadratically with disturbance and peaks at intermediate levels of disturbance. This result disagrees with Townsend et al. (1998), in which web size decreases in more disturbed sites, but it supports the Intermediate-Disturbance Hypothesis (IDH, Grime 1973; Connell 1978) for two related trophic levels. We indeed expected this pattern based on earlier studies of this plant-herbivore system, in which we found quadratic relationships both of host plant and of herbivore richness with disturbance levels (see chapters 1 and 2). We have shown that Asteraceae richness peaked significantly at intermediate disturbance levels (chapter 1), whereas endophagous richness did not (chapter 2). Here, we found a marginally significant peak of web size at intermediate disturbance levels.

Our findings on the number of interactions support an extension of the IDH for the interactions diversity (Thompson 1994), rather than species richness per se. In other words, not only is species richness quadratically related to anthropogenic disturbance, but also the number of trophic links between species. We predicted this effect of disturbance on the number of interactions based on the well-known fact that as more species are sampled more interactions can be recorded.

As far as we know, this study is the first to explicitly propose and demonstrate this simple relationship. However, further studies are needed to establish whether the effect of anthropogenic disturbance on the number of interactions can be generalized for other systems.

### *Connectance*

In accordance with the recent literature on the connectance in ecological networks (Bersier et al. 1999; Montoya & Solé 2003), we also found this property to be proportionally lower in more speciose networks. Fonseca et al. (2005) found a similar scale-dependent behavior for connectance on asteracean host plants and a subset of flower head endophagous insects in Brazilian cerrados, though that study focused only on well-preserved cerrado remnants over a wider geographical span. The ecological interpretation of this scale-dependent effect is that herbivores at richer sites consume, on average, proportionally fewer host plants than their counterparts in sites with lower species richness.

Our initial prediction that disturbance would have a U-shaped relationship with connectance was supported by a significant result after the removal of an outlier (Fig. 2a). This quadratic relationship can be ascribed to the high correlation between species richness and connectance values, shown by the regression between the number of possible against the number of observed interactions. If species richness tends to peak at intermediate disturbance levels, as predicted by the IDH (Grime 1973; Connell 1978; but see Mackey & Currie 2001), and the scale-dependent relationship between species richness and connectance proves a widespread property of food webs (Bersier et al. 1999; Montoya & Solé 2003; Fonseca et al. 2005), then we can presume that connectance may be consistently higher at the extremes of disturbance gradients.

After accounting for the effect of matrix size on connectance through the community allometry approach (Fonseca & John 1996), the remaining effect of disturbance on connectance was negative. If we assume that disturbance also tends to be positively related to degree of variability of the physical environment, then our result aggress with those of Briand (1983), who found significantly lower connectance in fluctuating ecosystems.

### *Nestedness*

The investigation of nestedness in ecological networks formed by two sets of species is a recent approach in studies regarding the structure of interactions (see Bascompte et al. 2003; Dupont et al. 2003). Apart from the paper of Lewinsohn et al. (2006), in which they showed an example of nestedness within compartments between plants (Asteraceae: Vernonieae) and a subset of their flower head feeding insects (Diptera: Tephritidae), to our knowledge no other study has investigated nestedness in trophic interactions. Furthermore, this is the first study that explores how anthropogenic disturbance affects this network property.

Contrasting with suppositions that nestedness should be rare in networks formed by specialized interactions (Bascompte et al. 2003), we found indications of nestedness in seven Asteraceae-endophagous networks. Moreover, contrary to our initial prediction that nestedness would increase in more disturbed sites, the degree of nestedness was significantly lower in sites with higher levels of anthropogenic disturbance (Fig. 5). This result means that the proportion of specialist endophagous species consuming those host plants that are used by the generalist ones did not increase in more disturbed sites.

### *Compartmentation*

A simple ecological explanation for compartmented interactions is the preferential or constrained use of distinct habitats (Pimm & Lawton 1980; Pimm 1982). In a study on tephritid flies associated to flower heads of Vernonieae (Asteraceae), Prado & Lewinsohn (2004) found significant non-random trophic compartments. According to them, the high level of tephritid specialization is probably the major cause of compartment formation. This hypothesis is, in fact, an application of the "preferential habitat use" proposed by Pimm & Lawton (1980; Pimm 1982).

Depending on how the degree of compartmentation is measured, specialist and generalist species can have distinct effects on degree of compartmentation. If our main concern is with totally disconnected sub-networks, then one super-generalist species suffices to unify any number of sub-networks into a single super-web, whereas any reciprocally exclusive herbivore-plant link can be considered a new sub-network. This high sensitivity to super-generalist or specialist species is an unavoidable consequence of this simple approach. Memmott et al. (1994) evaluated compartmentation in a leaf miner parasitoid web by using this approach and they found no evidence for compartments. Although compartments have been demonstrated in mutualistic interactions (Fonseca & Ganade 1996; Dicks et al. 2002), Bascompte et al. (2003) argued that mutualistic networks are highly nested, and for this reason, they are not compartmented. Ours results show that ecological networks can be both significantly nested and compartmented. Lewinsohn et al. (2006) also found both compartments and nestedness for interactions between tephritids and Asteraceae. They pointed out that this hierarchically combined structure occurs when species within each compartment are themselves nested, forming nested compartments. Compartments in plant-herbivore interactions arise when host plant use is strongly regulated by morphological, functional or phylogenetic constraints, but at the same time, herbivores consume plants according to proximate factors, such as plant abundance or temporal availability (Lewinsohn et al. 2006).

Finally, we found that species richness is more related to compartmentation than to disturbance (Table 2). Thus, if we examine the relationship between disturbance and compartmentation without taking species richness into account, we find a similar relationship of that found between disturbance and species richness, i.e. a hump-backed relationship. Our initial prediction that disturbance decreases the degree of compartmentation was not supported by our results. We hypothesised that as the proportion of typical Asteraceae species from cerrados decreases from less to more disturbed sites, the number of opportunistic and generalist herbivore insects would increase and, consequently, tend to interconnect compartments, but found no evidence of this being so.

***Concluding remarks***

To summarize, our data support the general prediction that anthropogenic disturbance affects the structure of trophic interactions between plants and their herbivore insects. However, species diversity per se gives few reliable indications on the effects of disturbance on other community attributes. Thus, if we want to assess the effects of disturbance on biodiversity, we need to expand our focus on other aspects of biodiversity beyond species diversity.

## ACKNOWLEDGEMENTS

We are grateful to various colleagues for their valuable help with fieldwork. We also thank Maria V. Urso-Guimarães, Marina R. Braun, Valéria C. Maia, Sérgio Vanin, and José R. Mermudes for their taxonomic support. This manuscript was improved by comments by Glauco Machado, Carlos R. Fonseca, André V.L. Freitas, Rafael D. Loyola, and Gustavo Q. Romero. This study was supported by FAPESP grants # 98/05085-2 to TML within the BIOTA-FAPESP Program, # 04/15482-1 to TML, # 03/02541-0 to MAN, and CNPq grant # 306049/2004 to TML.

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# 5

# Does anthropogenic disturbance affect the risk of co-extinctions in plant-herbivore networks?

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## SUMMARY

Topological studies of ecological networks have shown that the risk of local co-extinctions or secondary extinctions attendant on species loss is mediated by the structure of interactions. A simple way to explore the topological consequences of species removal in food webs is through the simulation of species extinctions. In this study, we explored the effect of anthropogenic disturbance on the susceptibility to secondary extinctions of endophagous species feeding on Asteraceae flower heads. The goal of this study was to examine whether the extinction level of herbivores following on plant removal is affected by disturbance, host plant richness, community connectance and nestedness. In order to evaluate the effects of these four predictor variables, we simulated three levels of plant extinction (10, 25 and 50%) for four deletion sequences of host plant species: (1) from the most- to least connected; (2) from the least- to most- connected; (3) from the least- to most-abundant; and (4) random removal. Removal from the most- to least-connected host plant species had the strongest impact on herbivore extinctions at all levels of host plant loss. Disturbance had distinct effects on the proportion of extinct herbivores depending on the host plant deletion sequence and on the level of plant loss. Host plant richness was positively correlated with the proportion of extinct herbivores ensuing on random plant removal. Nestedness was negatively correlated with herbivore co-extinction when host were lost from the most- to least-connected species. Connectance had no consistent correlation with herbivore co-extinction. Thus, disturbance is predicted to affect the risk of species loss in interactive communities, but its effects depend on network structural features as well as on the mode of host loss.

