LUCIMAR SOARES DE ARAUJO

ECOLOGIA DE BESOUROS MICETÓCOLOS: NOVAS PERSPECTIVAS PARA BIOMAS DA AMÉRICA DO SUL E ÁFRICA

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de Doctor Scientiae.

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Orientador

“Ninguém ignora tudo. Ninguém sabe tudo. Todos nós sabemos alguma coisa. Todos nós ignoramos alguma coisa. Por isso aprendemos sempre.”
Paulo Freire

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RESUMO

ARAUJO, Lucimar Soares de. D.Sc., Universidade Federal de Viçosa, fevereiro de 2014. **Ecologia de besouros micetócolos: novas perspectivas para biomas da América do Sul e África.** Orientador: Cristiano Lopes Andrade.

Modificações ambientais que alterem o ciclo natural de decomposição vegetal por fungos saprófitos podem afetar a estrutura de comunidades de besouros micetobiontes, que são organismos que utilizam basidiomas de macrofungos como hábitat e alimento. O táxon mais diverso e abundante de besouros micetobiontes é Ciidae, com cerca de 650 espécies descritas em 43 gêneros. Com o objetivo de entender quais os processos que determinam a diversidade de besouros micetobiontes em biomas tropicais e subtropicais, esta tese apresenta dois capítulos. No primeiro, foi estudado se haveria algum padrão de utilização de fungos por ciídeos em biomas brasileiros (Cerrado e Mata Atlântica no Brasil) e africanos. No segundo capítulo foi avaliado o efeito da fragmentação da Mata Atlântica sobre a riqueza e composição de espécies de besouros micetobiontes e seus recursos. No primeiro capítulo concluímos que os ciídeos dos biomas tropicais e subtropicais podem ser organizados em grupos de utilização de fungos. Isto facilita o entendimento do papel dessas espécies no ambiente e permite a discussão sobre os processos ecológicos e evolutivos que dirigem o estabelecimento de populações e comunidades, melhorando o entendimento sobre a conservação da fauna desses besouros e seus hospedeiros. No segundo capítulo, chegamos à conclusão que a fragmentação da Mata Atlântica afeta a riqueza de besouros micetobiontes, diminuindo em fragmentos menores e mais isolados. Isso afeta também a disponibilidade de recursos, que está estreitamente relacionada à presença desses besouros no ambiente.

ABSTRACT

ARAUJO, Lucimar Soares de. D.Sc., Universidade Federal de Viçosa, February, 2014. **Ecology of saproxylic beetles: New perspectives to biomes from Southern America and Africa.** Advisor: Cristiano Lopes Andrade.

Environmental changes that alter the natural cycle of plant decomposition by saprophytic fungi may affect the community of micetobiont beetles, which are organisms that use basidiomes of macrofungi as habitat and food. The most diverse and abundant taxon if micetobiont beetles is Ciidae, with about 650 described species in 43 genera. In order to understand what processes determine the diversity of micetobiont beetles in tropical and subtropical biomes, this thesis presents two chapters. At first, we studied whether there was any pattern of use of fungi by ciids in Brazilian (Cerrado and Atlantic Forest) and African biomes. In the second chapter, the effect of fragmentation of the Atlantic Forest on the richness and species composition of beetles micetobiont and its resources has been reported. In the first chapter we concluded that ciids of tropical and subtropical biomes can be organized in groups of host-fungi. This facilitates the understanding of the role of these species in the environment and allows discussion on the ecological and evolutionary processes that drive the establishment of populations and communities, improving the understanding of wildlife conservation of these beetles and their hosts. In the second chapter, we concluded that the fragmentation of the Atlantic forest affects the richness of micetobiont beetles, decreasing in smaller and more isolated fragments. This also affects the availability of resources, which is closely related to the presence of these beetles in the environment.

INTRODUÇÃO

Os animais micetócolos que dependem de macrofungos como hábitat e alimento em todas as fases de seu desenvolvimento são considerados micetobiontes. Os macrofungos usados por animais micetobiontes são normalmente Basidiomycetes e Ascomycetes, principais grupos causadores de doenças em plantas e decompositores de matéria orgânica vegetal (Webster & Weber 2007).

Dentre os animais micetobiontes, destacam-se pela diversidade e abundância alguns grandes grupos de Diptera (Cecidomyidae, Mycetophilidae, Drosophilidae, Dolichopodidae, dentre outros), Coleoptera (Ciidae, Tenebrionidae, Diaperini, Ptinidae, Dorcatominae, dentre outros) e Lepidoptera (Tineidae) (Jonsell et al. 1999; Jonsell & Nordlander 2002). Os Coleoptera micetobiontes mais diversos são: Ciidae (Ceracis spp., Cis spp. e Xylographus spp., dentre outros), Tenebrionidae (ex., Neomida spp., Platydema spp. e Diaperis spp.), Erotylidae e Ptinidae (principalmente os Dorcatominae) (Jonsell & Nordlander 2002; Komonen 2003; Komonen et al. 2003).

Em biomas tropicais e subtropicais, o táxon mais diverso e abundante de besouros micetobiontes é Ciidae (L. S. Araujo & C. Lopes-Andrade, obs. pes.). Atualmente, há cerca de 650 espécies descritas de ciídeos, em 43 gêneros (Oliveira et al. 2013). Contudo, o número de espécies reconhecidamente novas presentes em coleções científicas supera em muito esse número (C. Lopes-Andrade com. pes.). Ainda não há um consenso sobre a classificação supragenérica da família, mas duas subfamílias são reconhecidas: Sphindociinae e Ciinae. Sphindociinae é monospecífica e ocorre somente na Califórnia (EUA) (Lawrence 1974b, a). Ciinae é cosmopolita e dividida nas tribos Ciini, Orophiini e Xylographellini (Lopes-Andrade 2008). As duas primeiras tribos têm distribuição mundial, enquanto Xylographellini é basicamente tropical.

Na região Neotropical ocorrem mais de 150 espécies descritas de ciídeos e pelo menos 50 delas já foram encontradas no Brasil (Lopes-Andrade 2008; Lopes-Andrade & Lawrence 2011; Oliveira et al. 2013; Sandoval-Gómez et al. 2014). Contudo, o número de espécies de ciídeos neotropicais é certamente muito superior. Os besouros Ciidae, assim como os demais micetobiontes, fazem parte da grande guilda dos saproxílicos, um importante grupo funcional em diversos sistemas florestais, em especial em florestas boreais e temperadas da Europa. De acordo com Grove (2002) "O termo saproxílicos engloba uma ampla variedade de guildas de insetos que compartilham uma associação com os ambientes de madeira antiga – essencialmente árvores grandes e velhas – e a madeira em decomposição que estas geram".

A maior parte dos dados sobre o uso de macrofungos por ciídeos é para espécies neárticas (Lawrence 1973), européias (Reibnitz 1999) e japonesas (Kawanabe 1995, 1996, 1998, 1999). Na região tropical existem pouca informação sobre o uso de macrofungos pelos ciídeos (Gumier-Costa et al. 2003; Gumier-Costa 2004; Graf-Peters et al. 2011). A maioria dos ciídeos vive em fungos orelhas-de-pau (Basidiomycetes Aphyllophorales: Schizophyllaceae, Stereaceae, Polyporaceae, Ganodermataceae, Hymenochaetaceae) (Graf-Peters et al. 2011), e alguns poucos em cogumelos (Basidiomycetes: Agaricales: Pleurotaeae, Tricholomataceae, Bolbitiaceae). Há pouquíssimos relatos sobre ciídeos encontrados fora de basidiomas, e a maioria desses registros é para espécies micrópteras em serrapilheira (Lopes-Andrade 2007).

Alguns autores propõem que os fungos utilizados por espécies de ciídeos atuais podem ser filogeneticamente próximos dos fungos explorados por suas espécies ancestrais (Gumier-Costa et al. 2003; Orledge & Reynolds 2005). Além disso, algumas espécies de ciídeos são muito especializadas em utilizar apenas uma ou poucas espécies de basidiomicetos, principalmente por tolerância aos compostos tóxicos presentes em

alguns basidiomas, apesar de existirem espécies que são generalistas e amplamente distribuídas (Graf-Peters et al. 2011).

Há poucos estudos sobre animais associados a macrofugos (micetócolos), especialmente em florestas tropicais, onde se concentra a maior diversidade deles. Estudos realizados em áreas com intenso manejo florestal mostram que as populações de muitos animais micetócolos vêm decaindo como consequência direta da redução da disponibilidade de árvores mortas, que são substratos para o desenvolvimento dos macrofungos (Gumier-Costa 2004; Komonen & Kouki 2005; Jonsson & Nordlander 2006). Empiricamente, podemos concluir que parte do proceso de decomposição e ciclagem de nutrientes também sofre alteração nessa perda de besouros micetócolos, pois eles ao consumirem fungos como alimentos eles liberam para ambientes produtos da disgestão de compostos químicos que outros organismos não são capazes de assimilarem. Entretanto, ainda não se encontra na literatura o quão importante e qual o impacto disso no ambiente natural.

Modificações ambientais que alterem o ciclo natural de decomposição vegetal por fungos saprófitos podem afetar os animais micetobiontes tanto por redução da disponibilidade de recursos quanto por alteração de fatores microclimáticos como, por exemplo, umidade e consistência dos basidiomas (Paviour-Smith 1960). Um marco no estudo dessa dinâmica ecológica foi o estudo realizado por Rukke (2000) em florestas temperadas da Noruega, que demonstrou que a fragmentação e o manejo florestal afetam negativamente a presença de espécies de insetos micetócolos, especialmente de besouros Ciidae, reduzindo a probabilidade de colonização do fungo Fomes fomentarius (L.). Isso provocaria uma redução no processo de degradação desse fungo no ambiente. Entretanto, pouco se sabe sobre os efeitos da fragmentação sobre a diversidade e a

composição, além daestrutura de populações de espécies que anteriormente eran bem distribuídas.

Com o objetivo de entender quais os processos que determinam a diversidade de besouros micetobiontes em biomas tropicais e subtropicais, esta tese apresenta dois trabalhos com diferentes focos. No primeiro capítulo o objetivo é verificar se há algum padrão de utilização de fungos por ciídeos em biomas brasileiros (Cerrado e Mata Atlântica) e africanos. Para isso foi feito um levantamento dos dados disponíveis na literatura e dados não publicados de coleções científicas, além dos dados obtidos na execução do Capítulo 2. Dessa forma, foi possível analisar e comparar os agrupamentos formados pelas espécies de Ciidae, baseado no registro de utilização dos fungos pelos ciídeos em diferentes biomas. No segundo, o objetivo é avaliar o efeito da fragmentação da Mata Atlântica sobre a riqueza e composição de espécies de besouros micetobiontes e seus recursos. Para isso foram coletados os basidiomas de fungos decompositores de madeira, hospedeiros dos besouros micetobiontes, em 12 unidades de conservação dos estados de Espírito Santo, Minas Gerais e Rio de Janeiro.

CAPÍTULO 1: Patterns of utilisation of host fungi by Ciidae (Coleoptera) in subtropical and tropical biomes

(Plos one)

Patterns of utilisation of host fungi by Ciidae (Coleoptera) in subtropical and tropical biomes

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Abstract

Ciids (Coleoptera: Ciidae) are minute tree-fungus beetles occurring in almost all terrestrial ecosystems. They feed and live inside persistent basidiomes of macrofungi, and are thus considered to be micetobiont organisms. Ciid species have different host fungi, and they can be grouped in sets of utilization of host species. Here we address a comprehensive analytical study of patterns of utilization of host fungi by ciids of African and Brazilian biomes. We describe separately the structure found in four datasets: South African Subtropical Forests, Brazilian Subtropical Atlantic Forest, Brazilian Tropical Atlantic Forests and Cerrado (Brazilian Savannah). We registered 37 host fungi genera and more than 120 ciid species. Some host fungi species were used by only one ciid species and many ciids were recorded from one or two hosts. Approximately 80% of the ciid species and 60% of the host genera of this study were included in twenty two host affinity clusters in our analyses. These were gathered in six host-use groups, as follows: Ganoderma, Lenzites, Mycobonia, Phellinus, Trametes and Rigidoporus group. We compare our results with host-use groups recognized for the Holarctic Ciidae, discuss the composition and structure of host-use groups in the studied tropical and subtropical biomes, and the ecological importance of these host-use groups.

Introduction

Ciids (Coleoptera: Ciidae) are minute tree-fungus beetles occurring in almost all terrestrial ecosystems. They feed and live inside persistent basidiomes of macrofungi, and are thus considered being micetobiont organisms and the most diverse and abundant taxon of this guild in tropical and subtropical lands [1,2,3,4]. There are few registers of ciids utilizing other resources or living outside fungi, the most common are micropterous and apterous species sometimes found in leaf litter or associated to dead wood [5 see for a summary]. However, there is no register about their association to another resource instead of fungi [6,7]. Such dependence makes them strictly vulnerable to variations of quantity and quality of fungi resources. When a species is more specialized, more seldomly it explores other resources [8,9,10]. Based on this, many studies have proposed that there are physic-chemical characteristics of fungi that stimulate ciids to establish a population, or prevent when they are in a resource to which they are not adapted for [1,11,12,13].

Ciid species can be grouped in sets of utilization of fungi [1,11,12]. Fungi species used by ciid species can be the same or close related to those utilized by their ancestors. Lawrence [1] considered that a fungi successfully utilized by a ciid was the one in which they bred and sustained a population. This issue has been addressed previously by Paviour-Smith [12] through a subjective recognition of assemblages of fungal taxa from British and continental Europe data, exploited by subsets of ciid species. They were considered in more detail by Lawrence [1,14], who described four host preference groups from North American data. Such groups have been discussed by other authors, but have not received further detailed attention merited by their ecological interest.

Lawrence [1,15] introduced the conception of host preference group for the comparable patterns of ciid host-use described by himself and by Paviour-Smith [12]. The word “preference” referred simply to the recorded frequency of breeding records, but it was not considered appropriated by Orledge and Reynolds [11], because it suggested a behaviour of choice of particular fungal hosts by the ciids, what was not tested by any author until that time. The term host-use was suggested by Orledge and Reynolds [11] and as they described, it does not refer to choice and better represent the idea of group of fungi genera suitable for certain subsets of a give ciid assemblage. Therefore, the concept of host-use applied to ciid beetles in their studies does not refer to their fundamental and/or realized niche, but it is rather a description of which genera of fungi sustain the population of recorded species through their life cycle [11].

The relationship between beetles and fungi is barely studied in Neotropical and Afrotropical biomes [16]. Most of the data available in the literature are for Nearctic [1,14,15], European [11,17,18] and Asian species [19,20,21,22]. The places registered in this current work are listed on the biodiversity hotspots and correspond to places suffering high intervention of human activity and have high quantity of endemic species [23]. On the other hands, such biodiversity is still barely studied and only recently the studies about diversity of Ciidae species [2,24,25,26,27] and their fungi relationship [16,28] have been carried out.

Here we address a comprehensive analytical study of patterns of utilization of host fungi by ciids of African and Brazilian biomes, and evaluate whether such patterns are comparable to the ones observed in Holarctic biomes. We describe separately the structure found in four datasets on the African Subtropical Forest, Subtropical Atlantic Forest, Tropical Atlantic Forest and Cerrado (Brazilian Savannah). Our discussion focused on the composition and structure of host-use groups, conservational and

evolutionary issues and statistical approaches to established ecological concepts and biological characteristics of ciids. We hypothesized that group could be formed differently those formed in the arctic and nearctic region because of the composition of fungi. And they should be similar between African and Brazilian regions depending on biomes where we did the studies.

Material & Methods

Identification of ciids and nomenclature

Most ciid species were identified by us, including those of previous researches [16,29] and used to construct part of the datasets analysed here. The species of the Cis taurus group and the genus Xylographus Mellié were identified by E. H. Oliveira and V. E. Sandoval-Gómez, who are conducting revisionary works and examined all their type-specimens. Brazilian and African ciids were first identified to genus-level and separated in morphospecies. Then, all morphospecies were checked in order to identify them to species-level, using available taxonomic works on African and American ciids [2,3,4,6,14,15,26,27,30,31,32,33,34,35,36,37] and comparison to type-specimens or specimens compared to the type of most ciid species, available at the Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera (CELC; Universidade Federal de Viçosa, Viçosa, Brazil). We have taken care to check whether there were species described from other biogeographic regions, mainly in the cases of well-known invasive species (e.g. Antunes-Carvalho & Lopes-Andrade 2013; Lopes-Andrade 2008a). It means that the ciid species cited here without specific epithets are all possibly new to science.

