UNIVERSIDADE FEDERAL DE SANTA CATARINA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Talita Rosa Otilia Simões Clivatti

Metacomunidades de Besouros Escarabeíneos em Monoculturas de *Pinus* e Florestas Nativas na Microrregião de Tabuleiro – SC, sul do Brasil

Florianópolis
2020

Talita Rosa Otilia Simões Clivatti

Metacomunidades de Besouros Escarabeíneos em Monoculturas de *Pinus* e Florestas Nativas na Microrregião de Tabuleiro – SC, sul do Brasil

Dissertação submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do título de Mestre em Ecologia
Orientadora: Profª. Drª. Malva Isabel Medina Hernández

Florianópolis
2021

Ficha de identificação da obra elaborada pelo autor,

através do Programa de Geração Automática da Biblioteca Universitária da UFSC.

Simões Clivatti, Talita Rosa Otilia
Metacomunidades de Besouros Escarabeíneos em Monoculturas de Pinus e Florestas Nativas na Microrregião de Tabuleiro - SC, sul do Brasil / Talita Rosa Otilia Simões Clivatti ; orientadora, Malva Isabel Medina Hernández, 2021.
56 p.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Programa de Pós Graduação em Ecologia, Florianópolis, 2021.

Inclui referências.

1. Ecologia. 2. Indicação ecológica. 3. Conservação da biodiversidade. 4. Ecologia de comunidades. 5. Dispersão. I. Hernández, Malva Isabel Medina. II. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. III. Título.

Talita Rosa Otilia Simões Clivatti

Metacomunidades de Besouros Escarabeíneos em Monoculturas de *Pinus* e Florestas Nativas na Microrregião de Tabuleiro – SC, sul do Brasil

O presente trabalho em nível de mestrado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

Prof.ª Malva Isabel Medina Hernández, Dr.ª
Orientadora
Universidade Federal de Santa Catarina

Prof.ª Rosa Menéndez Martínez, Dr.ª
University of Lancaster

Prof. Nivaldo Peroni, Dr.
Universidade Federal de Santa Catarina

Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de mestre em Ecologia.

ICP-Edu
Documento assinado digitalmente
Nei Kavaguichi Leite
Data: 20/12/2021 10:10:40-0300
CPF: 629.700.972-49
Verifique as assinaturas em https://v.ufsc.br

Prof. Dr. Nei Kavaguichi Leite
Coordenação do Programa de Pós-Graduação

ICP-Edu
Documento assinado digitalmente
Malva Isabel Medina Hernandez
Data: 17/12/2021 23:14:55-0300
CPF: 013.658.487-01
Verifique as assinaturas em https://v.ufsc.br

Profª. Drª. Malva Isabel Medina Hernández
Orientadora

Dedico este trabalho ao meu filho Vitor Antônio

AGRADECIMENTOS

Gostaria de agradecer primeiramente ao meu esposo Michael Clivatti por todo apoio e incentivo em realizar e concluir essa nova etapa. Também sou imensamente grata por todo o seu auxílio durante o cansativo e pesado trabalho de campo, o que em alguns momentos, e por motivos de força maior (que veio a ser o Vitor), teve de ser realizado sem minha presença.

Agradeço também aos meus pais, Elvira e Cesário, pelo suporte, torcida e paciência durante todo o processo, mas principalmente no meu período de gestação, a qual concomitou com as minhas exaustivas coletas de campo.

Ao meu filho Vitor, o qual dedico todo este trabalho, a razão de toda minha caminhada passada e também futura. Obrigada filho, pelos constantes ensinamentos e paciência, tendo que dividir seu tempo comigo com este trabalho, o qual espero te dar um pouco de orgulho.

A minha orientadora Malva, quem me guiou e impulsionou a ir além, mostrando que eu era bem mais capaz do que acreditava ser. Agradeço pela compreensão e empatia.

Gratidão a todos os meus colegas do LECOTA que de alguma forma me auxiliaram durante estes anos, seja em campo, em análises, triagem de material coletado ou sendo um ombro amigo e oferecendo suporte emocional. Dr. Eduardo Giehl e Dr. Pedro da Silva no auxílio das análises e programação em R. Ao Dr. Maurício Graipel nas identificações de mamíferos e ao Dr. Fernando Vaz de Melo pelas identificações dos besouros.

Também sou grata aos donos de terras onde foram realizadas as coletas, por permitirem o acesso às áreas de estudo e disponibilizarem de bom grado o uso das mesmas. Ao programa de Pós-Graduação em Ecologia, todos os colegas e professores, agradeço o apoio, suporte e torcida recebidos. E a FAPESC, pela bolsa de mestrado durante o período de 22 meses.