# INTRODUCTION

The availability of adequate food resources is a primary requirement for the occurrence of a given species in any habitat. When there are no more prey for a consumer species to feed on, this species will go locally extinct. For this reason, any factor that causes local extinction of one or more species can promote a cascading effect throughout the food web to which those species belong (McCann et al. 1998; Schmitz et al. 2000). Both empirical and theoretical studies have supported this assertion by showing cascades of secondary extinctions following on the loss of one or more species, and subsequent changes in the trophic structure of ecological communities (e.g., Paine 1966; Borrvall et al. 2000; Solé & Montoya 2001; Dunne et al. 2002; Ebenman et al. 2004). Moreover, species loss and the consequent secondary extinctions can themselves alter the resistance of a community to future perturbations due to changes in community structure (Ives & Cardinale 2004). Since habitat disturbance by human activities is by now ubiquitous and has caused alarming rises in species extinction levels (Vitousek et al. 1997), an important issue to be addressed is whether disturbance affects the susceptibility of interaction networks to secondary extinctions or co-extinctions (Koh et al. 2004a,b).

Topological investigations of ecological networks have shown that both the risk and frequency of secondary extinctions provoked species losses are mediated by the structure of interactions (Dunne et al. 2002; Melián & Bascompte 2002; Bascompte et al. 2006). A feature of ecological networks that is liable to affect their fragility to species loss is connectance, which is the fraction of possible interactions that do occur in a community (see chapter 4). The relationship between connectance, as a measure of complexity, and stability of ecological communities is an issue of intense debate in ecology (e.g., MacArthur 1955; May 1972; Pimm 1984; Hall & Raffaelli 1993; Warren 1994; McCann 2000; Dunne et al. 2002). Recent studies have pointed out that interaction asymmetry also can promote higher resistance (Bascompte et al. 2006; Jordano et al. 2006). Nestedness is a particular kind of structure in which more specialized species interacts with a proper subset of those species connected with most generalist ones (Bascompte et al. 2003; Lewinsohn et al. 2006). According to Jordano et al. (2006), nestedness may affect network tolerance to species loss due to two characteristics of nested interactions: (1) specialist species, that often are rare, tend to interact with the generalistic and abundant ones, while (2) generalists, commonly the most abundant species, tend to interact among themselves forming a dense core of cohesive interactions. Both properties provide higher redundancy and increase the resistance of networks to random species loss. However, when generalist and abundant species are loss, the risk of secondary co-extinctions is expected to be greater in highly nested than in randomly connected networks.

A simple way to explore the topological consequences of species removal in food webs is through simulation of species loss (Solé & Montoya 2001; Dunne et al. 2002; Memmott et al. 2004; Jordano et al. 2005). However, this makes sense only if we are confident on the identity of the prey species for each consumer. This requirement constitutes a major obstacle for studies in large food webs with omnivorous species, in which network structure is blurred by uneven taxonomic aggregation into trophospecies. An effective solution to this difficult is to focus on taxonomically well-resolved subsets of networks, such as interactions between plant and vertebrate frugivores (Jordano et al. 2003) and between herbivores and their host plants (Prado & Lewinsohn 2004). In fact, plant-herbivore food webs are promising systems for topological investigations of networks because the majority of insect species, mainly the endophagous ones, are hosted by a reduced number of phylogenetically close plants (Price 1980; Gaston et al. 1992; Ødeggard et al. 2005; Novotny et al. 2006).

In this study, we focus on the effect of anthropogenic disturbance on the susceptibility of co-extinctions of endophagous insects feeding on Asteraceae flower heads following on the loss of a subset of their host plants. By susceptibility to co-extinction we mean the proportion of herbivore species that are expected to be lost due to the deletion of their host plant species. This plant-herbivore system is ideal for this kind of investigation because the immature stages of the endophagous insect species associated to asteracean flower heads are in effect restricted to this plant structure and, consequently, to this plant family. In fact, the majority of Asteraceae flower head endophages are restricted to only one genus (see chapters 2 and 3). Thus, when the host plant species of these endophagous insects go locally extinct, their own local extinction is inevitable. In this study, we set out examine the following questions: (1) is the proportion of extinct herbivores following one the extinction of host plants affected by environmental disturbance?; (2) how do host plant richness, connectance and nestedness affect the susceptibility of herbivores to co-extinction?; (3) how do distinct modes of host plant extinction sequences affect the risk of herbivore to co-extinction?

This paper is part of a series of comparative field studies on the effects of anthropogenic disturbance on the species diversity and structure of interactions between Asteraceae and their flower head feeding insects (see chapters 1 to 4). In previous studies we found that both plant and endophagous insect richness showed quadratic relationships with disturbance. Nonetheless, while the plant richness peaked at intermediate disturbance levels, the richness of endophagous insects apparently did not. In fact, host plant richness explained almost 80% of the variation in endophagous richness, and the direct effect of disturbance on insects was negative instead of quadratic (see chapter 2). Furthermore, anthropogenic disturbance affected negatively the degree of nestedness and showed a U-shaped relationship with connectance. When we controlled for the influence of species richness on connectance, it decreased at higher disturbance levels (see chapter 3). In sites with higher connectance values, the endophagous species have, on average, more host plants than in sites with lower connectance (see chapter 4). Based on these already established relationships, we predict that the proportion of secondary extinctions should be greater in sites with higher total richness and, consequently, lower connectance, i.e. at intermediate disturbance levels.

## METHODS

### *Study sites*

The field data for this analysis were obtained in remnants of cerrado vegetation located in three adjacent counties in the state of São Paulo, Southeastern Brazil (see chapter 1 for details). The cerrado is the largest savanna formation in South America, being considered a global biodiversity hotspot (Myers et al. 2000). Currently, cerrado vegetation is being converted at alarming rates into pasture and cash-crop agriculture (Sano et al. 2002; Klink & Machado 2005). We selected the sites in order to maximize the length and coverage of the disturbance gradient and to minimize the influence of additional factors, such as shade and humidity (see details in previous chapters). The studied sites are spaced apart from 0.6 to 41.4 km, at elevations between 600 to 950 m a.s.l. The surrounding landscape is constituted of pastures, sugar cane and other monocultures, forest plantations, and urbanized areas.

### *Sampling*

Asteraceae is the second largest plant family in Brazilian cerrados (Mendonça et al. 1998), and their flower heads are food resources of a speciose endophagous insect fauna in many habitats in the world (Redfern 1983; Zwölfer 1988; Zwölfer & Romstöck-Volkl 1991; Lewinsohn 1991; Gagné 1994; Prado et al. 2002; Almeida et al. 2006). Plant sampling and flower head collection were performed from April 2004 to February 2005. Since both abundance and composition of flower heads vary along the year, we used two strategies to minimize sampling bias: (1) each site was sampled in three periods (April/May, August/September, and January/February), and (2) all sites were sampled within 35 days in each sampling period (see details in chapter 1).

We estimated the density of each host plant species by counting the number of flowering/fruiting individuals of each Asteraceae species in 15 randomly placed transects of 30 x 5 m per period. We randomised two coordinates to place transects: (1) the position along the border of the sites with a minimal spacing of 10 m between two transects, and (2) the starting position perpendicular to the border from a minimum of 5 up to 55 m. In order to spread our sampling into sites, we collect roughly 80 ml of flower heads (or less, if not available) per individual plant and we endeavoured to sample 20 individual plants per Asteraceae population. We spent circa four person hours collecting flower heads in each period and site. Both total sampled weight of flower heads and number of sampled host plant individuals were highly correlated with our estimates of average plant and average flower head density per transect (Pearson correlation coefficients > 0.85 and $P <$ 0.0001 for all correlations).

In the laboratory, the flower head samples were kept in plastic containers covered with fine mesh lids, where adult herbivore emergence was checked weekly for a period of two months. The insects were identified to the lower taxonomic category. Several undescribed species and poorly known insect groups, mainly cecidomyiids and microlepidoptera, were analysed using a morphospecies approach.