We made a few updates to the identifications provided by Graf-Peters et al. [16]. The species “Strigocis sp.” is here called “Cis sp. 6”. There were doubts on whether the species belonged to Strigocis Dury by the time that the study was published, but now we sustain the opinion that it better fits in the genus Cis Latreille, among the species in the bilamellatus group. “Ceracis sp.1 (aff. multipunctatus)” is indeed Porculus vianai (Pic), which we confirmed after examining the type. Cis kawanabei Lopes-Andrade and Cis testaceimembris (Pic) are here treated as Cis aff. kawanabei and Cis aff. testeceimembris. Both belong to the taurus species-group, which was recently revised [37].

The identifications provided by Neser [29] remains essentially the same, except for Ceracis cucullatus (Mellié), which is here treated as Ceracis tabellifer (Mellié). The limits of the species were recently revised in a broad paper on the cucullatus species-group [24]. The name Ceracis tabellifer was reinstated and applies to the invasive species occurring in Africa and Asia (with a few records in Europe). The name Ceracis cucullatus applies to the invasive species found in Galapagos. They are very closely related species and have a Neotropical origin [24].

Codification

We opted to keep the same codification to morphospecies provided in the published datasets [16,29] analysed here. The additional South African morphospecies we recognized were coded following the same sequence provided by Neser [29]. The other two datasets are on the ciids from the Cerrado and the Atlantic Forest, and each had its own sequences. All these datasets are the result of independent studies. It means, for

instance, that a morphospecies named “Cis sp.E” from the Cerrado would not necessarily correspond to a “Cis sp.E” from South Africa.

In order to circumvent this problem, we added a code to indicate to which dataset a morphospecies belonged, as follows: SA, to the South African dataset; SFP, to the species from São Francisco de Paula National Forest; TAF, to Tropical Atlantic Forest; and CER to Cerrado. This code was also added to species with specific epithet; for instance, Ceracis cornifer-CER and Ceracis cornifer-TAF are the same species, but refer to individuals collected in different biomes.

Morphospecies from all datasets were compared, and the conspecifics received a unified code. Priority was given to codes used in published studies [16,29]. When a species occurred in two biomes, we kept the morphospecies’ code from published sources and added the codes from both biomes. For instance, Cis sp.ZB-TAF is the same of Cis sp.5-SFP. The latter is published in Graf-Peters et al. [16], so we kept it and added “TAF”, leading to Cis sp.5-SFP-TAF. When referring to individuals of this species collected in TAF, the code TAF is cited at first and then SFP, leading to Cis sp.5-TAF-SFP.

Identification of fungi and nomenclature

Identification of fungi from the African (SA) and the Subtropical Atlantic Forest (SFP) datasets are explained by Neser [29] and Graf-Peters et al. [16], respectively. Fungi from the Cerrado and the Tropical Atlantic Forest (TAF) were identified by the senior and junior authors, respectively. Fungi species names from all datasets were updated by consulting the online database Index Fungorum (http://www.indexfungorum.org/).

The TAF dataset

TAF ciids and their host fungi were collected during expeditions to 12 Conservation Units in the Brazilian states of Espírito Santo, Minas Gerais and Rio de Janeiro, made between Oct 2011 and Jan 2012. The ciids were reared under laboratory conditions in order to obtain sufficient specimens for identification and to confirm they breed in the fungi species where they were collected. All obtained ciids were examined and separated in morphospecies, a few individuals of each were mounted and the remaining was kept in alcohol. Ciids were obtained from more than 800 samples of fungi. Voucher specimens are deposited at CELC.

The SFP dataset

This dataset is the result of a comprehensive survey on the fungi and the ciid beetles of the National Forest of São Francisco de Paula, in the state of Rio Grande do Sul, southern Brazil, conducted between Aug 2006 and Mar 2007. A total of 376 individual fungi (sensu Graf-Peters et al.[16]) were collected, comprising 40 species. The fungi were maintained in laboratory in order to breed the ciids and other beetles. Among the material, ciids were obtained from 152 individual fungi of 33 species. A key to the fungi of SFP was made available by [38]. A list of the ciids of SFP and their respective host fungi, including detailed information on number of occurrences and feeding habits, was made available by Graf-Peters et al. [16]. Voucher specimens are deposited at CELC and at Fundação Zoobotânica do Rio Grande do Sul (MCNZ; Porto Alegre, RS, Brazil).

The CER dataset

This dataset was obtained from an unpublished survey on the ciids from Alto Paranaíba, in the state of Minas Gerais, Brazil, conducted between Dec 2011 and Jul 2012 [39; Lopes-Andrade pers. comm.]. A total of 69 individual fungi were collected in four phytophysiognomies of Cerrado. They were maintained in laboratory and ciids reared in 66 individual fungi. The ciid fauna of the Brazilian Cerrado is barely studied and the few published data on them is spread in the literature and is not robust enough to be included in our analyses. Voucher specimens are deposited at CELC.

The SA dataset

This dataset is the result of a long-term study on species of Astichus Förster (Hymenoptera: Eulophidae) parasitizing ciids in South Africa, with field collections in 20 localities, two in the southwest (Western Cape province) and 18 in northeast (Limpopo, North West, Gauteng, Mpumalanga and Kwazulu-Natal). Most collections took place between May 2002 and Jul 2010, but the dataset includes a few data from 1984, 1986 and 1990. The fungi were maintained in laboratory to breed the ciids and their parasitoids. The ciids from fungal samples that yielded parasitoids totalized approximately 800 specimens, and label data with information on their host fungi were published in the work of Neser [29]. One invasive ciid species found among these specimens, Ceracis tabellifer (Mellié), was also included on a broad study on invasive Ceracis Mellié of the cucullatus species-group [24]. Then, we had access to the ciids from fungal samples that did not yield parasitoids, and also to other ciids deposited in the South African National Collection of Insects (SANC), totalizing more than 2800 specimens. Voucher specimens are deposited at CELC and SANC.

The southern Africa, mostly South Africa, is considered to comprise the Afrotemperate zoogeographic region of the Austral kingdom [see 40]. Here we follow this biogeographic classification.

Data criteria

We recorded only breeding data based on the criteria proposed by Lawrence [1] and further recommendations of Orledge & Reynolds [11]. We considered as breeding record if at least one of following criteria was met: (i) at least 10 pigmented adults, (ii) two or more teneral adults (i.e. recently ecloded, light-coloured adults), or (iii) one teneral and two or more mature (fully pigmented) adults were found in the fungi. Another important criteria was presence of adults from eggs, larvae or pupae after bred out. On the way, we could eliminate the erroneous breeding records based only on casual presence of adult ciids in the basidiomes. In the absence of data on which to base any informed modifications of these criteria, Lawrence [1] and Orledge & Reynolds [11] is followed here.

Data format

The number of occurrences corresponds to the times a ciid species was found in a particular host fungus in each biome. The sum of the source scores for each ciid/host genus pair was then expressed as a proportion of a ciid species's total occurrence.

Individual dataset structure

Cluster analysis: Ciids were clustered with respect to host-use in analyses performed on each dataset in turn using Mesquite Software. We performed 1000 repetitions and employed Jackknife to reach the best dendrogram and so evaluate the consistence of groups formed by cluster analysis and Jackknife value. For each dataset, dendrograms were obtained using all possible combinations by Unweighted Pair-Group Matrix Analysis (UPGMA) with arithmetic averages [41,42]. It is important to note that this analysis was chosen based on the comparison of different clustering methods made by Orledge & Reynolds [11] for host-use datasets of ciids from the Nearctic and Palearctic regions. They compared four different clustering methods and did not find any statistic difference between them, but concluded that UPGMA was the most suitable for these kind of data. From dendrograms obtained using this best fit method, we identified ciid clusters, each comprising two or more ciids that together formed a discrete cluster in most, if not all, of their dataset dendrograms. Each of these clusters was colour coded and given a single-letter identifier [11]. These identified ciid clusters are referred to below as coloured clusters.

Recognition of host affinities: To recognize the host affinities, we used the tabulated data for proportions. Each dataset was considered separately, with each host genus taken in turn, and with only those ciids belonging to the coloured clusters considered. To consider a specific fungus genus as a part of a group, it had to be used by ciid below 30% by chance because it was the average that polyphagous ciids appear in the most favourite fungus. The cluster was comprised when the majority of the ciids was supported by the host. In some cases the ciids that belong to different hosts were split equally between two coloured clusters, or almost equally between three clusters. In these cases, we recognized a multiple host affinity to ciid with these clusters.

Comparing dataset structures

To characterized a core affinity profile, we followed Orledge & Reynolds [11] criteria, as follows: (i) fungi genera with affinity data for all four datasets to have at least three affinities in common; (ii) fungi genera with affinity data for three datasets only to share at least two affinities with all other group members; and (iii) fungi genera with affinity data for two datasets only to share both of these affinities with all other group members. On that way, host affinities for all datasets were combined to give an affinity profile supporting one or more ciids from the coloured clusters. We numbered the affinities group in turn to place together the hosts with similar profiles.

During this process, each of several of the ciids that failed to cluster in one of the coloured clusters was placed in the ciid host-use group containing the fungi associated with a clear majority of its breeding host data. Ciids belonging to coloured clusters, but with ambiguous data in terms of the recognised ciid host-use groups, were left ungrouped. Also left ungrouped were hosts with no, or ambiguous, affinity data, and the remaining ciids that failed to cluster in one of the coloured clusters.

Results

The data

We coded the clusters formed to facilitate comparison of the tables and figures provided in this paper. Our data has been assigned with the same colour across all datasets. For table and figures reference, the clutters were colour coding as: I, II, VI, XVIII and XXII

(red); III, IX, XII and XV (blue); IV and XVII (green); V (rose pink); VIII, XI, XIV, XVI, XIX and XX (purple); VII, XIII and XXI (orange); and X (yellow).

The TAF dataset is the biggest of this work, comprising 51.2% of the total ciid species. This corresponds to 64 species with breeding records, of 15 genera (Table 4). Following it there are the SA, SFP and CER datasets with 26, 22 and 14 species of Ciidae, respectively. We registered 37 host fungi genera. They are all lignicolous basidiomycetes, representing only Holobasidiomycetidae. Among the host fungi, there is only one family of Agaricales, Pleurotaceae (genus Pleurotus), and the other basidiomes are all Aphylophorales, of the families Hericiaceae, Meripilaceae, Russulaceae, Stereaceae, Schizophyllaceae and Thelephoraceae (each with one genus, respectively: Laxitextum, Rigidoporus, Russula, Stereum, Schizophyllum and Telephoraceae), Gloeophyllaceae and Ganodermataceae (two genera each: Lenzites and Mycobonia, and Ganoderma and Amauroderma, respectively), Meruliaceae (three genera: Podocypha, Junghuhnia and Flaviporus), Fomitopsidaceae (four genera: Fomitopsis, Fomes, Bjerkandera and Phaelous), Hymenochaetaceae (five genera: Cyclomyces, Hymenochaete, Inonotus, Phellinus and Trichaptum) and Polyporaceae (14 genera: Coriolus, Coriolopsis, Daedaleopsis, Datronia, Earliella, Favolus, Funalia, Hexagonia, Laetiporus, Lentinus, Perenniporia, Polyporus, Pycnoporus, Trametes). Some genera of host fungi were used by only one ciid species and many ciids were recorded from only one or two hosts. Otherwise, some ciids can be considered polyphagous, because their breeding records were in many genera of fungi of different families (see tables 1–4).

Cluster analyses

We accepted only the clusters with high Jackknife value. Dendrograms with scoring coefficients are shown in Figs 1–4. Substantial similarities within each set of dendrograms defined a large-scale structure for each dataset. These structures are described by the coloured ciid clusters, of which there are three, six, five, and two in the SA, SFP, TAF and CER datasets, respectively (Figs. 1–4). For each dataset, these clusters were composed by grouping ciids that use the same resource; and after that we joined the ciid species similar between datasets. There were few exceptions, as follows: (1) Cis sp.A-SA, Cis sp.B-SA, Cis sp.N-SA and Xylographus madagascariensis-SA, that belong to the Trametes group, was registered in Ganoderma fungus; (2) Xylographus sp.-SA found in Hymenochaete was kept in the Lenzites group; (3) Ceracis limai-SFP was kept in the Rigidoporus group, even though it was also found in Phellinus; (4) The Pycnoporus group and Trametes group were placed together in the final analysis due to the biological similarities of their species and phylogenetic proximity (Table 5).

Host-use groups

Twenty two affinity groups were formed by the cluster analyses. Host fungi were grouped when they recurrently appeared together in the clusters, indicating they share ciid species. The affinity groups were gathered in six host-use groups, as follows: (a) Ganoderma group (group numbers III, IX, XI and XV) formed by the fungi genera Ganoderma, Fomitopsis, Inonotus and Perenniporia; (b) Lenzites group (group numbers IV and XVII) formed by the genus Lenzites; (c) Mycobonia group (group number V) formed by Mycobonia, Junghuhnia and Coriolopsis; (d) Phellinus group (group

numbers VIII, XI, XIV, XVI, XIX, XX) formed by Cyclomyces, Phellinus, Polyporus and Hymenochaete; (e) Trametes group (group numbers I, II, VI, VII, XIII, XVIII, XXI and XXII) formed by Hexagonia, Trametes, Phaeolus, Telephora, Russula, Funalia, Pycnoporus, Earliella, Schizophyllum and Stereum; (f) Rigidoporus group (group number X) formed by Rigidoporus (See Table 5). We recognized three host-use groups in SA (Ganoderma, Lenzites and Trametes groups), six in SFP (Ganoderma, Lenzites, Mycobonia, Phellinus, Trametes and Rigidoporus), four in TAF (Ganoderma, Lenzites, Phellinus and Trametes groups) and two in CER (Phellinus and Trametes groups).

Discussion

The number of studied ciid species surpassed the number of described species known to occur in each of these faunas, with 11 and 54 species, respectively [4,43]. However, the number of fungi genera is an approximation of the actual diversity of these organisms, because fungi without ciids were not registered. Most parts of the datasets were composed by groups of ciids that use one or few fungi genera. A few species are clearly polyphagous, as Ceracis tabelifer-SA, an invasive species in Africa (Antunes-Carvalho & Lopes-Andrade 2013), Ceracis sp.2-SFP, Ceracis aff. bicornis-TAF and Ceracis tabellifer-CER, all using host fungi of different genera and being the unique ciid species registered in several fungi genera.

Composition and structure of host-use groups

Six host-use groups were recognized and they together represent the taxomomic diversity of ciids and the wood-rotting basidiomycetes (13 families and 37 genera) used by them as breeding hosts. Our data is composed mostly by ciid species which are new to science, and none of them is presented in the datasets examined by Orledge and Reynolds [11] to define host-use groups for the Holarctic Ciidae fauna. But several host fungi genera are presented in ours and theirs datasets, and thus host-use groups are comparable. Orledge and Reynolds [11] recognized the Stereum host-use group, but in our dataset it is a subgroup of the Trametes group, because most part of the ciid species occurring in Stereum also occurred in Trametes, such as Ceracis cornifer-CER and Cis sp.B-CER. We did not recognize a Trichaptum group or an Auricularia group. In our clusters, Trichaptum was used only by ungrouped ciid species and Auricularia was not presented in our datasets. Orledge and Reynolds [11] predicted that when data from other biogeographic regions were available, further host-uses groups would be defined. We confirmed this prediction, finding three host-use groups not previously recognized: the Mycobonia, Lenzites and Rigidoporus groups.

Among the six host-use groups we recognize, only Trametes appeared in all datasets. The lack of host-use groups in SA, TAF and CER, in comparison to SFP, may be a reflection of the absence or low abundance of host fungi genera that compose the lacking groups. For instance, the Ganoderma group is absent only in Cerrado, where big basidiomes, such as the ones of Ganoderma and Fomitopsis, are rarely found. The ciid species that eventually use Ganoderma as host in CER occur more frequently in hosts of other groups or are polyphagous species, which can deal with the unpredictability and low abundance of this resource in CER.

Approximately 80% of the ciid species and 60% of the host genera listed in this study are included in a host-use group. The grouped ciids come from a particular host or a range of hosts that belongs to the same family of fungi. In a few cases, ungrouped ciids are extreme polyphagous species, for instance Ceracis tabellifer in CER and SA and Ceracis aff. bicornis in CER, TAF and SFP, both from the cucullatus species-group, and Cis pubescens in CER and TAF, from the taurus gp. These species were already known to use a wide range of host fungi, without any evident pattern of utilization and even exploring fungi not consumed by other ciids [1,33].Therefore, the grouped ciids comprise mostly monophagous and oligophagous species, rather than polyphagous ones. However, it shall be noted here that polyphagous species may comprise host-use groups in specific situations, at least theoretically, and so it is necessary to include them in cluster analyses. A ciid species is considered polyphagous when the percentage of occurrences in a single fungus family is less than 90% of the recorded occurrences [16]. But even though a species consumes fungi of different families and, consequently, is classified as polyphagous, several of the host fungi may belong to a single host-use group. For instance, the Ganoderma host-use group include fungi genera not only of Ganodermateceae, but of Polyporaceae, Fomitopsidaceae and Hymenochaetaceae. Therefore, a ciid species of the Ganoderma host-use group may be polyphagous if it consumes fungi of these families, but still belong to a host-use group. The classification of ciid species in host-use groups does not necessarily reflect their degree of specialization in host use.

The definition of host-use groups may be extended to others obligate fungivorous beetles [1], as some taxa of Tenebrionidae, Ptinidae, Mycetophagidae, Erotylidae and even of other insects, such as Diptera, Lepidoptera and Hymenoptera [17,44,45]. The basic method to reach such grouping is obtaining the data registers in

scientific literature and making field samplings. It is important to determine whether host-use groups of Ciidae detected in a biome applies only to ciids or to other unrelated taxa, because in order to evaluate whether it depends mostly on the evolutionary history of a fungivorous taxon or it is a major property of an ecosystem.

Ecological Considerations

The present paper documents patterns of ciid host-use over wide geographic areas. But these patterns were not detected in preserved landscapes, but mostly in forest remnants of degraded biomes. Species of fungivorous beetles and their hosts might have been lost before our study and that certainly affected the structures of these communities [26,46]. It means that the host-use groups we have found reflects not only ecological interactions and evolutionary history of ciid species and host fungi, but also forest fragmentation and other anthropogenic interferences in these environments. The National Forest of São Francisco de Paula (SFP) is a well preserved area, but most importantly it is in a landscape made of several well preserved and interconnected large forest remnants [16]. In the other hand, the studied remnants of the Atlantic Forest (TAF), Cerrado (CER) and subtropical forests of South Africa (SA) are surrounded by highly degraded or even urbanized areas. We suppose that the number of host-use groups is a reflection of the degree of forest conservation or environmental quality, an important issue that shall be evaluated in the future. These biomes still shelter a high diversity of ciid beetles, and certainly of other fungivorous insects [16,39]. Most ciid species we studied are new to science and sometimes their populations are restrict to one or a few forest patches. It is important to understand how the structure of landscapes, with their forest remnants and

matrix of open areas highly modified by humans, affect these small, geographically restricted populations.

The host-use groups vary between biomes and the host-use group of one species is not necessarily the same in different biomes. The SFP and TAF datasets share species that fit different host-use groups in these biomes. For instance, Porculus vianai in SFP has not grouped, while in TAF it appeared in the Ganoderma group. Cis sp.5 in SFP appeared in the Mycobonia group, while in TAF was included in the Phellinus group. Xylographus contractus appeared in the Trametes and in the Phellinus group in CER and TAF, respectively. However, some species did not change their resources, as Gen. 1 sp.-TAF-SFP and Gen. 2 sp.-TAF-SFP, that were grouped in both datasets in the Phellinus and in the Ganoderma group, respectively.

Another recognized pattern was the presence of at least one polyphagous species in all datasets. The unique species shared by Brazilian and South African biomes, Ceracis tabellifer, is polyphagous. It is the most abundant and frequently encountered ciid species in Africa [35]. Ceracis tabellifer is a Neotropical species and possibly native to the Cerrado, where it is also polyphagous and the unique to occur in the four phytophysiognomies with known ciid fauna, indicating that it supports adverse conditions very well. It was introduced in Africa during the XIX century or before, and it is considered an invader there because there is no other Ceracis in the region and all the species in the cucullatus group are Neotropical [35]. It may be a good competitor, depleting resources and thus eliminating monophagous and oligophagous native ciid species [10,47]; or simply and opportunist that uses resources usually not consumed by native species. Anyway, its small size and fast development are possible advantages that permit it to explore available resources anywhere and possibly before native species [35]. Other common polyphagous species in Neotropical biomes are Cis pubescens (in

TAF and CER) and Ceracis aff. bicornis (SFP, TAF and CER). The latter is indeed a complex of morphologically related species, almost indiscernible, that deserve a careful and detailed taxonomic revision.

In SA and CER only three (Trametes, Ganoderma and Lenzites groups) and two (Trametes and Phellinus groups) host-use groups, respectively, were detected. The low number of host-use groups may be related to climatic conditions of both biomes. These biomes are in areas of dry weather and have typical Savannah vegetation with patches of forests [29,39]. Even the subtropical forest formations of SA are dryer in comparison to TAF and SFP. Ciids depend on dry a microclimatic condition of the basidiomes, but the basidiomes on their ways depend on high humidity to develop [48]. The total mass of basidiomes and frequency of occurrence of species of host fungi are possibly very low in SA and CER, and these parameters of resource availability shall be evaluated in future works.

The association with fungi, which are ephemeral and aggregated organisms, depends on a high ability for locating them and establishing populations in resources that are usually hazardous for other animals [13,49]. The evolution of different degrees of specialization of ciids to different host fungi may have shaped what is now seen as host-use groups [16]. The ultimate mechanism maintaining these groups may be the beetles' abilities to recognise particular host odours. The composition of volatiles released from host basidiomes can differ between fungi genera [13,49,50]. Also, both walking and flying ciids can be strongly attracted to odours of their particular hosts, whilst failing to respond to odours of hosts they do not use [13,49,51]. Some similarities and differences between the volatiles from Piptoporus and Ganoderma, and Trametes, indicate that the volatiles emitted by a particular fungus may share chemical attributes mostly with those fungi that belong to the same host-use group [13,49]. Thus, the

volatile emissions may have a chemical signature only shared by distinct groups of fungi that only ciids from the same host-use group and those that use several genera of fungi can recognize and respond. Not only volatiles of basidiomes, but also their structure, hardness, moisture content, time of exposure, presence/absence of chemical components that are difficult to degrade, seasonality, rot degree and presence of other fungivores, have been suggested as factors affecting the maintenance of ciid populations [1,12,16,45,52,53,54].

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Table 1: The South African dataset. Resource matrix for ciids (rows) from South Africa and their breeding hosts (columns), the ciids grouped according to the clusters in Fig. 1. Ciid clusters identifiers are in column 1. Host fungi are ordered to emphasise the similarities and differences between the data. These data are coloured to match the dendrogram clusters in Fig. 1. Numerical data are the summed record sources (see text) for each taxon pair expressed as a proportion of the ciid's total record sources.

	n	Coriolus Quél. 1886	Daedaleopsis J. Schröt. 1888	Favolus P. Beauv. 1805	FomitopsisP. Karst. 1881	FunaliaPat. 1900	Ganoderma P. Karst 1881	Hexagonia Pollini 1816	Stereum Hill ex Pers. 1794	Trametes Fr. 1836	Phaeolus Pat. 1900	Thelephora Ehrh. ex Willd. 1787	Hymenochaete Lév. 1846	Laetiporus Murr.	LaxitextumLentz 1956	Lentinus	Lenzites Fr. 1836	Phellinus Quél. 1886	Podoscypha Pat. 1900	Polyporus P. Micheli 1729	Pycnoporus P. Karst 1881	RussulaPers. 1796
Ceracis tabellifer-SA (gp. cucullatus)	90	0.01	0.01	0.01	0.01	0.02	0.19	0.01	0.06	0.43	0.03	0.02	0.01	0.01	0.01	0.01	0.09	0.02	0.01	0.01	0.03	
Cis sp.E-SA	42	0.02				0.02	0.06	0.02	0.06	0.46		0.02				0.02	0.17				0.15	
Cis sp.J-SA	12				0.08		0.33			0.42							0.17					
I																						
Cis pickeri-SA (gp. bilamellatus)	1									**1.0**												
Cis sp.A-SA	6						**0.16**	**0.17**		**0.67**												
Cis sp.B-SA	4						**0.25**		**0.25**	**0.50**												
Cis sp.C-SA	4									**1.0**												
Cis sp.D-SA	1									**1.0**												
Cis sp.F-SA	1									**1.0**												
Cis sp.G-SA	1									**1.0**												
Cis sp.H-SA	4									**0.75**	**0.25**											
Cis sp.I-SA	2									**0.50**		**0.50**										
Cis sp.K-SA	1									**1.0**												
Cis sp.L-SA	2								**0.50**	**0.50**												

Continuation Table 1:

		n	Coriolus Quél. 1886	Daedaleopsis J. Schröt. 1888	Favolus P. Beauv. 1805	Fomitopsis P. Karst. 1881	Ganoderma P. Karst 1881	Russula Pers. 1796	Funalia Pat. 1900	Hexagonia Pollini 1816	Stereum Hill ex Pers. 1794	Trametes Fr. 1836	Thelephora Ehrh. ex Willd. 1787	Hymenochaete Lév. 1846	Lenzites Fr. 1836	Laetiporus Murr.	Laxitextum Lentz 1956	Lentinus	Phaeolus Pat. 1900	Phellinus Quél. 1886	Podoscypha Pat. 1900	Polyporus P. Micheli 1729	Pycnoporus P. Karst 1881
	Cis sp.Q-SA	12				0.08	0.08				0.17	0.43	0.08	0.08	0.08								
II																							
	Cis sp.M-SA	1							1.0														
	Cis sp.N-SA	4					0.25		0.25			0.50											
	Cis sp.P-SA	3								0.33	0.33	0.34											
	Cis sp.R-SA	1										1.0											
	Cis sp.W-SA	2						0.50				0.50											
	Cis sp.O-SA	1										1.0											
	Cis sp.Y-SA	2										1.0											
	Xylographus madagascariensis-SA	8					0.12					0.63	0.25										
III																							
	Cis sp.T-SA	2				0.50	0.50																
IV																							
	Orthocis sp.A-SA	1													1.0								
	Xylographus sp.-SA	1												1.0									

Table 2: The Subtropical Atlantic Forest dataset. Resource matrix for ciids (rows) from the National Forest of São Francisco de Paula (Rio Grande do Sul, Brazil) and their breeding hosts (columns), the ciids grouped according to the dendrogram clusters in Fig. 2. Ciid cluster identifiers are in column 1. Host fungi are ordered to emphasise the similarities and differences between the data. These data are coloured to match the dendrogram clusters in Fig. 2. Numerical data are the summed record sources (see text) for each taxon pair expressed as a proportion of the ciid's total record sources.

	n	Amauroderma Murril 1905	Bjerkandera P. Karst 1879	Datronia Donk 1966	Flaviporus Murril 1905	Coriolopsis Murril 1905	Junghuhnia Corda 1842	Lenzites Fr. 1836	Mycobonia Pat. 1894	Inonotus P.Karst 1879	Ganoderma P. Karst 1881	Perenniporia Murril 1942	Funalia Pat. 1900	Cyclomyces Kunze 1830	Phellinus Quél. 1886	PolyporusP. Micheli 1729	Rigidoporus Murril 1905	Pycnoporus P. Karst 1881	Trametes Fr. 1836	Trichaptum Murril 1904
Cis sp.1-SFP (gp. taurus)	36	0.03	0.03	0.03	0.03		0.03				0.06	0.09	0.06	0.10	0.31		0.06		0.06	0.17
Ceracis aff. bicornis-SFP (gp. cucullatus)	14					0.43							0.29				0.21		0..07	
Ceracis sp.2-SFP	10					0.10				0.10			0.20	0.10			0.30		0.10	0.10
Porculus vianai-SFP	31		0.16								0.65		0.03				0.16			
Cis aff. melliei-SFP-TAF (gp. melliei)	3									0.33				0.33						0.34
V																				
Ceracis sp.3-SFP	2					**0.50**			**0.50**											
Cis sp.5-SFP-TAF (gp. fagi)	3						**0.34**	**0.33**	**0.33**											
VI																				
Cis sp. 6-SFP (gp. bilamellatus)	11												**0.09**			**0.09**		**0.27**	**0.54**	
Cis sp.2-SFP (gp. vitulus)	10														**0.10**				**0.90**	
Cis sp.4-SFP (gp. tricornis)	20														**0.05**			**0.05**	**0.90**	
Grossicis diadematus-SFP	3																	**0.33**	**0.67**	

Table 2 Continuation

	n	Amauroderma Murril 1905	Bjerkandera P. Karst 1879	Datronia Donk 1966	Flaviporus Murril 1905	Coriolopsis Murril 1905	Junghuhnia Corda 1842	Lenzites Fr. 1836	Mycobonia Pat. 1894	Inonotus P.Karst 1879	Ganoderma P. Karst 1881	Perenniporia Murril 1942	Funalia Pat. 1900	Cyclomyces Kunze 1830	Phellinus Quél. 1886	Polyporus P. Micheli 1729	Rigidoporus Murril 1905	Pycnoporus P. Karst 1881	Trametes Fr. 1836	Trichaptum Murril 1904
VII																				
Ceracis simplicicornis-SFP (gp. furcifer)	10							**0.10**										**0.90**		
Cis sp.3-SFP (gp. comptus)	3							**0.33**										**0.33**	**0.34**	
VIII																				
Gen.1 sp.-SFP-TAF	8													**0.37**	**0.63**					
Xylographus gibbus-SFP	1														**1.0**					
IX																				
Xylographus corpulentus-SFP	10										**0.40**				**0.60**					
Cis aff. testaceimembris-SFP (gp. taurus)	16									**0.06**	**0.88**	**0.06**								
Gen2 sp.-SFP-TAF	4											**1.0**								
Scolytocis fritzplaumanni-SFP	19										**1.0**									
X																				
Ceracis limai-SFP (gp. singularis)	15														**0.93**		**0.07**			
Cis aff. kawanabei-SFP (gp. taurus)	4																**1.0**			

Table 3: The Tropical Atlantic Forest dataset. Resource matrix for ciids (rows) from Tropical Atlantic Forest remnants and their breeding hosts (columns), the ciids grouped according to the dendrogram clusters in Fig. 3. Ciid cluster identifiers are in column 1. Host fungi are ordered to emphasise the similarities and differences between the data. These data are coloured to match the dendrogram clusters in Fig. 3. Numerical data are the summed record sources (see text) for each taxon pair expressed as a proportion of the ciid's total record sources.

	n	Cyclomyces Kunze 1830	Fomes Fr. 1849	Funalia Pat. 1900	Formitopsis P. Karst. 1881	Ganoderma P. Karst 1881	Lenzites Fr. 1836	Hymenochaete Lév. 1846	Phellinus Quél. 1886	Polyporus P. Micheli 1729	Pycnoporus P. Karst 1881	Hexagonia Pollini 1816	Trametes Fr. 1836
Ceracis aff. bicornis-TAF (gp. cucullatus)	48		0.02		0.02		0.04	0.18	0.40		0.02	0.13	0.19
Ceracis aff. cucullatus-TAF (gp. cucullatus)	9		0.11			0.11	0.11	0.11					0.56
Ceracis sp.G-TAF	11						0.09	0.46				0.18	0.27
Porculus dufaui-TAF	14		0.07			0.65		0.07	0.21				
Cis pubescens-TAF (gp. taurus)	9					0.34		0.22	0.11			0.11	0.22
Xylographus gibbus-TAF	16			0.06		0.12		0.13	0.38			0.06	0.25
Xylographus corpulentus-TAF	17				0.06	0.18		0.23	0.41				0.12
Cis kawanabei-TAF (gp. taurus)	13				0.08			0.23	0.23	0.08			0.38
Cis sp.R-TAF (gp. taurus)	15				0.07			0.40	0.13				0.40
Cis sp.D-TAF (gp. taurus)	10				0.10			0.20	0.10				0.60
XI													
Strigocis vicosensis-TAF	06	**0.17**						**0.32**	**0.17**	**0.17**			**0.17**
Cis sp.S-TAF (gp. taurus)	11						**0.19**	**0.36**	**0.09**	**0.09**			**0.27**
Ceracis limai-TAF (gp. singularis)	13							**0.38**	**0.31**	**0.08**			**0.23**
Phellinocis romualdoi-TAF	33					**0.06**		**0.15**	**0.55**	**0.03**			**0.21**
Gen.B sp.B-TAF	5					**0.20**		**0.20**	**0.40**	**0.20**			