### *Disturbance measurement*

Disturbance level is a consequence of several concurrent and historical factors, and, for this reason, it is rarely feasible to isolate and measure a single cause of human disturbance in non-experimental studies. A common procedure to overcome this practical problem is to use one or more easily measurable variables as surrogates for disturbance, such as density of invasive weeds or pioneer species (De Pietri 1992; Molino & Sabatier 2001). This surrogate is justified because disturbance increases habitat invasibility (Hobbs & Huenneke 1992), and invasive species are itself a factor of disturbance (D'Antonio & Vitousek 1992).

We used the density of five African grasses that are the major invasive species in Brazilian cerrados (see details in chapter 1) as surrogate for human disturbance level. This indirect measure of human-induced disturbance is supported by studies that have shown a displacement of native grasses by invasive ones after disturbance in Brazilian cerrados (Pivello et al. 1999a,b). We assumed that percent cover of these African grasses should reflect the frequency and intensity of remote and recent disturbance events. For each transect, we recorded invasive grass cover in five classes: 1) 0%, 2) 1 to 25%; 3) 25 to 50%; 4) 50 to 75%, and 5) 75 to 100%. As an index of invasive grass cover (IGC) we used the average value for all 45 transects pooled over three sampling periods in each study site. Although the IGC values did not conform to a normal distribution in some sites, the use of mean, instead of median or mode, as a measure of central tendency is justified because there is no extreme value (range = 1 to 5). Furthermore, these three measures of central tendency are highly correlated (Pearson's correlation coefficients > 0.94).

### *Simulations*

For the local interaction network at each site, we simulated the loss of 10, 25 and 50 percent of host plant species using four criteria: removal from (1) the most- to least-connected species, (2) the least- to most-connected species, (3) the least- to most-abundant species, and (4) random removal (mean value for 1000 random deletion sequences). Removal of the most connected and random deletion have been called "attacks" (directed loses) and "errors", respectively in simulations on the internet and other webs (Albert et al. 2000; Jeong et al. 2000; Solé & Montoya 2001). The third scenario of extinction sequence is based on the widespread hypothesis that rare and uncommon species are generally at greater risk of extinction due to their small population sizes (MacArthur & Wilson 1967; Pimm et al. 1988; Hubble 2001). Finally, the deletion sequence from the least- to most-connected species was performed to compare our results with those of other recent studies on the fragility of real ecological networks (Dunne et al. 2002; Memmott et al. 2006). We assessed network fragility as the proportion of herbivore species that lose all their known host plant and are bound to go co-extinct. For sites with uneven number of host plant species, the preset host loss levels give us fractional numbers of host species. To overcome this, we calculated the proportion of herbivore extinction through the weighted mean number of deleted host plant. This weighted mean is exactly equal to the percentage of host loss. Randomizations were performed with the Resampling Stats spreadsheet macro (Blank et al. 2001).

### *Data analysis*

We first performed linear and quadratic regressions to check whether the relationship between disturbance level and the proportion of herbivore loss following on host plant deletion has a monotonic or unimodal shape. Models were chosen through comparison of the sum of squares for the quadratic and linear models following Zar (1999). We used Spearman rank correlations to examine the relationships between the proportion of secondary extinctions and three properties of the plant-herbivore networks, namely host plant richness, connectance and degree of nestedness. In order to reduce type I error, we applied a Bonferroni correction in correlation tables. Finally, we compared the effects of the four removal sequences through an ANOVA followed by a Tukey test for multiple comparisons.

Connectance was calculated by dividing the number of observed by the number of possible interactions. In any herbivore-plant system, the number of possible interactions is given by $P \times H$, where $P$ is plant richness and $H$ is herbivore richness. Degree of nestedness was measured by a modification of Brualdi & Sanderson's (1999) discrepancy metric ($d$) proposed by Greve et al. (2005). The discrepancy metric uses the number of interactions ("ones") that need to be switched to create a perfectly nested matrix from the observed matrix. The modification proposed by Greve & Chown (2006), called $d1$, standardizes $d$ by calculating $d/n$, where $n$ is the number of presences (interactions) in the matrix. We calculated $d1$ through the *Nestedness Programme* (see Greve & Chown 2006).

# RESULTS

The four deletion sequences of host plant species caused distinct levels of secondary extinctions of herbivorous insects (Fig. 1). As expected, removal of the most connected host plant species had the strongest impact on herbivore extinctions for all the three levels of host plant loss (Fig. 1). Additionally, the proportions of co-extinct herbivores were lower for all sequences of removal from least- to most-connected, as well as for two sequences of removal from least- to most-abundant hosts, than for random removals (Fig. 1).

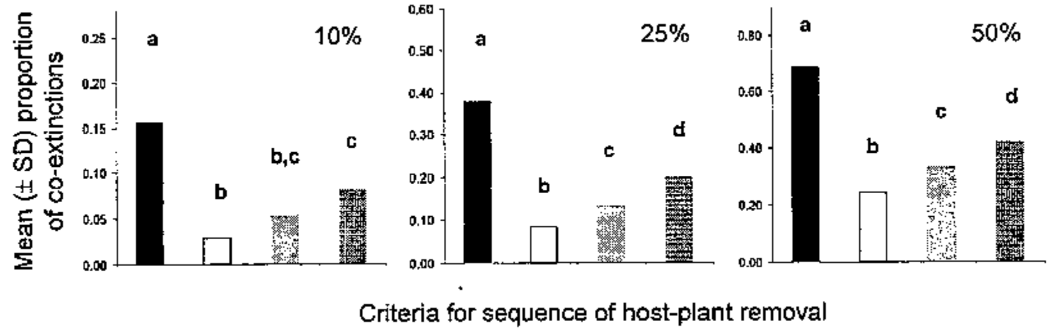

**Figure 1.** Mean (±SD) values of proportion of co-extinct endophages following on four sequences of asteracean host species removal at different levels of host loss (10, 25 and 50%): (1) from most- to least-connected (black bars); (2) from least- to most-connected (white bars); (3) from least- to most-abundant (light gray bars), and (4) random extinctions (dark gray bars). Bars marked with the same letter are not significantly different.

Disturbance level had no clear effect on the proportion of co-extinct herbivores followed by the removal of 10% of their host species (Fig. 2). However, when 25% of hosts were removed, we found a significant increase in the proportion of extinct herbivores for removal of the most-connected host species ($F_{1,18} = 4.9$, $P = 0.04$; Fig. 3a) and a quadratic, U-shaped, relationship for the other three criteria of removal sequences (Figs. 3b, c, d). Finally, when 50% of host species were removed, the random deletion had a positive linear relationship with disturbance level ($F_{1,18} = 6.3$, $P = 0.021$; Fig. 4d).

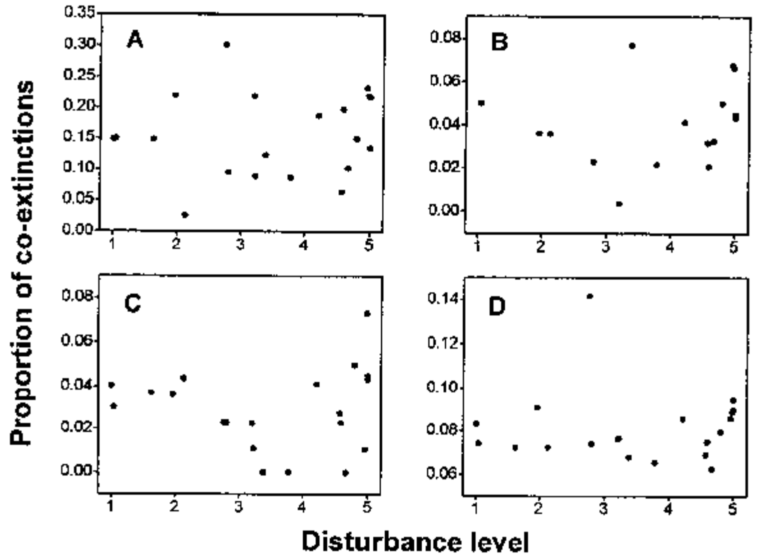

**Figure 2.** Effect of disturbance level on the proportion of extinct flower head feeding herbivores followed by four sequences of 10% of host plant (Asteraceae) removal: (A) from most- to least-connected; (B) from least- to most-connected; (C) from least- to most-abundant, and (D) random extinctions. The index of disturbance is based on the proportion of invasive grass cover, varying from 1 (low disturbance) to 5 (high disturbance).