Table 2 Continuation:

		n	Cyclomyces Kunze 1830	Fomes Fr. 1849	Funalia Pat. 1900	Formitopsis P. Karst. 1881	Ganoderma P. Karst 1881	Lenzites Fr. 1836	Hymenochaete Lév. 1846	Phellinus Quél. 1886	Polyporus P. Micheli 1729	Pycnoporus P. Karst 1881	Hexagonia Pollini 1816	Trametes Fr. 1836
	Xylographus brasiliensis-TAF	9					0.78			0.11				0.11
	Falsocis sp.B-TAF	3					0.33			0.67				
XII														
	Scolytocis paschoali-TAF	16				**0.06**	**0.88**	**0.06**						
	Porculus vianai-TAF	20				**0.05**	**0.95**							
XIII														
	Cis aff. pusillus-TAF (gp. comptus?)	2										**1.0**		
	Ceracis cornifer-TAF (gp. furcifer)	5										**0.60**		**0.40**
XIV														
	Cis sp.L-TAF (gp. tricornis)	7							**0.29**	**0.57**				**0.14**
	Xylographus contractus-TAF	15							**0.07**	**0.67**				**0.26**
	Gen.E sp.A-TAF	2								**0.50**				**0.50**
	Falsocis brasiliensis-TAF	4								**0.50**				**0.50**
XV														
	Gen.2 sp.- TAF-SFP	1					**1.0**							
	Gen.B sp.A-TAF	1					**1.0**							
	Cis sp.ZH-TAF (gp. taurus)	8					**1.0**							
	Grossicis sp.A-TAF	1					**1.0**							
XVI														
	Orthocis sp.A-TAF	1	1.0											
	Cis sp.F-TAF (gp. vitulus)	1									1.0			

Table 2 Continuation

		n	Cyclomyces Kunze 1830	Fomes Fr. 1849	Funalia Pat. 1900	Formitopsis P. Karst. 1881	Ganoderma P. Karst 1881	Lenzites Fr. 1836	Hymenochaete Lév. 1846	Phellinus Quél. 1886	Polyporus P. Micheli 1729	Pycnoporus P. Karst 1881	Hexagonia Pollini 1816	Trametes Fr. 1836
XVII														
	Cis sp.X-TAF (gp. taurus)	1						**1.0**						
	Scolytocis sp.D-TAF							**1.0**						
XVIII														
	Ceracis sp.D-TAF	2											**0.50**	**0.50**
	Cis sp.U-TAF (gp. taurus)	6											**0.17**	**0.83**
	Cis sp.W-TAF (gp. taurus)	3											**0.33**	**0.67**
	Scolytocis furieriae-TAF	1												**1.0**
	Cis sp.ZI-TAF (gp. taurus)	1												**1.0**
	Cis sp.ZE-TAF (gp. taurus)	8												**1.0**
	Cis sp.ZF-TAF (gp. taurus)	1												**1.0**
	Cis sp.A-TAF (gp. taurus)	1												**1.0**
	Cis sp.N-TAF (gp. taurus)	2												**1.0**
	Cis sp.ZC-TAF (gp. taurus)	1												**1.0**
	Cis sp.O-TAF (gp. taurus)	2												**1.0**
	Cis sp.M-TAF	1												**1.0**
	Cis sp.E-TAF (gp. tricornis)	1												**1.0**
	Cis sp.J-TAF	1												**1.0**
XIX														
	Porculus grossus-TAF	2							**1.0**					
	Malacocis sp.A-TAF (new sp.)	1							**1.0**					
	Cis sp.5-TAF-SFP	1							**1.0**					
	Cis sp.T-TAF (gp. bilamellatus)	1							**1.0**					
	Cis sp.V-TAF	1							**1.0**					

Table 2 Continuation

	n	Cyclomyces Kunze 1830	Fomes Fr. 1849	Funalia Pat. 1900	Formitopsis P. Karst. 1881	Ganoderma P. Karst 1881	Lenzites Fr. 1836	Hymenochaete Lév. 1846	Phellinus Quél. 1886	Polyporus P. Micheli 1729	Pycnoporus P. Karst 1881	Hexagonia Pollini 1816	Trametes Fr. 1836
Ceracis cucullatus-TAF (gp. cucullatus)	48		**0.02**		**0.02**		**0.04**	**0.18**	**0.40**		**0.02**	**0.13**	**0.19**
Cis sp.Z-TAF (gp. taurus)	4							**0.25**	**0.75**				
Gen.1 sp.- TAF-SFP	4							**0.75**	**0.25**				
Cis sp.Q-TAF (gp. taurus)	4							**0.75**	**0.25**				
Cis sp.G-TAF	2							**0.50**	**0.50**				
Cis sp.C-TAF (gp. taurus)	8							**0.25**	**0.75**				
Ceracis sp.I-TAF	1								**1.0**				
Ceracis sp.H-TAF	1								**1.0**				
Cis sp.ZA-TAF (gp. taurus)	1								**1.0**				
Cis sp.ZG-TAF (gp. taurus)	4								**1.0**				
Dolichocis sp.A-TAF	2								**1.0**				
Cis aff. melliei- TAF-SFP (gp. melliei)	1								**1.0**				

Table 4: The Cerrado (Brazilian Savannah) dataset. Resource matrix for ciids (rows) from four phytophysiognomies of Cerrado of Alto Paranaíba (Minas Gerais, Brazil) and their breeding hosts (columns), the ciids grouped according to the dendrogram clusters in Fig. 4. The Species of ciid are in column 1. Host fungi are ordered to emphasise the similarities and differences between the data. Numerical data are the summed record sources (see text) for each taxon pair expressed as a proportion of the ciid's total record sources. These data are coloured to match the dendrogram clusters in Fig. 4.

	n	Pleurotus (Fr.) Kumm. 1871	Hexagonia Pollini 1816	Lenzites Fr. 1836	Ganoderma P. Karst 1881	Earliella Murril 1905	Phellinus Quél. 1886	Pycnoporus P. Karst 1881	Schizophyllum Fr.1815	Stereum Hill ex Pers. 1794	Trametes Fr. 1836
Cis pubescens-CER (gp. taurus)	13	0.08	0.15		0.08	0.23	0.08	0.08		0.08	0.08
Ceracis tabellifer-CER (gp. cucullatus)	10		0.10	0.10	0.10	0.10		0.30		0.10	0.20
Ceracis aff. bicornis -CER (gp. cucullatus)	10		0.10	0.10	0.10			0.10		0.20	0.40
XX											
Ceracis sp.A-CER	1						**1.0**				
Ceracis sp.C-CER	1						**1.0**				
XXI											
Ceracis cornifer-CER (gp. furcifer)	14						**0.07**	**0.58**	**0.07**	**0.07**	**0.21**
Xylographus contractus-CER	3					**0.34**		**0.33**		**0.33**	
Strigosis vicosensis-CER	3					**0.33**		**0.33**			**0.34**
XXII											
Xylographus gibbus-CER	2				0.50		0.50				
Xylographus rufipes-CER	5				**0.20**		**0.20**	**0.20**			**0.40**
Cis sp.A-CER (gp. comptus)	2									**1.0**	
Cis sp.B-CER (gp. comptus)	1								**1.0**		
Malacocis sp.B-CER	1					**1.0**					

Table 5: Species of Ciidae and Host fungi members of host-use group.

	Host-use group* (Cluters of Ciidae Species and fungus affiliation group)							
	Ganoderma (III;IX;XI;XV)				Lenzites (IV; XVII)	Mycobonia (V)		
Fungi	Ganoderma	Fomitopsis	Inonotus	Perenniporia	Lenzites	Mycobonia	Junghuhnia	Coriolopsis
Ciidae Species	Cis sp.T-SA, Cis aff. testaceimembris-SFP (gp. taurus), Xylographus corpulentus-SFP, Scolytocis fritzplaumanni-SFP, Scolytocis paschoali-TAF, Porculus vianai -TAF, Gen.2 sp.-TAF-SFP, Gen.B sp.B-TAF, Cis sp.ZH-TAF (gp. taurus), Grossicis sp.A-TAF.	Cis sp.T-SA, Scolytocis paschoali-TAF, Porculus vianai-TAF.	Cis aff. testaceimembris-SFP (gp. taurus).	Cis aff. testaceimembris-SFP (gp. taurus).	Cis sp.E-SA, Orthocis sp.A, Cis sp.5-SFP, Cis sp.X-TAF (gp. taurus), Scolytocis sp.D-TAF.	Ceracis sp.3-SFP, Cis sp.5-SFP (gp. fagi).	Cis sp.5-SFP (gp. fagi).	Ceracis sp.3-SFP.
	Phellinus (VIII; XI; XIV; XVI; XIX; XX)				Trametes (I; II; VI; VII; XIII; XVIII; XXI; XXII)			
Fungi	Cyclomyces	Phellinus	Polyporus	Hymenochaete	Hexagonia	Trametes	Phaeolus	Telephora
Ciidae Species	Gen.1 sp.-SFP-TAF, Strigocis vicosensis-TAF (S. vicosensis), Orthocis sp.A-TAF.	Gen.1 sp-SFP, Xylographus gibbus, Strigocis vicosensis-TAF, Cis sp.S-TAF (gp. taurus), Ceracis limai-TAF (gp. singularis),	Strigocis vicosensis-TAF, Cis sp.S-TAF (gp. taurus), Ceracis limai-TAF (gp. singularis), Phellinocis romualdoi-TAF, Gen.B sp.B-TAF, Cis sp.F-TAF (gp. vitulus).	Xylographus sp.-SA, Strigocis vicosensis-TAF, Cis sp.S-TAF (gp. taurus), Ceracis limai-TAF (gp. singularis), Phellinocis romualdoi-TAF, Gen.B sp.B-TAF, Cis sp.L-TAF (gp. tricornis)	Cis sp.P-SA, Ceracis sp.D-TAF, Cis sp.U-TAF (gp. taurus).	Cis pikeri-SA, Cis sp.A-SA, Cis sp.B-SA, Cis sp.C-SA, Cis sp.D-SA, Cis sp.F-SA, Cis sp.G-SA, Cis sp.H-SA, Cis sp.I-SA, Cis sp.K-SA, Cis sp.L-SA, Cis sp.P-SA, Cis sp.R-SA, Cis sp.W-SA, Cis sp.O-SA, Cis sp.Y-SA, Xylographus madagascariensis-SA, Strigocis sp.-SFP,	Cis sp.H-SA	Xylographus madagascariensis-SA

	Phellinus (Cont.)	Hymenochaete (cont.)	Trametes (cont.)
	Phellinocis romualdoi-TAF, Gen.B sp.B-TAF, Cis sp.L-TAF (gp. tricornis), Xylographus contractus-TAF, Ceracis cucullatus-TAF (gp. cucullatus), Cis sp.Z-TAF (gp. taurus), Gen.1 sp.-TAF-SFP, Cis sp.Q-TAF (gp. taurus), Cis sp.G-TAF, Cis sp.C-TAF (gp. taurus), Ceracis sp.I-TAF, Ceracis sp.H-TAF, Cis sp.ZA-TAF (gp. taurus), Cis sp.ZG-TAF (gp. taurus), Dolichocis sp.A-TAF, Cis aff. melliei -TAF-SFP (gp. melliei), Ceracis sp.A-CER, Ceracis sp.C-CER.	Xylographus contractus-TAF, Cis sp.W-TAF (gp. taurus), Porculus grossus-TAF, Malacocis sp.A-TAF, Cis sp.5-TAF-SFP (gp. fagi), Cis sp.T (gp. bilamellatus), Cis sp.V-TAF, Ceracis cucullatus-TAF (gp. cucullatus), Cis sp.Z-TAF (gp. taurus), Gen.1 sp.-TAF-SFP, Cis sp.Q-TAF (gp. taurus), Cis sp.G-TAF, Cis sp.C-TAF (gp. taurus).	Cis sp.2-SFP (gp. vitulus), Cis sp.4-SFP (gp. tricornis), Grossicis diadematus-SFP, Cis sp.3-SFP (gp. comptus), Ceracis cornifer-TAF (gp. furcifer), Ceracis sp.D-TAF, Cis sp.U-TAF (gp. taurus), Scolytocis furieriae-TAF, Cis sp.ZI-TAF (gp. taurus), Cis sp.ZE-TAF (gp. taurus), Cis sp.ZF-TAF (gp. taurus), Cis sp.A-TAF (gp. taurus), Cis sp.N-TAF (gp. taurus), Cis sp.ZC-TAF (gp. taurus), Cis sp.O-TAF (gp. taurus), Cis sp.M-TAF, Cis sp.E-TAF (gp. tricornis), Cis sp.J-TAF, Ceracis cornifer-CER (gp. furcifer), Strigosis vicosensis-CER, Xylographus rufipes-CER, Cis sp.A-CER (gp. comptus).

	Trametes Cont. (I; VII; VIII; IX; XIV; XVI; XVII)						Rigidoporus (XI)
Fungi	Russula	Funalia	Pycnoporus	Earliela	Schizophylum	Stereum	Rigidoporus
Ciidae Species	Cis sp.W-SA	Cis sp.M-SA, Cis sp.N-SA.	Cis sp.6-SFP (gp. bilamellatus), Cis sp.4 (gp. tricornis)-SFP, Grossicis diadematus-SFP, Ceracis simplicicornis-SFP, Cis sp.3-SFP (gp. comptus), Cis aff. pusillus-TAF (gp.comptus?), Ceracis cornifer-TAF (gp. furcifer), Ceracis cornifer-CER (gp. furcifer), Xylographus contractus-CER, Strigocis vicosensis-CER.	Xylographus contractus-CER, Strigosis vicosensis- CER, Malacocis sp.B-CER.	Ceracis cornifer-CER (gp. furcifer), Cis sp.B-CER (gp. comptus).	Cis sp.P-SA, Ceracis cornifer-CER (gp. furcifer), Xylographus contractus-CER, Cis sp.A-CER (gp. comptus).	Ceracis limai-SFP (gp. singularis), Cis aff. kawanabei-SFP (gp. taurus).

*See text for further explanation.

Figures legends

Figure 1: UPGMA ciid dendrogram for the South African (SA) dataset obtained by Jackknife analysis. Each colored cluster comprises two or more species of Ciidae that belong to a host-use group. See text for colored cluster's identifiers. Abbreviations: SA = South Africa; gp. = species-group.

Figure 2: UPGMA ciid dendrograms for the Subtropical Atlantic Forest (SFP) dataset obtained by Jackknife analysis. Each colored cluster comprises two or more species of Ciidae that belong to a host-use group. See text for colored cluster's identifiers. Abbreviations: SFP = São Francisco de Paula; gp. = group; Gen. = undetermined genus.

Figure 3: UPGMA ciid dendrograms for the Atlantic Forest (TAF) dataset obtained by Jackknife analysis. Each colored cluster comprises two or more species of Ciidae that belong to a host-use group. See text for colored cluster's identifiers. Abbreviations: TAF = Tropical Atlantic Forest; SFP = São Francisco de Paula; gp. = species-group; Gen. = undetermined genus; aff. = affinis (resembling).

Figure 4: UPGMA ciid dendrograms for the Cerrado (CER) dataset obtained by Jackknife analysis. Each colored cluster comprises two or more species of Ciidae that belong to a host-use group. See text for colored cluster's identifiers. Abbreviations: CER = Cerrado; gp. = species-group; Gen. = undetermined genus.