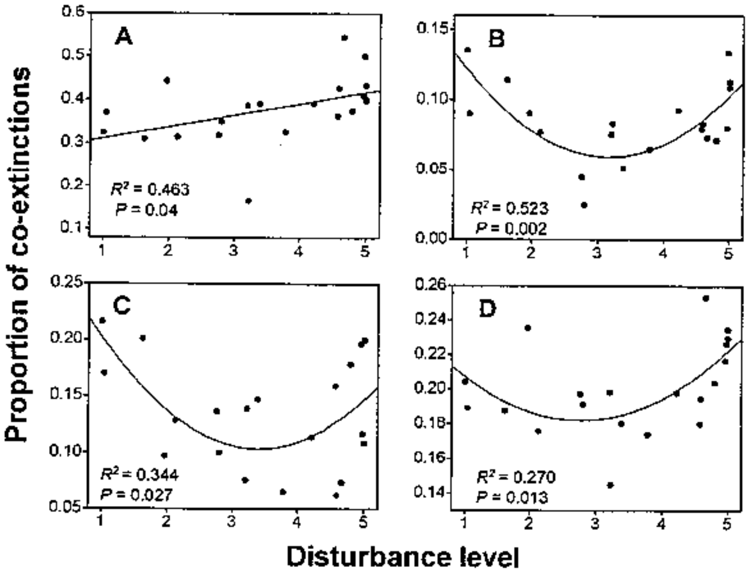

**Figure 3.** Effect of disturbance level on the proportion of extinct flower head feeding herbivores followed by four sequences of 25% of host plant (Asteraceae) removal (as in figure 2).

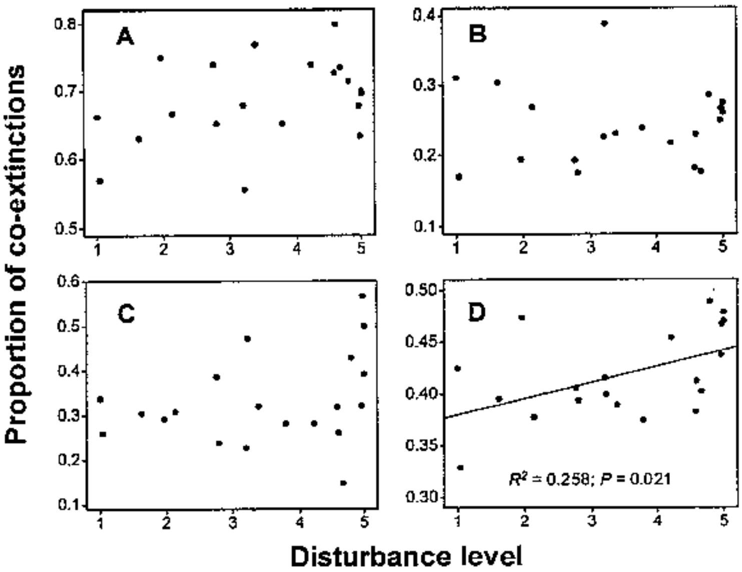

**Figure 4.** Effect of disturbance level on the proportion of extinct flower head feeding herbivores followed by four sequences of 50% of host plant (Asteraceae) removal (as in figure 2).

Host plant richness, connectance and degree of nestedness showed significant correlations with proportions of herbivore co-extinctions, according to removal sequences and level of host loss (Tables 1). Degree of nestedness was significantly related to proportion of herbivore co-extinction when hosts were deleted either from most- to least-connected or randomly (Table 1). On the other hand, when host plants were removed from least- to most-connected or from least- to most-abundant, only host plant richness showed a significant negative correlation with proportion of co-extinct herbivores, even so at different removal levels (Table 1). Host plant richness was also correlated with herbivore co-extinction after random removal of their hosts at all deletion levels (Table 1).

**Table 1.** Spearman rank correlations of proportion secondary extinctions of flower head endophagous insects with disturbance level, host-plant richness, connectance and degree of nestedness. We simulated the extinction of 10, 25 and 50 % of Asteraceae species using four criteria for removal sequence.

| | | Criteria for sequence of host-plant deletion | | | |
|---|---|---|---|---|---|
| Variables | Host-plant loss (%) | From most- to least connected | From least- to most-connected | From least- to most-abundant | Random |
| Disturbance level | 10 | 0.147 | 0.123 | −0.196 | 0.208 |
| | 25 | **0.621**** | 0.041 | −0.145 | 0.404 |
| | 50 | 0.264 | 0.118 | 0.373 | 0.495* |
| Host-plant richness | 10 | −0.354 | **−0.566**** | −0.425 | **−0.564**** |
| | 25 | −0.171 | −0.473 | −0.347 | **−0.589**** |
| | 50 | 0.073 | −0.310 | **−0.555*** | **−0.584**** |
| Connectance | 10 | 0.050 | 0.344 | 0.517 | 0.269 |
| | 25 | −0.014 | 0.284 | 0.486 | 0.241 |
| | 50 | 0.036 | 0.411 | 0.515 | 0.223 |
| Degree of nestedness | 10 | **−0.500**** | −0.378 | 0.392 | −0.515 |
| | 25 | **−0.704***** | −0.192 | 0.359 | −0.549 |
| | 50 | −0.406 | 0.166 | −0.149 | **−0.652**** |

A Bonferroni-corrected value of $P = 0.05/4$ was used to determine significance. Significant values are shown in bold. * $P < 0.0125$; ** $P < 0.01$; *** $P < 0.001$

## DISCUSSION

As a consequence of the high rates of habitat loss and anthropogenic disturbances, the diversity of herbivorous insects, mainly of endemic and rare ones, has been continually impoverished (Brooks et al. 2002). Pimm & Raven (2000) estimated 57,000 extinctions of insect species per million species on Earth in the next 50 years. Although there are some studies regarding the effects of anthropogenic disturbances on insect diversity (e.g. Holloway et al. 1992; Lawton et al. 1998), to date very few ones have examined whether plant extinction promotes secondary extinctions of their associated herbivores (see Koh et al. 2004a; Thacker et al. 2006). Nonetheless, there is a general expectation that species loss is bound to produce secondary extinctions and other kinds of cascade effects (Pimm 1980, 1982; McCann et al. 1998; Schmitz et al. 2000). In addition, fewer studies till now have explored how food web resistance to species loss is affected by environmental factors (see Dunne et al. 2002; Memmott et al. 2006). In this study we found partial support for the hypothesis of environmental control of food web resistance to co-extinction via disturbance level. In previous studies (see chapters 2 and 4) we had established that disturbance affects several aspects of the interactions between Asteraceae and their flower head feeding endophagous insects.

We showed that the susceptibility to secondary extinction of herbivores ensuing on removal of their host plants is differently affected by disturbance, depending on the sequence and extent of plant loss. Intriguingly, the proportion of extinct herbivores is similar to the proportion of removed host plants when we performed random removals. When we simulated preferential removal from most- to least-connected host plants the proportion of co-extinct herbivores surpassed the proportion of removed host plants. Conversely, when host species were removed from least- to most-connected and from least- to most abundant, the proportion of extinct herbivores was lower than the proportion of host plant removed. Given that rare species are often more specialized (less-connected), partly as a sampling effect, the agreement of these two removal criteria is to be expected. Our result contrasts with those of Memmott et al. (2004), who simulated extinction cascades in animal-pollinated networks. The proportions of secondary extinctions in their study were clearly lower than those produced in our simulations for all three connection-based removal criteria. We suppose that this difference may be due in part to the higher level of specialization of plant-herbivore than plant-pollinator interactions (see Bascompte et al. 2003; Novotny et al. 2006).

We assumed that the criterion of plant species removal based on their abundances is the most likely extinction scenario because small population sizes tend to increase the risk of extinction (MacArthur & Wilson 1967; Pimm et al. 1988; Hubble 2001). This criterion caused a higher proportion of herbivore loss than removal of least- to most-connected plants, but their effects were similar, when compared to those for random removal and removal of the most-connected species. This result was expected because plant abundance determines the number of herbivore individuals associated to a given plant species, and if most individuals are sampled more interactions can be recorded, as a passive sampling effect (Lewinsohn 1991; Gotelli & Colwell 2001).

Some authors have argued that high biodiversity, i.e. species-rich networks, can operate as an insurance against ecosystem perturbations (Walker 1992; Naeem 1998). On the other hand, according to MacArthur (1955), consumers feeding on many prey species should be less sensitive to variations in prey abundance than those more specialized consumers. This implies that the probability of extinction should be lower for more polyphagous consumer species. In fact, MacArthur's assertion is related both to connectance and diversity per se. The effect of connectance on community response to species loss has been supported by topological studies on empirical webs (Dunne et al. 2002, 2004) and theoretical ones focused on local stability analysis (Pimm 1980; Eklöf & Edanman 2006). Our results showed that networks with higher host plant richness are expected to suffer lower herbivore losses after random deletions of their hosts. However, connectance was weakly correlated with proportion of extinct herbivores in the majority of simulations, in contrast to Dunne et al.'s (2002) simulations on complete food webs.

In accordance with other results from theoretical and empirical studies on ecological networks (Solé & Montoya 2001; Bascompte et al. 2003), we found that nestedness is related to food web fragility when host plants are removed from most- to least-connected ones. However, the negative effect of nestedness on network fragility to random host removal was unexpected. This result contrasts with our initial expectation based on previous studies on nestedness (Bascompte et al. 2003; Memmott et al. 2004; Jordano et al. 2006). Networks with higher degree of nestedness showed higher expectations of herbivore co-extinction. Since it is obvious that higher nestedness promotes increased tolerance to random extinctions in idealized networks, we suggest that our measure of nestedness should be related to other food web properties that we have not examined, which would have a greater direct effect on fragility to species loss.

To sum up, disturbance is predicted to affect the resistance of communities to species loss, but its effects are not uniform. Moreover, diversity per se does not confer topological robustness in our plant-herbivore networks. On the contrary, networks with higher plant richness had higher expected levels of herbivore losses followed by the random removal of host plants. Our findings suggest that, in empirical networks the relationship of network fragility to their structural properties may diverge from those expected through theoretical studies based on idealized representations of ecological interactions. If co-extinctions promote decrease in food web resistance, we may expect increasing rates of extinctions in species-poor communities ensuing on host plant losses. This could indeed have serious implications for conservation strategies and estimates of future extinctions.

## ACKNOWLEDGEMENTS

We are grateful to various colleagues for their valuable help with fieldwork, and to Marina R. Braun, Valéria C. Maia, Maria V. Urso-Guimarães, Paulo I. Prado, Sérgio Vanin, José R. Mermudes, João Semir, Roberto L. Esteves and Mara Magenta for providing or confirming identification of insects and plants. This manuscript was improved by comments by Glauco Machado, Carlos R. Fonseca, André V.L. Freitas, and Gustavo Q. Romero. This study was supported by FAPESP grants # 98/05085-2 to TML within the BIOTA-FAPESP Program, # 04/15482-1 to TML, # 03/02541-0 to MAN, and CNPq grant # 306049/2004 to TML.

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# Anexo

## On nestedness analyses: rethinking matrix temperature and anti-nestedness

Mário Almeida-Neto, Paulo R. Guimarães Jr., and Thomas M. Lewinsohn

### SUMMARY

The analysis of nested structures in sets of species assemblages across different sites or in networks of interspecific interactions has become a common practice in ecological studies. Although new analyses and metrics have been proposed, few studies have look at the concepts derived from nestedness analysis. We note two important conceptual problems that can lead to terminological inconsistencies and flawed interpretations. First, the thermodynamic analogy related to the most common metric of nestedness, matrix temperature, is flawed and has lead some authors to incorrect interpretations. Second, the creation and usage of the term "anti-nestedness" is a potential source of confusion and inconsistencies. We list four concepts for anti-nestedness and showed how distinct they are. Matrices less nested than expected by chance, i.e. "anti-nested", may result from different ecological processes and show distinct structural patterns. Thus, "anti-nestedness" is not workable as the converse of nestedness. A more useful approach is to designate and test each distinct non-nested pattern according to their assumptions and mechanistic hypotheses.

## INTRODUCTION

In community ecology and biogeography, ecological systems usually are described as presence/absence matrices, often called incidence matrices (Diamond 1975, Gotelli 2000), or as networks (Pimm 1982, Pascual and Dunne 2005). By tradition, incidence matrices are used to investigate distributional patterns of species composition among different habitats or islands (Diamond 1975), whereas a network representation has been adopted in studies of species interactions (Pimm 1982, Jordano 1987). However, incidence matrices and bipartite networks are interchangeable representations for identical structures (Harary 1969, Lewinsohn et al. 2006) and measurements associated with one representation can be directly applied to the other. In this context, the analysis of nestedness, widely used to characterize matrices of species distributions, was recently applied to characterize ecological networks (Bascompte et al. 2003, Dupont et al. 2003, Ollerton et al. 2003, Guimarães et al. 2006, Lewinsohn et al. 2006).

The ecological concept of nestedness dates from Darlington (1957), but only after its development by Patterson and Atmar (1986) and Patterson (1987), it was formally defined and popularized among ecologists. According to Patterson and Atmar (1986), species assemblages are nested if the species present in species-poor sites are a proper subset of those present in species-rich sites. Perfect nestedness occurs when all species-poor sites are proper subsets of the assemblages found in species-rich sites (Figs. 1a,b), while a maximally nested matrix is a special case of a perfectly nested matrix with 50% fill in which presences occupy an upper-left triangle (Fig. 1a). Similarly, plant-animal networks will be nested if plants with few interactions are mostly associated with generalist animals, and vice-versa, so that generalist species tend to interact with each other, forming a dense core of interactions (Bascompte et al. 2003; Lewinsohn et al. 2006). The concept of nestedness has thus been used to indicate both distributional and interactive descriptions of community structure in ecological studies. Here, we use “presence” to designate species records in sites (e.g. islands, fragments, patches, hosts) or species interactions (e.g. mutualistic or antagonistic interactions). We also use “incidence matrix” to refer both to tabular and to network representations as bipartite networks (Harary 1969).

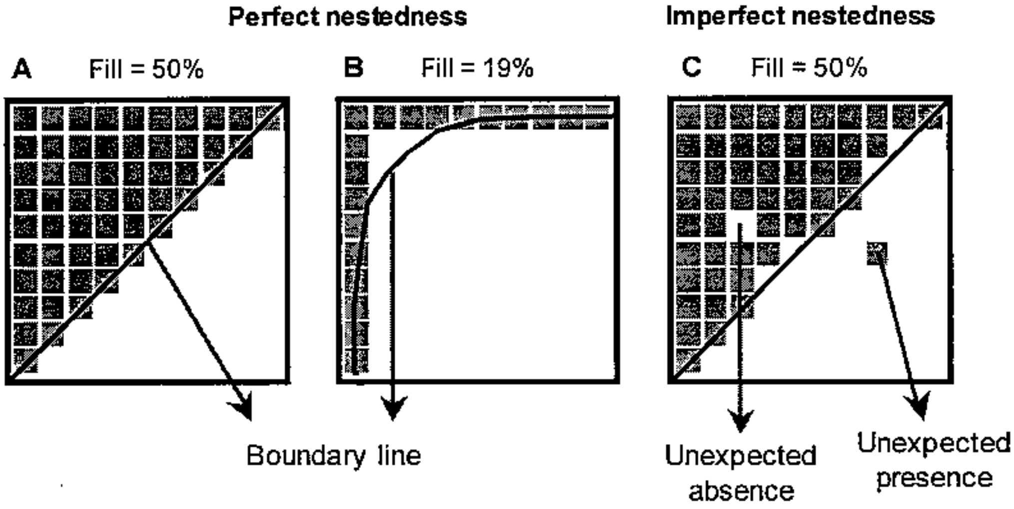

**Figure 1.** Three examples of nested matrices. Matrices A and B illustrated the extremes models of perfectly nestedness, a maximally informative matrix (A) and a minimally informative matrix (B). Matrix C illustrates unexpected absences and presences in relation to the boundary line.