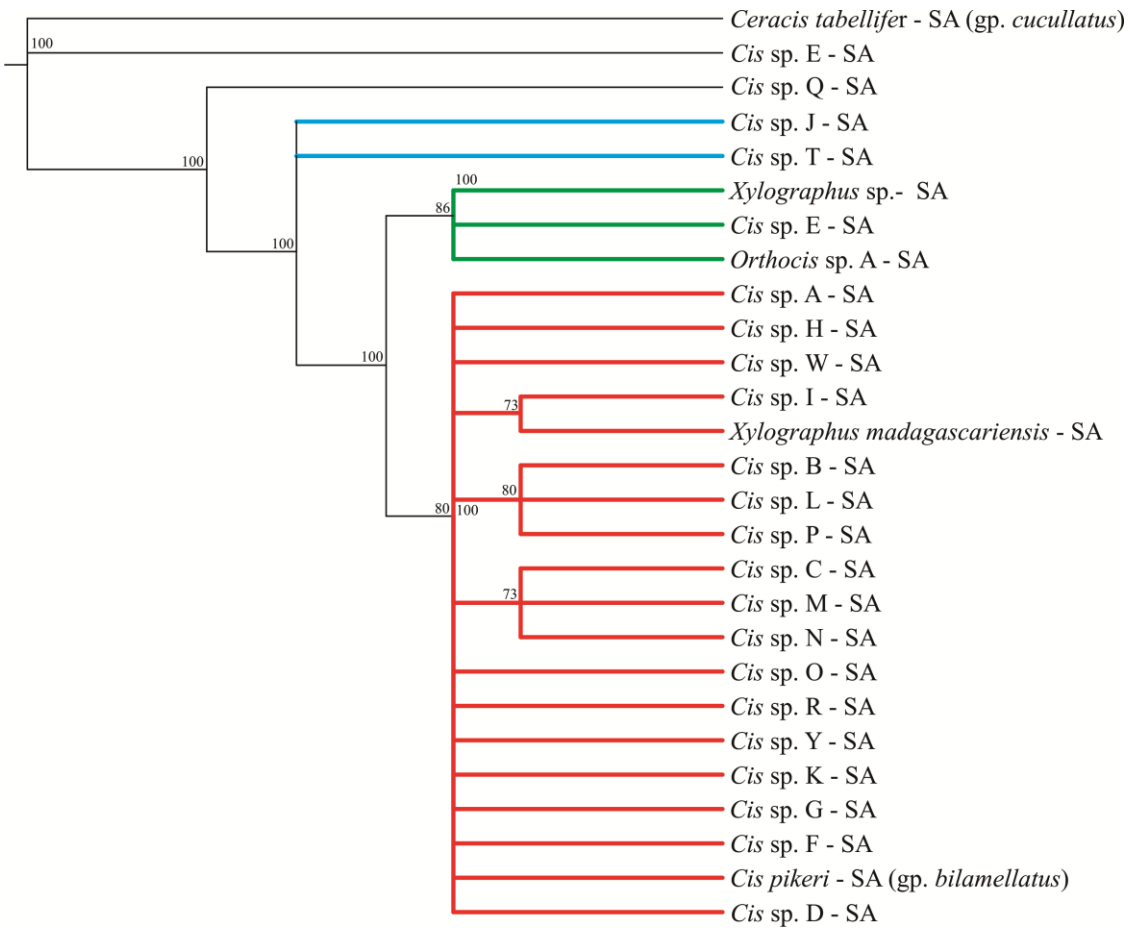

Ceracis tabellifer - SA (gp. cucullatus)
Cis sp. E - SA
Cis sp. Q - SA
Cis sp. J - SA
Cis sp. T - SA
Xylographus sp.- SA
Cis sp. E - SA
Orthocis sp. A - SA
Cis sp. A - SA
Cis sp. H - SA
Cis sp. W - SA
Cis sp. I - SA
Xylographus madagascariensis - SA
Cis sp. B - SA
Cis sp. L - SA
Cis sp. P - SA
Cis sp. C - SA
Cis sp. M - SA
Cis sp. N - SA
Cis sp. O - SA
Cis sp. R - SA
Cis sp. Y - SA
Cis sp. K - SA
Cis sp. G - SA
Cis sp. F - SA
Cis pikeri - SA (gp. bilamellatus)
Cis sp. D - SA
100
100
100
86
100
100
73
80
80
100
73

Figure 1

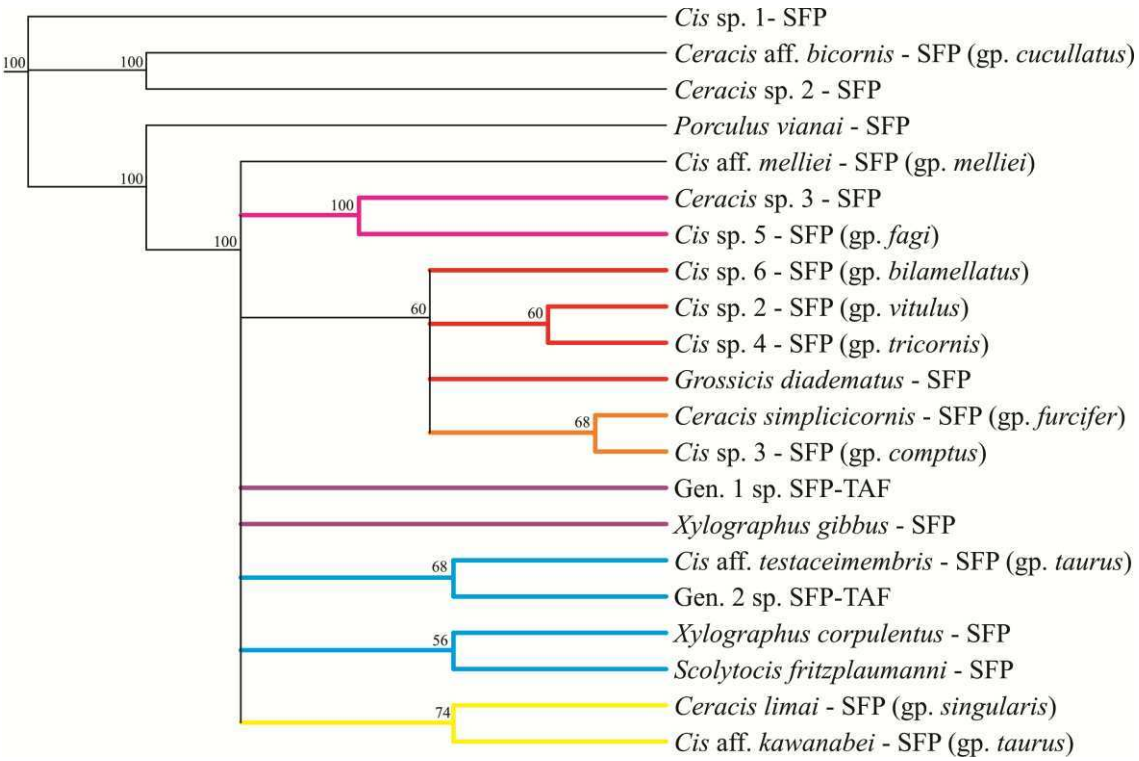

100
100
100
100
100
60
60
68
68
56
74
Cis sp. 1- SFP
Ceracis aff. bicornis - SFP (gp. cucullatus)
Ceracis sp. 2 - SFP
Porculus vianai - SFP
Cis aff. melliei - SFP (gp. melliei)
Ceracis sp. 3 - SFP
Cis sp. 5 - SFP (gp. fagi)
Cis sp. 6 - SFP (gp. bilamellatus)
Cis sp. 2 - SFP (gp. vitulus)
Cis sp. 4 - SFP (gp. tricornis)
Grossicis diadematus - SFP
Ceracis simplicicornis - SFP (gp. furcifer)
Cis sp. 3 - SFP (gp. comptus)
Gen. 1 sp. SFP-TAF
Xylographus gibbus - SFP
Cis aff. testaceimembris - SFP (gp. taurus)
Gen. 2 sp. SFP-TAF
Xylographus corpulentus - SFP
Scolytocis fritzplaumanni - SFP
Ceracis limai - SFP (gp. singularis)
Cis aff. kawanabei - SFP (gp. taurus)

Figure 2

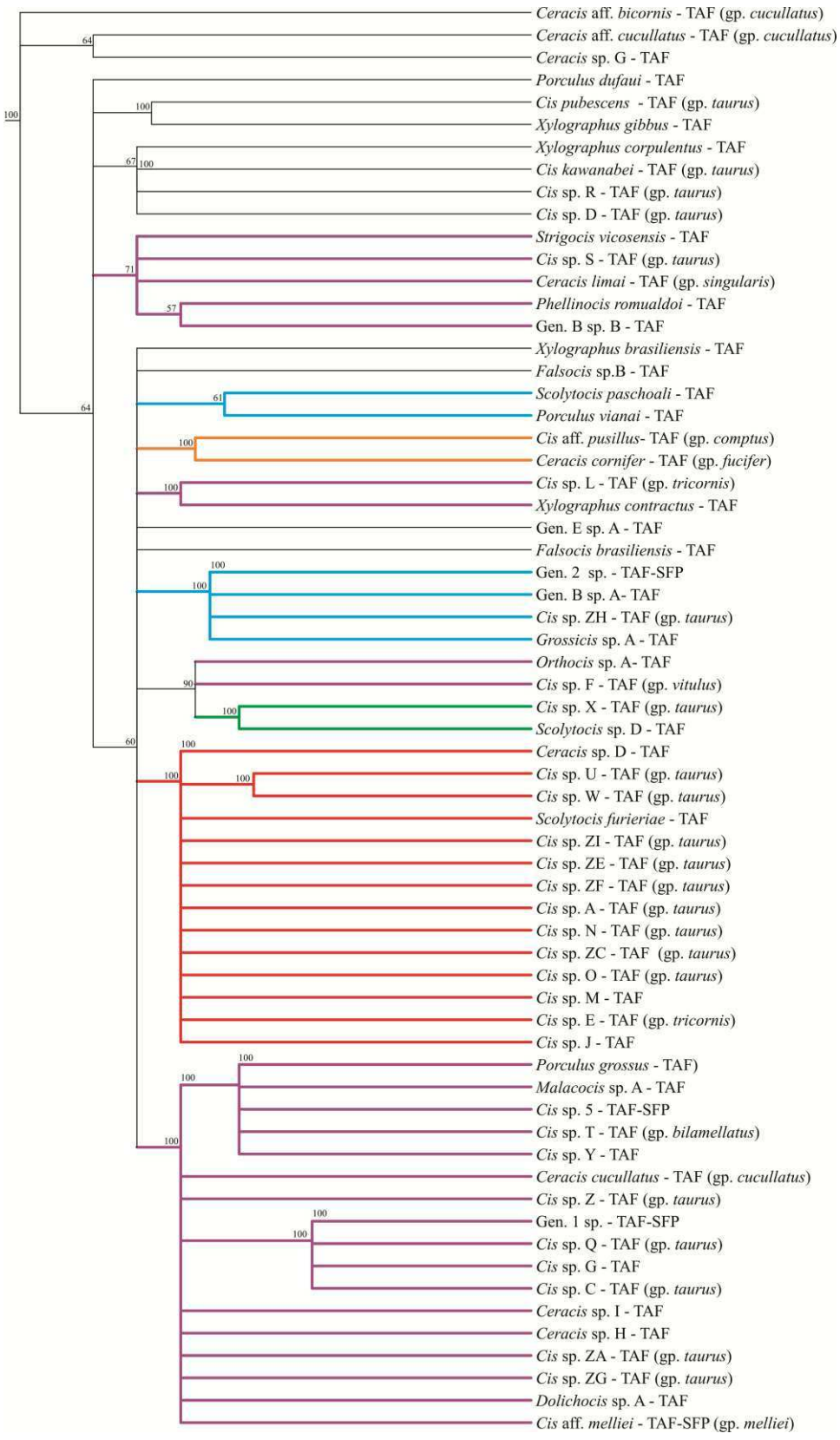
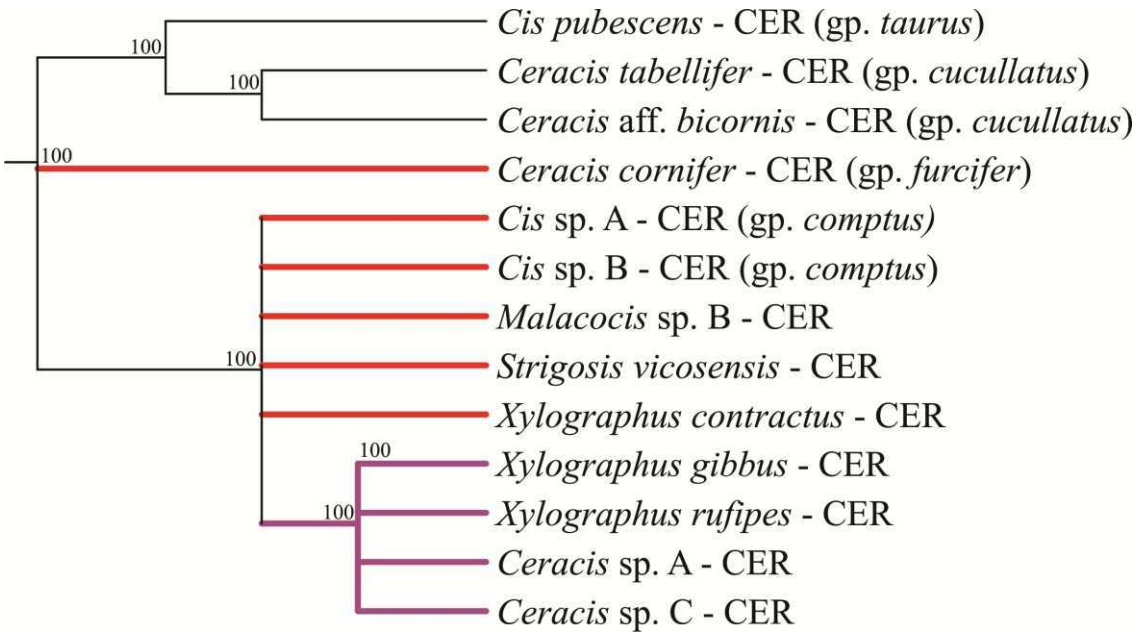

Ceracis aff. bicornis - TAF (gp. cucullatus)
Ceracis aff. cucullatus - TAF (gp. cucullatus)
Ceracis sp. G - TAF
Porculus dufaui - TAF
Cis pubescens - TAF (gp. taurus)
Xylographus gibbus - TAF
Xylographus corpulentus - TAF
Cis kawanabei - TAF (gp. taurus)
Cis sp. R - TAF (gp. taurus)
Cis sp. D - TAF (gp. taurus)
Strigocis vicosensis - TAF
Cis sp. S - TAF (gp. taurus)
Ceracis limai - TAF (gp. singularis)
Phellinocis romualdoi - TAF
Gen. B sp. B - TAF
Xylographus brasiliensis - TAF
Falsocis sp.B - TAF
Scolytocis paschoali - TAF
Porculus vianai - TAF
Cis aff. pusillus- TAF (gp. comptus)
Ceracis cornifer - TAF (gp. fucifer)
Cis sp. L - TAF (gp. tricornis)
Xylographus contractus - TAF
Gen. E sp. A - TAF
Falsocis brasiliensis - TAF
Gen. 2 sp. - TAF-SFP
Gen. B sp. A- TAF
Cis sp. ZH - TAF (gp. taurus)
Grossicis sp. A - TAF
Orthocis sp. A- TAF
Cis sp. F - TAF (gp. vitulus)
Cis sp. X - TAF (gp. taurus)
Scolytocis sp. D - TAF
Ceracis sp. D - TAF
Cis sp. U - TAF (gp. taurus)
Cis sp. W - TAF (gp. taurus)
Scolytocis furieriae - TAF
Cis sp. ZI - TAF (gp. taurus)
Cis sp. ZE - TAF (gp. taurus)
Cis sp. ZF - TAF (gp. taurus)
Cis sp. A - TAF (gp. taurus)
Cis sp. N - TAF (gp. taurus)
Cis sp. ZC - TAF (gp. taurus)
Cis sp. O - TAF (gp. taurus)
Cis sp. M - TAF
Cis sp. E - TAF (gp. tricornis)
Cis sp. J - TAF
Porculus grossus - TAF)
Malacocis sp. A - TAF
Cis sp. 5 - TAF-SFP
Cis sp. T - TAF (gp. bilamellatus)
Cis sp. Y - TAF
Ceracis cucullatus - TAF (gp. cucullatus)
Cis sp. Z - TAF (gp. taurus)
Gen. 1 sp. - TAF-SFP
Cis sp. Q - TAF (gp. taurus)
Cis sp. G - TAF
Cis sp. C - TAF (gp. taurus)
Ceracis sp. I - TAF
Ceracis sp. H - TAF
Cis sp. ZA - TAF (gp. taurus)
Cis sp. ZG - TAF (gp. taurus)
Dolichocis sp. A - TAF
Cis aff. melliei - TAF-SFP (gp. melliei)

Figure 3


100
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Cis pubescens - CER (gp. taurus)
Ceracis tabellifer - CER (gp. cucullatus)
Ceracis aff. bicornis - CER (gp. cucullatus)
Ceracis cornifer - CER (gp. furcifer)
Cis sp. A - CER (gp. comptus)
Cis sp. B - CER (gp. comptus)
Malacocis sp. B - CER
Strigosis vicosensis - CER
Xylographus contractus - CER
Xylographus gibbus - CER
Xylographus rufipes - CER
Ceracis sp. A - CER
Ceracis sp. C - CER

Figure 4

CAPÍTULO 2: Area and connectivity of conservation units influence the community structure of saproxylic organisms in the Brazilian Atlantic Forest

(Conservation Biology)

Area and connectivity influence the community structure of saproxylic organisms in the Brazilian Atlantic Forest

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Abstract

The Brazilian Atlantic Forest ecosystem is one of the most important global biodiversity hotspots. At the same time, it is the most explored biome in the country during last century. To develop efficient conservation measures, there is an urgent need to document biodiversity and investigate how human activities have affected, and still affect, natural biota. In this paper, we tested the relative importance of forest characteristics, area and connectivity of conservation areas on species richness of saproxylic (dead wood dependent) fungi and beetles associated with fungal basidiomes. Species richness of beetles increased the larger the area and the better the connectivity of conservation units. Our study indicates that the fragmentation of Brazilian Atlantic Forest has affected negatively the community structure of beetles associated with wood-decaying fungi, even in relatively large conservation areas. In addition of the effect of

reduced area and connectivity of conservation areas, the beetle community has also been affected by the reduction in resource availability at lower trophic levels, i.e. fungi and dead wood, whose decrease how strong was the fragmentation. This leads us to conclude that many species will be lost locally if the exploration of forest continues. Consequently, some services, i.e.: nutrient cycling and decomposition, may be affected in the natural system.