Distributional nestedness has been documented for a variety of taxonomical groups on several spatial scales in a range of distinct biogeographical regions and habitats (Wright and Reeves 1992, Patterson 1990, Wright et al. 1998, Gaston and Blackburn 2000). Interactive nestedness seems to be a common property for some mutualistic interactions, such as the interactions of plants with seed dispersers, pollinators and protective ants (Bascompte et al. 2003, Dupont et al. 2003, Ollerton et al. 2003, Guimarães et al. 2006). Nestedness also has been recorded for parasite species among conspecific host individuals (Worthen and Rohde 1996, Rohde et al. 1998, Gonzalez and Poulin 2005). This last system represents both an interactive and a distributional matrix.

Nestedness structures in ecological systems can reveal some cues about the ecological and evolutionary processes shaping interspecific interactions (Thompson 2005, Lewinsohn et al. 2006) and distribution of species among sites (Lomolino 1996). Additionally, nestedness can be a useful tool for species preservation and to establish priorities for conservation in fragmented landscapes (Patterson 1987, Boecklen 1997, Martinez-Morales 2005). Indeed, recent studies suggest that nested plant-animal networks are more robust to environmental perturbation (Fortuna and Bascompte 2006).

In this paper, we address two conceptual inconsistencies related to nestedness. First, we show that the thermodynamic analogy related to matrix temperature, a metric widely used to quantify the degree of nestedness, is not valid and we propose a new concept for matrix temperature based on its calculation procedures. Second, we demonstrate that "anti-nestedness", a term increasingly used for matrix patterns that depart from nestedness, actually describes several distinct biological patterns. Thus, anti-nestedness should be avoided in favor of more meaningful concepts that describe distinct departures from nestedness. Our objective is not to review issues related to nestedness measurement, as the use of appropriate metrics or null models (for these issues, see Wright and Reeves 1992, Cook and Quinn 1998, Brualdi and Sanderson 1999, Jonsson 2001, Rodríguez-Gironéz and Santamaría 2006, Greve and Chown 2006). We will deal with conceptual questions and their possible consequences for data interpretation.

## MATRIX TEMPERATURE: AN INADEQUATE ANALOGY

The degree of nestedness of a given matrix can be assessed through different metrics (Cutler 1994, 1998; Wright et al. 1998, Brualdi and Sanderson 1999). However, several metrics are frequently sensitive to matrix size, form and/or fill (Wright et al. 1998). This compromises comparisons of nestedness among different assemblages. Wright et al. (1998) suggested that these problems are less severe for matrix temperature, *T*, a metric developed by Atmar and Patterson (1993) (but see Rodríguez-Gironéz and Santamaría 2006, Greve and Chown 2006). The *T* metric has become established as the standard measurement of the degree of nestedness in studies of species distribution among sites (Fischer and Lindenmayer 2002) and of ecological interaction networks (Bascompte et al. 2003). Although we concur that *T* is a useful metric to describe nestedness, we take exception to its conceptual foundations.

Matrix temperature measures how much the incidence matrix departs from perfect nestedness. The calculation of this metric involves computational procedures to reorganize the incidence matrix into a state of "maximum packing", which means that the rows and columns are reordered so that nestedness is maximized, using different algorithms (Atmar and Patterson 1993, Guimarães and Guimarães 2006, Rodríguez-Gironés and Santamaria 2006). The "packed" matrix conventionally shows rows with more presences at the top of the matrix and columns with more presences at the left side (see Fig. 1 for an example). Then, a boundary line is calculated describing the expected distribution of presences if the matrix is perfectly nested (see Atmar and Patterson 1993 for details). Absences to the top and left of the line are defined as unexpected in a perfectly nested arrangement, and the same is true for presences below and to the right (Fig. 1c). The matrix temperature is calculated as the sum of squared deviations from the boundary line of unexpected presences and absences divided by the maximum value possible for the matrix, multiplied by 100. Thus, *T* is a standardized (i.e. non-dimensional) index of how much the matrix departs from the perfectly nested state, combining the number and distance of unexpected presences and absences from the boundary line. In fact, *T* is a percentage measure (Rodríguez-Gironéz and Santamaría 2006).

Atmar and Patterson (1993) coined the term matrix temperature in analogy to Ludwig Boltzmann's proposition that heat is equivalent to disorder and, additionally, to Shannon's (1948) definition of entropy as an informational measure of unexpectedness. Indeed, although *T* is a standardized index, Atmar and Patterson (1993) define an unnecessary unit for *T*, degrees, to reinforce the analogy. We believe that the incorporation of terms from physics and information theory into the analysis of incidence matrices causes conceptual problems for the understanding of matrix structure. The thermodynamic analogy is applied for instance in the statement "At 100°, no discernible extinction order remains; the presence-absence matrix has become a free-gas" (Atmar and Patterson, 1993). However, differently from what have been stated by many authors (e.g. Fernández-Juricic 2002, Fischer and Lindenmayer 2002, Heino and Soininent 2005, Donlan et al. 2005, Martínez-Morales 2005), matrix temperature does not measure presences as expected by the thermodynamical analogy of Atmar and Patterson (1993). According to the calculus of *T* as proposed by Atmar and Patterson (1993), matrix temperature increases with the proportion of unexpected absences and presences in the matrix with respect to the expectative of perfect nestedness. Therefore, $T = 100$ means the maximum proportion of unexpected presences and absences regardless of rearranging rows and columns. It is important to notice that randomly allocated presences will produce a matrix in which $T < 100$ (Rodríguez-Gironéz and Santamaría 2006). Since a matrix with temperature close to 100 cannot be randomly filled, the concept of maximally disordered matrix of Atmar and Patterson (1993) becomes inapplicable. Consequently, the analogy with thermodynamical or information systems, such as heat and entropy, should be viewed as unnecessary.

We propose that a more precise definition of matrix temperature according to what is actually calculated should be "a measure of the symmetry in the distribution of unexpected absences and presences, respectively, at both sides of the perfect nestedness boundary line". When $T = 0$, there is no symmetry, while $T = 100$ means the highest symmetry of unexpected absences and presences between both sides of the boundary line.

## ANTI-NESTEDNESS: A NON-CONCEPT

Anti-nestedness was firstly used by Wright et al. (1998) to designate "species communities that were more heterogeneous than expected by chance", but this same term has been used with distinct meanings in the literature (Table 1). Since in a perfectly nested matrix $T = 0$, we can expect that a perfectly anti-nested one should present a value of *T* very close or equal to 100. Thus, the affirmation of Atmar and Patterson (1993) that at $T$ = 100, a matrix presents maximally disordered presences can be interpreted as a non-explicit concept of anti-nested. We will call this model of anti-nested as random. The first explicit and unambiguous concept of anti-nestedness appears in Poulin and Guégan (2000), for whom anti-nestedness is an alternative departure from nestedness in which species are always absent from sites (in their case, host individuals) richer than the most depauperate one in which they occur. The second explicit usage of anti-nestedness is to indicate a checkerboard pattern. Jonsson (2001; see also Dupont et al. 2003, Lázaro et al. 2005) stated that at $T$ = 100, a matrix has a checkerboard pattern. Note that the checkerboard pattern can be rearranged into a matrix with two compartments (Gotelli 2000, Lewinsohn et al. 2006), and thus is a particular case of compartmented matrix, as are the non-inclusive anti-nestedness model listed above. Finally, other concept of anti-nestedness, called high-turnover, was proposed by Leibold and Mikkelson (2002). According to them, an anti-nested pattern occurs when there are more replacements of presences than would be expected by chance.

Although other variants are found in the literature, the concepts above illustrate the gamut of biological concepts that are called anti-nested.

## PROPERTIES OF DIFFERENT ANTI-NESTED CONCEPTS

We examined some properties derived of the distinct anti-nested representations to assess more formally the difference among the definitions of anti-nestedness and thus to evaluate the applicability of this concept. To facilitate comparisons of the distinct concepts of anti-nestedness, we illustrate both matrix and network representations of these concepts using the same dimension of 15 rows by 5 columns (Fig. 2). We did not attempt to depict the first usage of the term anti-nested by Wright et al. (1998) because their concept is vague and does not permit an unequivocal representation.