Keywords: Forest Fragmentation, Tropical Rain Forest, Coleoptera, Diversity.

Introduction

During the last few millennia, since the development of agriculture, humans have been a major force of modification of nature. Humans have transformed natural ecosystems into urban areas and agricultural landscapes, and the remaining natural areas have become small, isolated from each other, and subjected to adverse edge effects (Fahrig 2003; Kupfer et al. 2006). Indeed, habitat loss and fragmentation is considered one of the most influential factors contributing to species local and regional extinction (Ehrlich & Ehrlich 1981).

Smaller patches sustain smaller population sizes, which increases the likelihood of stochastic extinctions (Dunn 2005; Fahrig 2003). Increased isolation in turn decreases the likelihood of recolonization of empty patches (Fahrig 2003; Hanski & Simberloff 1997) or the rescue of small or sink populations (Brown & Kodrick-Brown 1977). The exploitation of natural resources affects habitat quality by removing resources that are

crucial for species as food, shelter or nesting sites. However, the realization of fragmentation effects may take years or even decades (Hanski 2013), particularly if the extent of natural habitat is still large in the landscape, individual habitat areas are large, and the species can tolerate moderate level of fragmentation (Rybicki & Hanski 2013).

The Brazilian Atlantic Forest ecosystem (AF) is a global biodiversity hotspot. It is also heavily fragmented and the most explored biome in the country during last century. Deforestation and forest degradation began already during the colonization by Europeans in the XVI century (Dean 1996) and by the end of the last century the pristine AF had practically vanished. Originally, the AF was approximately 130 million hectares, occupying more than 15% of area of the country. Currently, only ca. 12% of the original extent remains (Ribeiro et al. 2009) and most of it as small, isolated, unprotected or severely altered forest patches, embedded into the heavily degraded matrix (agriculture and cities) (Fonseca 1985; Silva & Tabarelli 2000).According to percolation theory of landscape ecology, 10-20% of remaining habitat is a threshold for many taxa that fragmentation effects become prominent (O'Neill et al. 1988). Thus, further fragmentation of the AF is likely to be detrimental for original biota.

Dead wood is a key resource for many organisms in forest ecosystems (Jonsell & Nordlander 2002; Jonsson & Nordlander 2006; Komonen & Kouki 2005; Komonen et al. 2000). There is no formal estimate about how many species in tropical forests are dependent on dead wood, but in relatively species-poor boreal and temperate forests, thousands of organisms are directly dependent on dead wood (Stokland & Larsson 2011; Stokland et al. 2012). Because dead wood is a major reservoir of energy in forests, taxonomically and trophically complex food webs are based on it. One example

of the dead wood based food web is wood decaying fungi and associated insects. Fungal basidiomes constitute a major source of shelter and food for a large variety of insects, especially beetles (Ackerman & Shenefel 1973; Matthewm & Pielou 1971; Pielou 1966; Pielou & Matthewm 1966). The insect community associated with basidiomes of wood-decomposing fungi consists of primary fungivores consuming the fungal tissue, and their parasitoids and predators (Jonsell & Nordlander 2002; Komonen et al. 2004). These organisms are usually strictly dependent on fungi for food, reproduction and shelter. Fragmentation may have direct and indirect effects on insects associated to bracket fungi (Komonen et al. 2000). Direct effects relate to reduced colonization between habitats, whereas indirect effects relate to reduced availability of substrate, i.e. fungal basidiomes. It is known that forest fragmentation can have cascading affects across the food chain, consisting of dead wood, fungi and insects (Komonen et al. 2000). For basic understanding and practical conservation, it is important to disentangle the independent effects of area and connectivity.

Associated community of dead wood is a good model system to study the effects of forest fragmentation, because the community is easy to delineate in an ecologically meaningful way and the patch-matrix approach is truly appropriate, since the organisms are strictly dependent on dead wood or fungal basiodiomes for reproduction. We studied the effects of area and connectivity of conservation areas on species richness of beetles associated to wood-decaying fungi in the Brazilian Atlantic Forest. We predicted that the area and connectivity would affect the richness of beetles and their resources. Based on that, we tested if these effects are caused by lose of suitable habitat or decrease of accessibility.

Material and methods

Study area

The study was carried out from October 2011 to January 2012, i.e. late spring to early summer, at the Atlantic Forest (AF) in Brazil. We chose 12 Conservation Units (see Fig. 1 for locations, names and abbreviations) with different area, ranging from 17ha to 37,000ha, with varying connectivity to other conservation areas. These Conservation Units are preserved patches of the originally continuous AF, and they are all located in highly fragmented landscapes (Fig. 1; see Appendix S1), in the midst of agricultural land, secondary plantation forests and urban areas. The climate types in these landscapes are Cwb and Cwa (mesothermal), mild to hot during all year, with humidity increasing closer to the sea(Peel et al. 2007). The terrain is flat to hilly, with declivity ranging from 0 to 45^{o}, with an average altitude of 1000 ma.s.l.

Sampling

We collected basidiomes of bracket fungi by establishing three transects in each forest patch. The locations of transects were chosen a priori from maps, based on accessibility and anthropogenic disturbance, i.e. to avoid tourist places. To avoid edge effects, transects were placed at least 50m from the edge of the conservation units. In these transects, we established fifteen 5m x 5m study plots separated from each other at least 15m, and placed where had at least one basidiome (Gumier-Costa 2004, modified). In each plot, we checked all fallen and living trunks as well as ground for basidiomes of bracket fungi, and all the basidiomes found were collected. Collected basidiomes were placed in plastic boxes and kept in lab conditions for about four months to rear out the beetles.

Measured variables

To explain the variation in species richness of beetles, we measured variables that characterized the conservation units and variables that were related to resources of fungi and saproxylic beetles. The landscape variables were the size (ha) and connectivity of patches. Connectivity was measured as the distance (km) to the nearest neighbor and as the area of suitable habitat (ha) in a radius of five, 10 and 20 kilometers around the sampling locations. The connectivity was calculated from map data obtained from the SOS Mata Atlântica Foundation and the Brazilian Ministry of Environment. We first created one map for each patch with their respective scale using ArcGis software. Then, we used the ImageJ software to standardize the distance and calculate the radius, the distance among patches and quantity of suitable area.

To test our hypothesis, we measured plot variables. They were the number of fungal species, number of basidiomes, volume of basidiomes (cm^3), number of dead wood items (minimum diameter of 15cm), circumference of dead wood (cm) and depth of litter (cm). These variables represented the direct and indirect resources used by saproxylic beetles. The circumference of wood is an indicator of forest naturalness and litter depth indicates site productivity. All measurements were made within the study plots from which we collected the basidiomes.

Identification of fungi and beetles

Fungal species were identified consulting the works of Ryvarden (2004). The nomenclature follows the fungal taxonomy available in the online database Index Fungorum. All emerged beetles species were primarily identified to family-level and, when pertinent, to subfamily and tribe, using a multi-entry key to world Coleoptera

(Lawrence et al. 1999). The Ciidae were identified to the highest possible level using the available keys and revisionary works on American genera and comparison to type-specimens or specimens compared to the type of most Neotropical ciid species (Lawrence 1971; Lopes-Andrade 2008; Lopes-Andrade 2011; Lopes-Andrade & Lawrence 2005). It means that the ciid species without specific epithets are possibly all new to science. Species of the other families were identified by comparison to the reference collection of the Laboratório de Sistemática e Biologia de Coleoptera (Viçosa, Brazil), where all beetles and fungi collected in the present study were deposited.

Statistical analyses

To analyze the relationship between the size and connectivity of patches and beetles and fungi (resources for beetles), we used Generalized Linear Models (GLM) with Poisson errors. Size and connectivity of patches may affect habitat characteristics, such as the amount and circumference of wood as well as the depth of litter, and the abundance (i.e. volume and number of basidiomes) and species richness of fungi, which will then influence beetles. Firstly, we analyzed whether the size (area) and connectivity of patches (Next Neighbor Distance (NND) and Area of Suitable Habitat (ASH) in radiuses of 5km, 10km and 20km) explain the richness of beetles and food resources. Food resources were included in the models as explanatory variable of beetle species richness. In all analyses, the full model included all variables, and the model simplification was done by removing the non-significant terms (Crawley 2007). All statistical analyses were performed in R software (R-Development-Core-Team 2013) with a significance level of 5%.

Results

We recorded 136 species of Coleoptera, associated to 30 species of fungi (n = 1800 basidiomes). About 70% of the collected beetle species were found in no more than three Conservation Unities. None of the collected species occurred in all patches and less than 6% of species were recorded in more than six of the patches. The most representative family was Ciidae, with 47% of the recorded beetles species (see Appendix S2). Almost 70% of all species of saproxylic beetles collected may be new species to science.

Area and connectivity alone did not have a significant effect on beetle species richness. However, models that included an interaction between area and connectivity explained significantly the species richness of beetles (Table 1). Models that included both area and next neighbor distance had a smaller qAIC than the models that included area and area of suitable habitat within different radiuses (Table 1; Figure 2A-C). The number of saproxylic beetles species increased the shorter the distance between patches (Figure 2A) and the greater the area of suitable habitat within 10km and 20km radius (Figures 2A and 2B).

Local resource availability, i.e. the number of basidiomes and volume of fungi, explained the species richness of saproxylic beetles (Table 2, Figure 3A and B); the number of fungal species did not have a significant effect (Table 2). From the plot variables that might affect the species richness saproxylic beetles, the circumference of wood and depth of litter did affect the number of saproxylic beetle species (Table 2, Figure 3C and 3D). Furthermore, the circumference of wood explained the number of basidiomes (Table 3), whereas there was neither a significant relationship between the

circumference of wood and volume of basidiomes, nor between the depth of litter and number or volume of basiodiomes.

We also analyzed the effects of connectivity and area on the local resources of beetles and fungi, i.e. the direct effects of fragmentation. Both the number of basidiomes and circumference of wood were larger the larger the size of the patch (Figure 4A and 4C), and the number of basidiomes was negatively affected by next neighbor distance (Figure 4B) and circumference of wood by area of suitable habitat inside of 10km (Figure 4D, see Supplementary material S3).

Discussion

Our main result is that the species richness of beetles was positively affected by an interaction between area and connectivity of conservation areas. This significant interaction indicates that small and isolated conservation areas have a smaller number of species than those bigger and connected areas, which may result from higher extinction and slower recolonization rates in these areas (Andren 1994; Fahrig 2003; Polus et al. 2007). Indeed, area and connectivity alone did not have a significant effect on beetle species richness. One reason might be that the most part of studied conservation units were relatively large. This characteristic may have promoted a slow lost of species, depending of several factors to construct a local diversity.

The food chain consisting of dead wood, fungi and beetles were all positively affected by the connectivity of areas, whereas the number of fungi and the number of species of beetles were affected by size of patch. The polypore fungi can be affected severely by

reduced area of suitable habitat, because the fragmentation of forests lead to a reduced number of decaying wood (Penttilä et al. 2006). Local habitat quality, i.e. availability of resources, did affect species richness and abundance across trophic levels. We found a relationship between different trophic levels e.g. circumference of wood affected positively volume of basidiomes, which in turn affected in the same way the richness of saproxylic beetles. Therefore, organisms directly associated with fungi are directly affected by fragmentation process, because they usually use basidiomes in most of their life cycle, as food and shelter for larvae and adults, for mating and as oviposition sites (Jonsell & Nordlander 2002, 2004).

The relationship between saproxylic beetles and their host fungi drives the establishment and maintenance of beetle populations (Graf-Peters et al. 2011; Komonen 2006). Many of these beetle species are specialists on a particular fungal species or genus, increasing their extinction risk (Hill et al. 2001; Lopes-Andrade 2007; Lopes-Andrade & Lawrence 2005; Saccheri et al. 1998). This may happen because smaller areas can't sustain an increasing of populations of species, which can result in strong competition forces and lead vulnerable populations to stochastic events, genetic impoverishment and even local extinction (DeSouza et al. 2001; Didham et al. 1996; Dunn 2005; Manel et al. 2003).

The effect of connectivity on the richness of beetles depends on how they can support an adverse condition and find a suitable area. An important factor in the dispersal of beetles is how long they need to disperse to find their substrate. An area must be within the flight range of individuals of a species to have some chance of being colonized, and the probability of colonization decreases as the distance between areas increases, which

has been shown also for fungivorous beetles (Aberg et al. 1995; Araujo 2010; Rukke 2000). Saproxylic insects are usually considered good dispersers (Lawrence 1971), a feature important for organisms whose breeding substrates are generally both ephemeral and unpredictable in space (Murlis et al. 1992). However, such dispersal ability is not expected to be equal for all saproxylic beetles. Jonsell et al. (1999) found that ciids associated with basidiomes of two polypore fungi placed in different distances were less successful colonizers, despite their higher abundance, compared to anobiid beetles, which readily flew over open fields. Therefore, species with the least dispersal ability are more prone to local extinction (Nieminen et al. 2001; Saccheri et al. 1998).

Some saproxylic beetle species may be threatened by extinction in the AF. For instance, available information suggests that Falsocis Genus is specialized in one or a few fungal species (Lopes-Andrade 2007; Lopes-Andrade & Lawrence 2011). Observations on Falsocis brasiliensis (Lopes-Andrade 2007), a species globally restricted to the AF, indicate they have low population density. Falsocis occultus, another species that occurs only in AF, is restricted to the best conservation forests and has recent registers only in a few coastal rainforests of mountain areas in the AF (Lopes-Andrade & Lawrence 2011). The past and current loss and fragmentation of the AF may have reduced and caused local extinctions of several populations of Falsocis species, due to reduction in availability and quality of deadwood and fungi(Lopes-Andrade 2007; Lopes-Andrade & Lawrence 2011). The case of Falsocis species is only an example and basic studies on other saproxylic beetles will certainly reveal much more species in risk of local or even regional extinction.

In Atlantic forest the process of fragmentation and reduction of forests was made in different time and way (Dean 1996; Liebsch et al. 2008). This means that some patches may be suffered more anthropogenic pressure than others, affecting the composition of species in different way, turning particular each set of species. Such result can show the importance of preservation of Atlantic Forest remnants, because they can have a unique composition of species (most part of them are new for science registers) that depends of a specific region to sustain their population and do not extinct.

Conclusions

Land use changes over the past centuries have led to a steady loss of habitat and increasing isolation of habitat patches in the AF. Our results support the general observation that habitat loss and fragmentation are the most likely major causes of the increasing rates of extinctions of tropical forests' species in recent decades. Interestingly, our results indicate that even relatively large conservations areas have fewer species if they are not well connected to other respective areas. The negative effects of fragmentation on biota even in relatively large conservation areas may be related to the long fragmentation history of the AF. The relative importance of local and landscape factors in shaping forest biodiversity in different trophic levels should be better understood for the setting of conservation priorities.

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Tables

Table1. Analysis of deviance of the complete generalized linear model compared with the null model (model with only constant), to explain the variation of richness of saproxylic beetles in relation to patch size and connectivity.Error distributions were quasi-Poisson. The symbol ":" indicates that the model includes an interaction between the variables and the symbol "+" indicates only independent effects of these variables.

Explanatory variable	Dev. df	Residual df	F	p	qAIC	
Area:NND**	11.29	8	4.94	0.031	79.06	*
Area+NND**	11.35	9	12.18	0.011	77.12	*
Area:ASH† (5 km)	20.16	8	1.44	0.302	85.42	n.s.
Area:ASH† (10 km)	13.80	8	3.69	0.040	81.46	*
Area:ASH† (20 km)	13.02	8	4.14	0.048	80.77	*

* Significant model ($p<0.05$)
**NND = Next Neighbor Distance
†ASH = Area of suitable habitat

Table 2. Analysis of deviance of the complete generalized linear model compared with the null model (which is the variation of beetles explained by random, statistically means 1) to explain the variation in richness of saproxylic beetles in relation to their direct and indirect resources.

Explanatory variable	Dev.	Residual df	F	p	AIC	
N of basidiomes	16.78	10	8.90	0.013	79.82	*
N of fungal species	6.52	10	2.51	0.144	83.94	n.s.
Volbasidiomes	18.81	10	14.35	0.004	76.56	**
Circumf. of wood	15.65	10	9.94	0.010	79.16	*
N of dead wood	4.84	10	1.78	0.212	84.85	n.s.
Depth of litter	12.86	10	6.44	0.030	80.25	*

Table 3: Analysis of deviance of the model that explained the variation of the indirect resource of saproxylic beetles in relation to their own resources. All models were compared to null model.

Model	Residual df	F	p	
Nbasidiomes~ circumfof wood	10	1.99	0.188	n.s.
Vol.basidiomes~ circumf of wood	10	18.08	0.002	**
N basidiomes~ depth of litter	10	1.34	0.275	n.s.
Volbasidiomes~ depth of litter	10	1.00	0.341	n.s.
Circumf. of wood ~ Depth of litter	10	0.34	0.572	n.s.

Figure legends

Figure 1: Brazil (major map) showing the remaining Atlantic Forest patches in dark. Minor maps show the study locations (Conservation Units) in the states of Espírito Santo (ES), Minas Gerais (MG) and Rio de Janeiro (RJ): A = RPPN Zaca; B = Parque Estadual do Rio Doce (PERD); C = Parque Nacional Serra do Caparaó (PNC); D = Parque Estadual Serra do Brigadeiro (PESB); E = Estação de Treinamento Mata do Paraíso (ETMP); F = Área de Proteção Ambiental São José (APASJ); G = Floresta Nacional do Rio Preto (FNRP); H = Reserva Biológica de Sooretama (RBS); I = Estação Biológica de Santa Lúcia (EBSL); J = RPPN Bacchus; K = Parque Nacional Serra dos Orgãos (PNSO); L = Parque Nacional de Itatiaia (PNI).

Figure 2: Relationship between the number of saproxylic beetles species and habitat area interacting with different measurements of connectivity: A) next neighbor distance – NND, B) area of suitable habitat –ASH measured within a radius 10 km and C) 20 km. The connectivity in 5km radius was not shown because it was not significant.

Figure 3: Relationship between the number of saproxylic beetle species and (A) number of basidiomes of fungi, (B) volume of basidiomes, (C) circumference of wood and (D) depth of litter.

Figure 4: Effects of patch variables on (A&B) the number of basidiomes and (C & D) the circumference of dead wood: relationship between the number of basidiomes and (A) area of patch and (B) next neighbor distance, and relationship between the circumference of dead wood and (C) area of patch, and (D) area of suitable habitat inside 10 km radius.

Figure 1

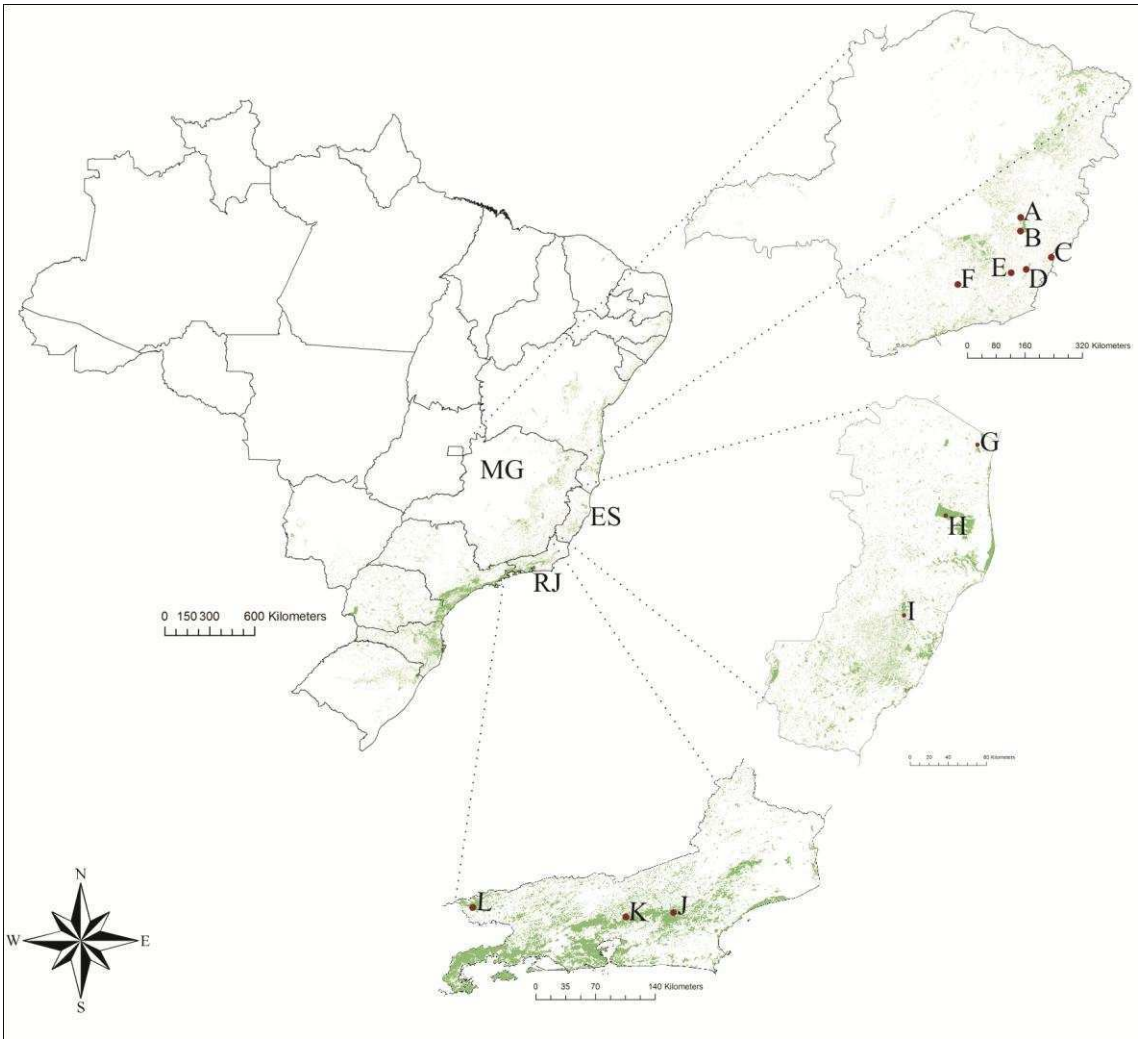

A
B
C
D
E
F
0 80 160 320 Kilometers
MG
ES
RJ
0 150 300 600 Kilometers
G
H
I
L
K
J
0 35 70 140 Kilometers
N
W
E
S

Figure 2

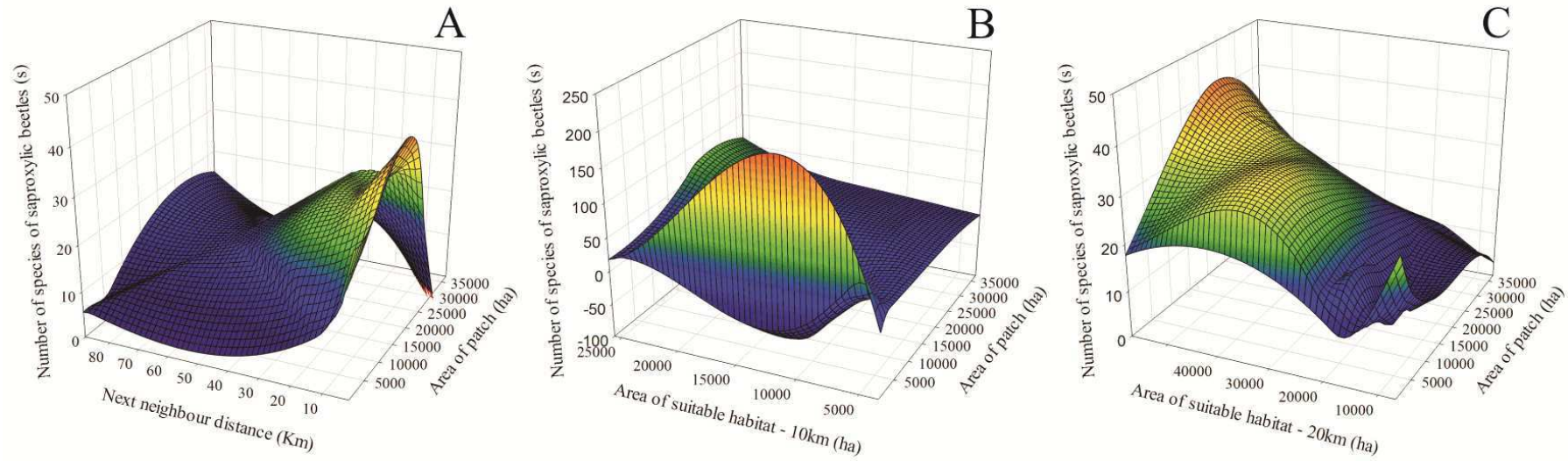

A
Number of species of saproxylic beetles (s)
50
40
30
20
10
0
80
70
60
50
40
30
20
10
Next neighbour distance (Km)
35000
30000
25000
20000
15000
10000
5000
Area of patch (ha)
B
Number of species of saproxylic beetles (s)
250
200
150
100
50
0
-50
-100
25000
20000
15000
10000
5000
Area of suitable habitat - 10km (ha)
35000
30000
25000
20000
15000
10000
5000
Area of patch (ha)
C
Number of species of saproxylic beetles (s)
50
40
30
20
10
0
40000
30000
20000
10000
Area of suitable habitat - 20km (ha)
35000
30000
25000
20000
15000
10000
5000
Area of patch (ha)

Figure 3

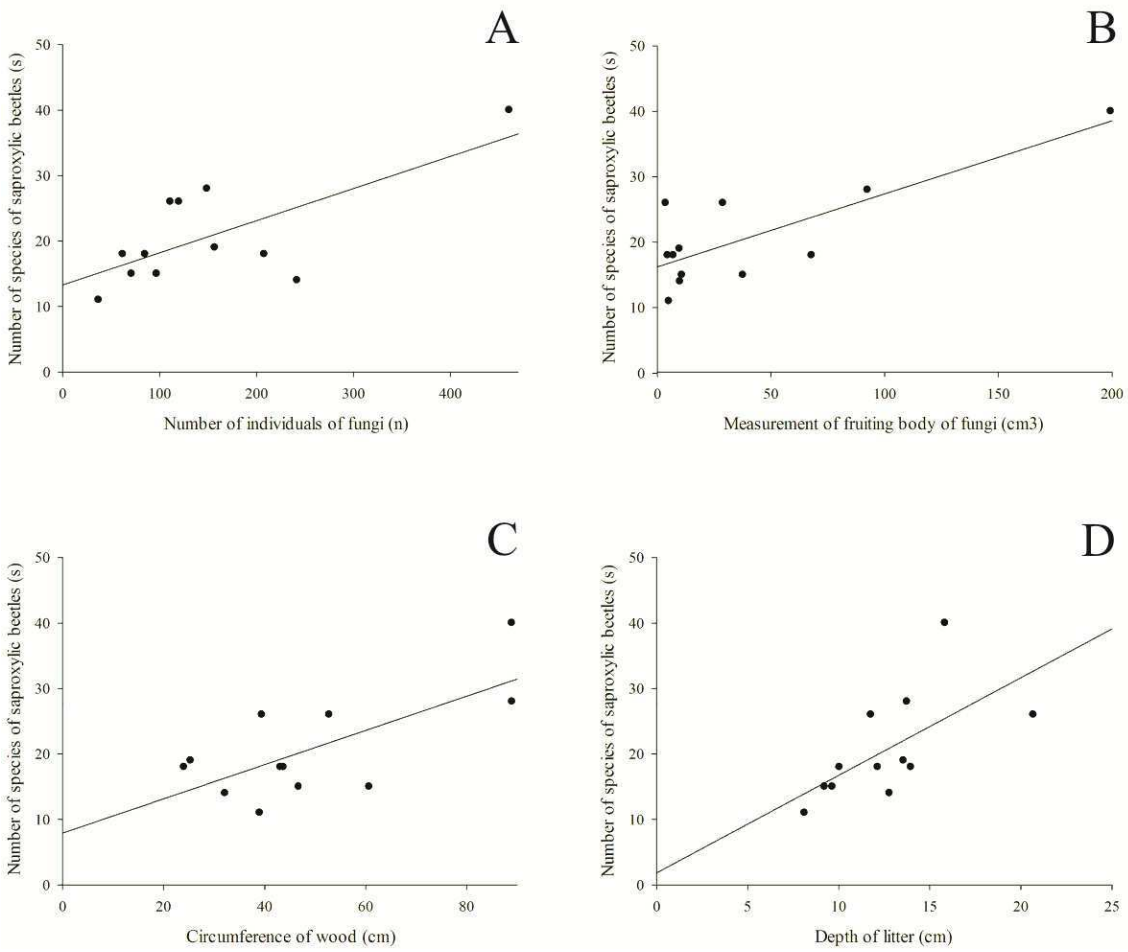
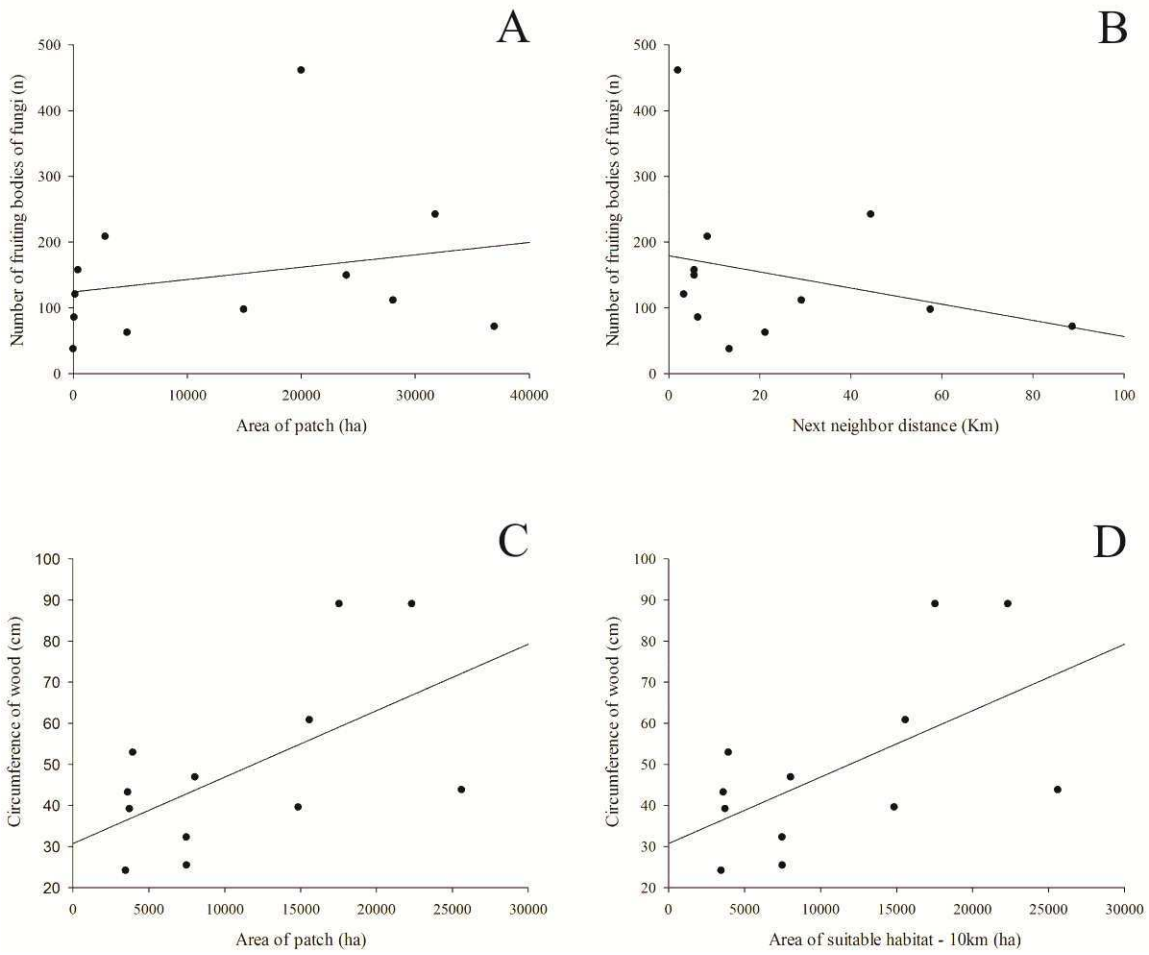

A
Number of species of saproxylic beetles (s)
Number of individuals of fungi (n)
B
Number of species of saproxylic beetles (s)
Measurement of fruiting body of fungi (cm3)
C
Number of species of saproxylic beetles (s)
Circumference of wood (cm)
D
Number of species of saproxylic beetles (s)
Depth of litter (cm)

Figure 4


A
Number of fruiting bodies of fungi (n)
Area of patch (ha)
B
Number of fruiting bodies of fungi (n)
Next neighbor distance (Km)
C
Circumference of wood (cm)
Area of patch (ha)
D
Circumference of wood (cm)
Area of suitable habitat - 10km (ha)

Supplementary material

S1: Characteristics of Conservation Unities where were made the collections.