We initially compared the other four anti-nested models by contrasting some general properties and relationships derived of these four concepts (Table 1). To evaluate further the differences among the anti-nestedness models, we assess two additional properties: equality and overlap. We define equality as the percentage of pairs of columns (or rows) with identical number of presences. Overlap was defined as the percentage of presences recorded in less filled columns (or rows) also present in more filled columns for all paired combinations of columns.

Then, we compare the value and significance of nestedness degree of the four concepts by using a standardized matrix size of 10 columns by 55 rows. This specific matrix dimension was chosen to compare the mean number of presences in rows and columns, and the model derived of the Poulin and Guégan (2000) concept of non-inclusive with unequal sizes produce at least 55 rows for 10 columns. To evaluate whether a matrix is significantly less nested than expected by chance, we used four null models and performed the analysis in the $C^{++}$ program ANINHADO (Guimarães and Guimarães, in press) based on the original code of the NTC program of Atmar and Patterson (1995). The four null models used are: (1) random matrices in which the probability of a presence in a given cell is constant and estimated from data as the overall proportion of occupied cells (this null model is practically identical to that of NTC); (2) random matrices in which the number of presences in a given row is estimated from data as the proportion of occupied cells within the row; (3) random matrices in which the number of presences in a given column is estimated from data as the proportion of occupied cells within the column, and (4) random matrices in which the probability of a given cell being occupied is the average of the probabilities of occupancy of its row and column (Bascompte et al. 2003). Since the calculus of nestedness degree by the *T* metric of Atmar and Patterson (1993) seems to be less affected by fill than by matrix dimensions (Wright et al. 1998; Greve et al. 2006), we standardized all comparisons among the models using matrices with the same dimensions (rows and columns).

Table 1. General properties and relationships of four models of anti-nestedness based on distinct concepts.

| Anti-nested model | References | Fill | Equality | Overlap | Relationship between size and fill | No. of components |
|---|---|---|---|---|---|---|
| Maximum randomness | Atmar and Patterson 1993 | Variable | Variable | Variable | Constant | Variable |
| Non-inclusive sets of unequal sizes | Poulin and Guégan 2000 | < 50% | 0% | 0% | Inverse | = no. of columns or rows** |
| Checkerboard presences | Jonsson 2001 | ≈50% | ≈100% | ≈50% | Constant | 2 |
| High turnover | Leibold and Mikkelson 2002 | Variable | 100% | Variable | Variable* | 1 |

* Constant when n° of columns = n° of rows, inverse when n° of columns > n° of rows and positive when n° of columns < n° of rows

** The number of components is equal the number of the smallest side (columns or rows).

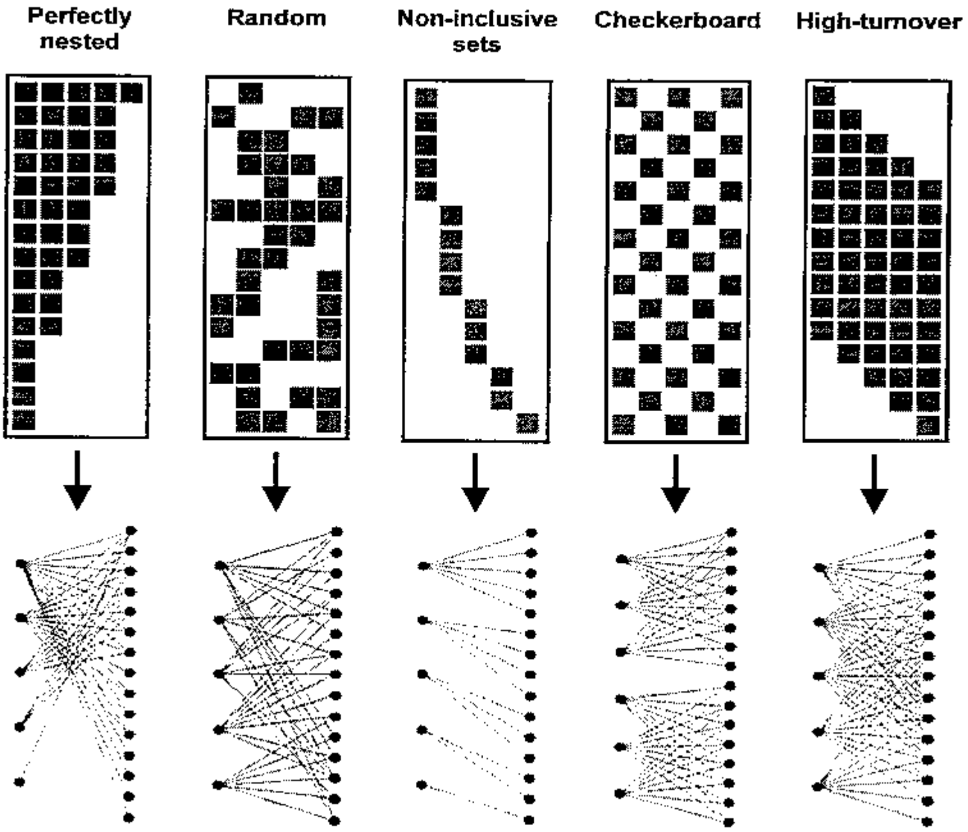

**Figure 2.** Matrix and network representations of perfectly nested and four anti-nested models based on distinct concepts. All models have the same dimensions (5 columns and 15 rows), although fills differ.

To compare the anti-nested models as bipartite networks (see Jordano et al. 2003, Lewinsohn et al. 2006), we used three properties best visualized in network representation: (1) number of components, i.e. the number of non-connected sub-networks or discrete compartments; (2) the size the largest component, i.e. the number of nodes (columns and rows) that constitute the component with the largest number of nodes, (3) average degree (and standard deviation), i.e., the average number of links (presences) per node. As we are dealing here with networks of two exclusive sets, we compare average degree for both columns and rows. To visualize both matrix and network properties, we depicted an idealized representation for each anti-nested model (Fig. 2). An initial comparison of the figures of each model showed us clearly that they present distinct properties, such as the number of components and connectance.

The four anti-nested models showed marked differences in their level of nestedness (Table 2). The difference between the lowest (the non-inclusive model) and the highest nestedness degree (the checkerboarding model) was approximately 85 (Table 2). Only checkerboard and high-turnover models were significantly less nested than expected by null model in which the probability of a presence occur in a given cell is constant and estimated from data as the proportion of occupied cells (Table 2). The model of non-inclusive sets of unequal sizes proposed by Poulin and Guégan (2000) did not showed higher levels of nestedness degrees than expected by any null model. Therefore, its degree of nestedness is similar to those expected by randomly filled matrices of similar dimensions.

These models also vary markedly in other properties such as number of components and average degree. These properties lead to important consequences for dynamics of the studied system (see Albert and Barábasi 2002 for a review in the context of complex networks). For example, the effects of environmental disturbance may not propagate through distinct components in an interactive network since there is no connection between their species groups. Moreover, differences in the degree lead to the idea that different species or sites may be more important than other to the overall stability of the system (Jordano et al. 2003, Fortuna and Bascompte 2006). It is important to note that *T* is a single metric and we should not expect capture all aspects of matrix properties using it. However, the highly different matrices that are usually called anti-nestedness suggest that they apparently only share a higher degree of symmetry in their patterns of presences. Therefore, few, if any, conclusions should be derived from the fact that a matrix is less nested than expected by chance.