Conservation Unity	Location	Area (ha)	Connectivity (NND*/Km)	Height (m)
Mata do Paraíso	Viçosa/Minas Gerais	194	3.39	650
Parque Nacional de Itatiaia	Itatiaia/Rio de Janeiro	28084.10	29.21	600
Parque Nacional Serra dos Órgãos	Teresópolis/Rio de Janeiro	20020.54	2.06	147
RPPN** Bacchus	Nova Friburgo/Rio de Janeiro	105.57	6.47	800
Parque Nacional do Caparaó	Alto Caparaó/Minas Gerais	21578.60	44.46	997
Estação Biológica de Santa Lúcia	Santa Teresa/Espírito Santo	440	5.66	650
Reserva Biológica de Sooretama	Sooretama/Espírito Santo	24000	5.68	200
Floresta Nacional de Rio Preto	Conceição da Barra/Espírito Santo	2830.63	8.56	50
RPPN** do Zaca	Ipatinga/Minas Gerais	17.34	13.37	500
Parque Estadual do Rio Doce	Marliéria/Minas Gerais	36970	88.73	297
Parque Estadual Serra do Brigadeiro	Araponga/Minas Gerais	14984	57.55	750
APA^{+} São José	Tiradentes/Minas Gerais	4758	21.24	1000

*NND: Next Neighbor Distance
**RPPN: Reserva Particular do Patrimônio Natural
+APA: Área de Proteção Ambiental

S2: List of species found at conservation unities in Atlantic Forests with their respective host fungi. The Conservatio Unities abbreviations mean: APA = Area de Proteção Ambiental (Area of Environmental Protection); EB = Estação Biológica (Biological Station); FN = Floresta Nacional (National Forest); PE = Parque Estadual (State Park); PN = Parque Nacional (National Park); RB = Reserva Biológica (Biological Reserve) and RPPN = Reserva Particular do Patrimônio Natural (Private Reserve of Natural Heritage). The fungi abbreviations mean: Cycl. = Cyclomyces; Fom. = Fomes; Fom. = Fomitopsis; Fun. = Funalia; Gan. = Ganoderma; Hex. = Hexagonia; Hym. = Hymenochaete; Lenz. = Lenzites; Phell. = Phellinus; Pol. = Polyporus; Pyc = Pycnoporus and Tram. = Trametes.

	Conservation Unities											
	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Species of Coleoptera												
Anobiidae												
Dorcatominae sp. A								Gan.				
Dorcatominae sp. B		Gan.						Gan.				
Dorcatominae sp. C								Hym. Tram				
Dorcatominae sp. D							Gan.					
Dorcatominae sp. E											Gan.	

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Dorcatominae sp. F				Gan.								
Dorcatominae sp. G				Gan.								
Dorcatominae sp. H					Phell. Hex.						Hym.	
Dorcatominae sp. I										Phell.		
Dorcatominae sp .J										Lenz.		
Dorcatominae sp .K											Phell.	Phell. Tram.
Dorcatominae sp .L					Hym.					Poly.		
Dorcatominae sp. M									Fom.			
Dorcatominae sp .N					Tram.							
Dorcatominae sp. O			Tram.									
Dorcatominae sp. P						Phell.						
Dorcatominae sp. Q						Phell.						
Anthribidae												
Anthribidae spA										Tram.		
Biphylidae												
Biphylidae sp. A								Gan.				
Biphylidae sp. B							Hym.					
Biphylidae sp. C			Tram.									

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Biphylidae spD				Tram.								
Carabidae												
Carabidae sp. A								Gan.				
Carabidae sp. B		Gan.					Hym.	Gan.	Tram. Phell.			
Carabidae sp. C			Phell.						Hym.			
Carabidae sp. D								Gan.				
Cerambycidae												
Cerambycidae sp. A		Tram.										
Ciidae												
Ceracis aff. cucullatus (gp. cucullatus)				Hym.					Tram. Gan. Lenz. Fom.			
Ceracis limai (gp. singularis)			Phell. Tram. Hym. Pol.	Phell.						Hym. Tram.		

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Ceracis aff. bicornis (gp. cucullatus)	Hex. Tram Hym. Phell.		Phell. Hym.	Lenz.	Tram. Hex. Hym. Lenz. Phell. Pyc.	Hex. Tram.			Tram. Phell. Hex. Fom. Gan. Hym.	Hym. Phell.		Phell. Tram. Fomi.
Ceracis sp. D						Tram. Hex.						
Ceracis cornifer (gp. furcifer)	Pyc.				Tram. Pyc.							
Ceracis cucullatus (gp. cucullatus)												Phell. Fomi.
Ceracis sp. G	Hym. Tram.				Hex. Tram. Hym. Lenz.		Tram.					
Ceracis sp. H								Phell.				
Ceracis sp. I			Phell.									

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Cis sp. A (gp. taurus)			Tram.									
Cis pubescens (gp. taurus)		Gan.	Phell.		Hym.	Hex.			Tram.		Tram.	
			Hym.								Gan.	
Cis sp. C (gp. taurus)	Hym.								Hym.			Phell.
	Phell.								Phell.			
Cis sp. D (gp. taurus)			Hym.	Hym.					Tram.			Tram.
									Phell.			Fomi.
Cis sp. E (gp. tricornis)								Tram.				
Cis sp. F (gp. vitulus)										Pol.		
Cis sp. G										Phell.		
										Hym.		
Cis aff. pusillus (gp. comptus)					Pyc.							
Cis aff. melliei (gp. melliei)												Phell.
Cis sp. J										Tram.		
Cis sp. L (gp. tricornis)		Hym.				Phell.	Phell.				Tram.	
											Hym.	
											Phell.	
Cis sp. M											Tram.	
Cis sp. N (gp. taurus)							Tram.					
Cis sp. O (gp. taurus)							Tram.					

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Cis kawanabei (gp. taurus)			Phell. Tram. Fomi.	Hym.			Tram.	Hym.		Pol.	Tram. Phell.	
Cis sp. Q (gp. taurus)					Hym.			Hym. Phell.				
Cis sp. R (gp. taurus)	Hym.	Hym.	Tram. Phell. Hym. Fomi.					Hym.		Hym. Tram.	Tram.	
Cis sp. S (gp. taurus)			Tram. Pol.	Hym. Phell. Lenz.	Hym. Tram. Lenz.							
Cis sp. T (gp. bilamellatus)										Hym.		
Cis sp. U (gp. taurus)			Tram.				Tram.	Hym.		Tram.		
Cis sp. W (gp. taurus)											Hym. Tram.	
Cis sp. X (gp. taurus)										Lenz.		
Cis sp. Y										Hym.		
Cis sp. Z (gp. taurus)		Phell.							Hex.			Phell.
Cis sp. ZA (gp. taurus)												Phell.

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Cis sp. ZB				Hym.								
Cis sp. ZC (gp. taurus)			Tram.									
Cis sp. ZE (gp taurus)						Tram.						
Cis sp. ZF (gp. taurus)						Tram.						
Cis sp. ZG (gp. taurus)						Phell.						
Cis sp. ZH (gp. taurus)								Gan.				
Cis sp. ZI (gp. taurus)			Tram.									
Dolichocis sp. A	Phell.											
Falsocis brasiliensis			Tram.						Phell.	Phell.		
										Tram.		
Falsocis sp. B									Gan.			
									Phell.			
Gen. B sp. A		Gan.										
Gen. B sp. B						Phell.		Gan.		Pol.		
										Hym.		
Gen. C sp. A									Gan.			
Gen. D sp. A		Hym.		Hym.				Hym.				
								Phell.				

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Gen. E sp. A						Tram. Phell.						
Grossicis sp. A		Gan.										
Malacocis sp. A									Hym.			
Orthocis sp. A								Cyc.				
Phellinocis romualdoi	Phell. Hym.			Hym.	Tram. Phell.	Phell.			Hym. Phell.	Tram.	Tram Phell. Lenz.	Phell.
Porculus vianai		Gan. Fomi.					Gan.	Gan.				
Porculus grossus								Hym.		Hym.		
Porculus dufaui								Gan. Phell.		Hym. Fom.		
Scolytocis paschoali		Gan. Fomi.					Gan.	Gan.		Lenz.		
Scolytocis furieriae									Tram.			
Scolytocis sp. D											Lenz.	

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Strigocis vicosensis		Hym.		Tram.	Phell. Cyc. Pol. Hym.							
Xylographus corpulentus		Fomi. Phell.	Phell. Hym.	Phell. Hym.			Hym.	Phell. Gan.	Phell. Gan. Tram.	Hym. Tram.		
Xylographus gibbus	Hex. Hym. Phell.		Tram. Phell.	Fun. Hym.				Gan.	Phell. Gan.	Phell.	Tram.	Tram. Phell.
Xylographus contractus	Phell.		Phell.		Tram. Phell.				Phell. Hym.	Tram. Phell.		Phell.
Xylographus brasiliensis		Gan.						Gan. Phell.			Gan. Tram.	
Curculiomidae												
Curculionidae sp. A								Tram.				
Curculionidae sp. B			Phell									

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Endomycidae												
Endomycidae sp. A						Tram.						
Erotylidae												
Erotylidae sp. A							Hym.	Gan.				
Erotylidae sp. B									Gan.			
Erotylidae sp. C						Phell.						
Erotylidae sp. D					Tram.							
Erotylidae sp. E						Tram.						
Histeridae												
Histeridae sp. A												Phell.
Melandryidae												
Melandryidae sp. A								Phell.				
Mycetophagidae												
Mycetophagidae sp. A				Hym.								
Nitidulidae												
Nitidulidae sp. A						Phell.						
Nitidulidae sp. B										Pyc.		
Nitidulidae sp. C			Phell.									

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Nitidulidae sp. D									Phell.			
Nitidulidae sp. E						Tram.						
						Phell.						
Nitidulidae sp. F			Tram.									
Pitilidae												
Pitilidae sp. A	Phell.							Gan.				
Pitilodactylidae												
Pitilodactylidae sp. A						Phell.						
Rhysodidae												
Rhysodidae sp. A									Gan.			
Staphylinidae												
Staphylinidae sp. A		Gan.						Gan.				
Staphylinidae sp. B								Gan.				
Staphylinidae sp .C		Fomi.			Tram.	Phell		Tram.				
Staphylinidae sp. D					Tram.		Tram.					
Staphylinidae sp. E					Tram.							Pyc.
Staphylinidae sp. F												Tram.
Staphylinidae sp. G								Gan.				

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Tenebrionidae												
Lelegeis nigrifrons			Phell.									
Lelegeis sp. A									Fom.			
Lelegeis sp. B									Fom.			
Neomida sp. A			Pol.									
Neomida sp. B			Hym.									
Neomida sp. C					Phell.							
Neomida sp. D								Hym.				
Neomida sp. E				Gan.								
Neomida sp. F											Tram.	
Neomida sp. G				Gan.								
Neomida sp. H									Tram Gan			
Neomida sp. I											Gan.	
Neomida sp. J									Gan.			
Neomida sp. K		Gan. Hym.					Gan.	Gan.				
Phipidandrus sp. A					Phell. Cycl.							
Platydema sp. A								Gan.				

S1 Continuation

	RPPN Zaca	RPPN Bacchus	Mata do Paraiso	EB Santa Lucia	FN Rio Preto	APA São José	PE Serra do Brigadeiro	PN Serra dos Órgãos	RB Sooretama	PN de Itatiaia	PN Serra do Caparaó	PE do Rio Doce
Platydema sp. B								Tram.				
Platydema sp. C								Gan.				
Platydema sp. D									Tram.			
Platydema sp. E					Cycl.							
Platydema sp. F				Gan.								
Platydema sp. G	Tram											
Platydema sp. H									Hym.			
Zopheridae												
Zopheridae sp. A			Phell.									
Zopheridae sp. B			Phell.									
Zopheridae sp. C								Gan.		Tram.		Phell.
Zopheridae sp. D								Tram.				
Coleoptera												
sp. A									Phell.			
sp. B						Tram.						
Total	11	18	26	19	18	18	15	40	28	26	14	15

S3: Simplification of Analysis of deviance of the complete generalized linear model compared with the null model (model with only constant), to explain the variables local that explain the richness in relation to patch size and connectivity. Error distributions were fit to that more adequate. The symbol ":" indicates that the model includes an interaction between the variables and the symbol "+" indicates only independent effects of these variables.

Explanatory variable	**Model selected**	**Residual df**	**F**	**P**	**AIC**	
Number of fungi	Area+Next Neighborhood Distance	8	6.9979	0.02668	*qaic	*
Number of fungi	Area:Area of Suitable habitat (5m)	8	4.9424	0.59100	*qaic	n.s
Number of fungi	Area:Area of Suitable habitat (10m)	8	0.5205	0.68000	*qaic	n.s.
Number of fungi	Area:Area of Suitable habitat (20m)	8	0.8711	0.49500	*qaic	n.s.
Volume of wood	Area:Next Neighborhood Distance	8	1.4846	0.29060	135.04	n.s.
Volume of wood	Area:Area of Suitable habitat (5m)	8	1.2834	0.34430	135.63	n.s.
Volume of wood	Area of Suitable habitat (10m)	10	8.4364	0.01571	129.01	*
Volume of wood	Area:Area of Suitable habitat (20m)	8	3.3773	0.07490	130.53	n.s.
Circumference of wood	Area:Next Neighborhood Distance	8	1.3282	0.33140	111.75	n.s.
Circumference of wood	Area:Area of Suitable habitat (5m)	8	2.6793	0.11790	108.26	n.s.
Circumference of wood	Area:Area of Suitable habitat (10m)	8	4.6202	0.03709	104.54	*

S2 Continuation:						
Circumference of wood	Area:Area of Suitable habitat (20m)	8	2.8165	0.10740	107.95	n.s.
Depth of litter	Area+Next Neighborhood Distance	8	4.3761	0.04704	62.285	*
Depth of litter	Area:Area of Suitable habitat (5m)	8	1.2257	0.36190	67.898	n.s.
Depth of litter	Area:Area of Suitable habitat (10m)	8	1.011	0.43680	68.579	n.s.
Depth of litter	Area:Area of Suitable habitat (20m)	8	1.1271	0.39430	68.206	n.s.

CONCLUSÕES

O presente trabalho buscou introduzir novas referências a respeito da fauna de besouros micetobiontes (Coleoptera) e seus hospedeiros (Basidiomyceta – Homobasidiomycetes) dos biomas tropicais e subtropicais. No primeiro capítulo concluímos que os ciídeos dos biomas tropicais e subtropicais podem ser organizados em grupos de utilização de fungos. Isto facilita o reconhecimento do papel dessas espécies no ambiente e permite a discussão sobre os processos evolutivos e ecológicos que dirigem o estabelecimento de uma população, melhorando o entendimento sobre a conservação da fauna desses besouros e seus hospedeiros. No segundo capítulo, chegamos à conclusão que a fragmentação da Mata Atlântica afeta a riqueza de besouros micetobiontes, diminuindo em fragmentos menores e mais isolados. Isso afeta também a disponibilidade de recurso que está estreitamente relacionada com a presença e ausência desses besouros no ambiente. Assim, essa tese cumpre seu objetivo de prover conhecimento sobre a diversidade de besouros associados a fungos em biomas tropicais e subtropicais. Além disso, espera-se que esta tese ajude o estabelecimento de uma linha de pesquisa em ecologia de organismos saproxílicos no Brasil, especialmente para o estudo das relações entre besouros e fungos decompositores de madeira.

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