**Table 2.** Some matrix and network properties of four models of anti-nestedness based on distinct concepts. *CRO* = completely random occupancy; *FRT* = fixed row totals; *FCT* = fixed column totals; *APO* = average probability of occupancy. The *P*-values correspond to the probability of a matrix to have a nestedness degree lesser than expected by chance according to each the null model. All matrices have 55 rows by 10 columns. The nestedness degree for the maximum random model is the mean value (± SD) for 1000 randomly generated matrices. The nestedness degree varies from 0 (no nestedness) to 100 (maximum nestedness).

| **Anti-nested model** | **Fill (%)** | **Nestedness degree (100 – $T$)** | ***P*-values for each null model** | | | |
|---|---|---|---|---|---|---|
| | | | ***CRO*** | ***FRT*** | ***FCT*** | ***APO*** |
| Maximum randomness | 50 | 36.03 ± 3.9 | 0.546 | 0.760 | 0.934 | 0.148 |
| Non-inclusive sets of unequal sizes | 10 | 62.95 | 0.958 | 0.998 | 0.630 | 0.830 |
| Checkerboard presences | 50 | 3.19 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| Highly filled high turnover* | 83.60 | 48.69 | 0.548 | 0.966 | 1.000 | 0.192 |
| Poorly filled high turnover* | 18.18 | 15.69 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |

*In order to test the effect of fill, we used two alternative models of high turnover.

**Table 3**. Some network properties of five idealized models of anti-nestedness based on distinct concepts. All matrices have 55 rows by 10 columns.

| Anti-nested model | No. of components | Size of the largest component | Average number of presences per columns | Average number of presences per rows |
|---|---|---|---|---|
| Maximum randomness | 1 | 65 | 25 | 5 |
| Non-inclusive sets | 10 | 10 | 5.5 | 1 |
| Checkerboard presences | 2 | 28 | 27.5 | 5 |
| Highly filled high turnover | 1 | 65 | 46 | 8.36 |
| Poorly filled high turnover | 1 | 65 | 10 | 1.82 |

Since several distinct kinds of structured incidence matrices are less nested than expected by chance, test anti-nestedness by counting the probability of a matrix to be less nested than expected by chance (e.g. Whright et al. 1998, Poulin and Guégan 2000) is not a test for a specific anti-nested concept, but only a test for an alternative non-random incidence matrix. Therefore, we suggest that future studies on distributional and interactive species pattern change the use of "anti-nested" to other more specific concepts based on testable and comparable patterns.

## CONCLUSION

Since the metric of matrix temperature proposed by Atmar and Patterson (1993) is in wide use in studies on distributional and interactive nestedness, we propose a concept to revise the underlying of this metric. More specifically, we argue that (1) there is no reason to maintain the analogy between matrix temperature and thermodynamic systems, and (2) authors should not state that when $T = 100$ a matrix presents a random distribution of presences, since this only applies to matrices with symmetric (i.e. non-random) distribution of unexpected absences and presences at both sides of the boundary line.

What is the motivation to use the term "anti-nested" to describe so distinct patterns? We believe that this can be explained by two major motivations: (1) some degree of nestedness seems to be a widespread ecological pattern, and (2) to measure and test nestedness is easier than to measure and test the majority of other structured patterns on species distribution and species interaction due to computational availability (several free available programs). These motivations have promoted nestedness to a status of "pattern to be tested a priori", in spite of several other structured species distribution (or interactions) also occur in a data set. Since matrices that are less nested than expected by chance may be a result of different ecological processes and show distinct structural patterns, there is no convincing reason to designate "anti-nestedness" as the inverse of nestedness. In that way, the logic underlying anti-nestedness could lead to anti-concepts for each structured model (e.g., anti-turnover, anti-checkerboard).

Finally, several other structures for species distribution and species interactions have been proposed (e.g. Diamond 1975, Wilson 1987, Gotelli and Graves 1996, Sanderson et al. 1998, Gotelli 2000), but these structures rarely are tested as alternative or complementary structures for nestedness. As pointed by Leibold and Mikkelson (2002) and Lewinsohn et al. (2006), there is no general a priori reason to test matrices only for nestedness. Following this assessment, recently some studies have tested diverse patterns related to species distribution among sites or species interactions (Leibold and Mikkelson 2002, Feeley 2003, Heino 2005, Hylander et al. 2005, Lewinsohn et al. 2006). A more promising approach is to name and test each distinct non-random pattern according to their assumptions and mechanistic hypotheses.

## ACKNOWLEDGEMENTS

We thank Sérgio F. dos Reis, Paulo Inácio Prado, Rafael D. Loyola and Miguel A. Fortuna for valuable discussion and comments. The three authors were founded by grants of Fundação de Amparo à Pesquisa do Estado de São Paulo (#03/02541-0 to MAN, #03/03857-8 to PRG, #04/15482-1 to TML). TML also was founded by CNPq grant # 306049/2004.

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# Conclusão Geral

O número de espécies é apenas um dos muitos componentes da biodiversidade (Wilson 1988; Gaston 1996; Faith 2003). Embora o conceito e os limites do termo biodiversidade ainda sejam objeto de debate (e.g., Gaston 1996; Ricotta 2004; Myers & Patil 2005), há um consenso de que o termo expressa a diversidade em vários níveis hierárquicos. A biodiversidade de uma dada região expressa a sua diversidade estrutural, funcional e histórica em diferentes níveis de sua organização biológica (ou seja, desde genes até comunidades). Nesse sentido, a maior parte dos estudos sobre os efeitos da degradação antrópica têm examinado um aspecto bastante limitado da biodiversidade: a variação na diversidade de espécies (veja Mackey & Currie 2001). Embora o enfoque sobre a diversidade de espécies seja indispensável e muitas vezes constitua o primeiro passo para outras abordagens, para aprofundar o entendimento da dinâmica da biodiversidade é necessário expandir o foco para outros de seus componentes, como a diversidade funcional de espécies e a diversidade de interações. Essas abordagens complementares podem nos ajudar na compreensão de diversas questões relacionadas aos mecanismos reguladores da biodiversidade, tais como a estruturação das interações e suas conseqüências sobre a dinâmica de extinções.

No presente estudo, examinei o efeito da degradação antrópica sobre diferentes aspectos da biodiversidade usando um subconjunto de comunidades naturais formado por um grupo monofilético de plantas (Asteraceae) e os insetos que se desenvolvem no interior de suas inflorescências. As questões abordadas e os resultados encontrados no presente estudo trazem várias implicações sobre os efeitos da degradação antrópica na diversidade, estrutura e integridade de interações entre insetos fitófagos e plantas. Na opinião do autor, os principais resultados são deste estudo são: (1) tanto a densidade de espécies quanto a riqueza de plantas da família Asteraceae foram maiores em áreas com níveis intermediários de degradação antrópica, corroborando a Hipótese da Perturbação Intermediária (Grime 1973; Connell 1978); (2) a riqueza de insetos fitófagos apresentou uma relação quadrática com a degradação, mas essa relação por sua vez deve ser mediada pela riqueza de plantas; (3) o efeito direto da degradação antrópica sobre a riqueza de herbívoros foi negativo; (4) a proporção média de plantas hospedeiras consumidas por herbívoros foi menor em níveis intermediários de degradação antrópica; (5) a proporção de espécies de herbívoros que seriam extintos em conseqüência da extinção de suas plantas hospedeiras tende a ser maior em áreas com maior riqueza de plantas, ou seja, em áreas com níveis intermediários de degradação antrópica; (6) a degradação antrópica não apresentou uma relação monotônica com o nível de fragilidade das redes de interações entre plantas e insetos herbívoros.

Como em toda tese, há outras questões que poderiam ser examinadas, e foi necessário fazer opções sobre o que tratar primeiro. Para o leitor mais curioso, adianto algumas questões que serão examinadas em breve: (1) qual o efeito de outras características das áreas (e.g. intensidade de fogo recente, densidade de gado, propriedades do solo e cobertura do dossel) sobre a composição de Asteraceae?; (2) a degradação promove uma homogeneização de espécies e/ou interações, i.e. áreas mais degradadas apresentam maior similaridade na composição de plantas, de insetos endófagos e de interações?; (3) o grau de especialização dos insetos endófagos afeta a sua suscetibilidade à extinção ao longo do gradiente de degradação?

Tendo em vista os efeitos potencialmente negativos da degradação antrópica sobre a biodiversidade, e os efeitos resultantes sobre a qualidade dos serviços ecossistêmicos, a demanda por informações relacionadas às conseqüências das mudanças na biodiversidade deve aumentar cada vez mais nos próximos anos. Caberá aos ecólogos e pesquisadores afins a elaboração de uma teoria mais robusta sobre os padrões e processos relacionados à biodiversidade em um mundo cada vez mais antropizado.

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