RESUMO

Besouros detritívoros da subfamília Scarabaeinae são comumente utilizados em estudos sobre os efeitos de mudanças ambientais, sendo considerados bons indicadores ecológicos. As metacomunidades podem ser estruturadas através de efeitos de massa ou de alocação de espécies, sendo influenciadas pelo habitat, bem como pela dispersão de indivíduos entre áreas distintas. Na região da Serra Catarinense, as florestas nativas vêm sendo alteradas pela pressão antrópica e a monocultura de *Pinus* ganha forte destaque. Nosso objetivo é entender a estruturação das metacomunidades de besouros escarabeíneos em monoculturas de *Pinus* e em matas nativas próximas. Para tanto, conferimos a capacidade de dispersão das espécies e sua fidelidade ao habitat, para depois observarmos os fatores que influenciam essas metacomunidades, como a disponibilidade de recursos alimentares, variáveis microclimáticas e da estrutura da vegetação. No município de Anitápolis, SC, sul do Brasil, realizamos coletas em 12 localidades, incluindo seis áreas de monoculturas de *Pinus* e seis áreas nas matas nativas próximas às mesmas, sendo três áreas de monocultura de *Pinus* contiguas às áreas de mata nativa e as outras três afastadas. Para o teste de dispersão e fidelidade dos besouros ao habitat, instalamos 10 armadilhas para atração de escarabeíneos vivos em cada área e aplicamos o método de marcação e recaptura mensalmente por três meses durante o verão 2018/2019. Para avaliação da diversidade, instalamos 10 armadilhas de queda em amostragens padronizadas nas mesmas áreas, repetindo a captura em duas campanhas. Registramos a presença de mamíferos através de armadilhas fotográficas (para avaliar recursos alimentares dos escarabeíneos), bem como a temperatura ambiental e do solo e variáveis da vegetação. A análise dos dados incluiu um modelo de classificação multinominal para classificar as espécies em generalistas e especialistas e curvas de rarefação e extrapolação para comparar e estimar a riqueza de espécies, diversidade e suficiência amostral entre os diferentes habitats de cada área. Para comparar as comunidades de mata nativa e de monocultura de *Pinus*, calculamos e particionamos a diversidade beta verificando a importância relativa de cada espécie nos padrões de diversidade de cada local. Finalmente, para medir quais fatores influenciam as comunidades, utilizamos modelos de equações estruturais, onde a riqueza e abundância de besouros foram as variáveis respostas e o ambiente, a temperatura, a estrutura da vegetação e a riqueza de mamíferos foram as variáveis explicativas. Como resultado do experimento de dispersão obtivemos 18 recapturas, das quais três ocorreram em habitats diferentes, demonstrando a dispersão dos besouros entre habitats. Também foram registradas atividades comportamentais que confirmam a utilização tanto das áreas de mata nativa como as de monocultura de *Pinus* para estocagem de alimento e construção de ninhos. Nas armadilhas de queda coletamos um total de 3222 besouros de 41 espécies. A diversidade alfa não mostrou diferenças significativas entre os diferentes habitats, mas a diversidade beta mostrou existir dissimilaridade entre as comunidades das monoculturas de *Pinus* e das matas nativas devido à troca de espécies, havendo 24 espécies importantes na contribuição para a dissimilaridade entre os habitats. A influência dos fatores ambientais sobre as metacomunidades não mostrou nenhum preditor relacionado com a riqueza dos besouros, porém vários influenciaram sua abundância, com destaque para a temperatura. Este trabalho nos possibilitou demonstrar que os índices de riqueza e de diversidade de espécies de assembleias de besouros escarabeíneos não refletiram a grande diferença de qualidade ambiental dos habitats, já que através deles não foi possível verificar diferenças entre as comunidades dos diferentes habitats. Dessa forma, a utilização destes índices por si só não seria suficiente para avaliar de forma eficaz a indicação dos besouros. Entretanto, na partição da diversidade beta conseguimos perceber as diferenças na estrutura das comunidades, havendo espécies especialistas de cada habitat. Além disso, podemos afirmar que o trânsito de besouros entre um habitat e outro mostra que a estruturação das comunidades locais também é produto da dispersão entre as áreas, existindo interação entre as populações.

Palavras-chave: Bioindicadores. Conservação da biodiversidade. Ecologia. Dispersão. Nicho.

ABSTRACT

Detritivorous beetles of the subfamily Scarabaeinae are commonly used in studies on the effects of environmental changes, being considered good ecological indicators. Metacommunities can be structured through mass effects or species sorting, being influenced by habitat, as well as the dispersion of individuals between different areas. In the region of Serra Catarinense, native forests have been altered by anthropic pressure and the *Pinus* monoculture gains strong prominence. Our aim is to understand the structuring of dung beetles metacommunities in *Pinus* monocultures and in nearby native forests. To do so, we check the dispersal capacity of the species and their fidelity to the habitat, and then observe the factors that influence these metacommunities, such as food resources' availability, microclimatic variables and vegetation structure. In Anitápolis county, SC, southern Brazil, we carried out samples in 12 locations, including six areas of *Pinus* and six areas in native forests nearby, being three areas of *Pinus* contiguous to the native forest areas and three apart. To test the dispersion and fidelity of the dung beetles to the habitat, we installed 10 attracting traps for live beetles in each area and applied monthly the marking and recapture method for three months during the summer 2018/2019. To assess diversity, we installed 10 pitfall traps in standardized samplings in the same areas, repeating the capture in two campaigns. We recorded the presence of mammals using camera traps (to assess food resources of scarabs), as well as environmental and soil temperature and vegetation variables. Data analysis included a multinominal classification model to rank species into generalists and specialists, and rarefaction and extrapolation curves to compare and estimate species richness, diversity and sampling sufficiency among the different habitats in each area. To compare native forest and *Pinus* monocultures communities, we calculated and partitioned the beta diversity verifying the relative importance of each species in the diversity patterns of each location. Finally, to assess which factors influence the communities, we used equation models, where the richness and abundance of beetles were the response variables and the environment, temperature, vegetation structure and mammal richness were the explanatory variables. We had 18 recaptures from the dispersal experiment, three of which occurred in different habitats, demonstrating the dispersal of beetles between habitats. We also registered dung beetles' behavioral activities, confirming the use of both native forest and *Pinus* areas for food storage and nesting. We collected 3222 beetles from 41 species in the pitfall traps. Alpha diversity did not show significant differences between the two habitats, but beta diversity showed that there is dissimilarity between *Pinus* and native forests communities due to the exchange of species, with 24 important species contributing to the dissimilarity. The influence of environmental factors on metacommunities did not show any predictor related to beetles’ richness, but several influenced their abundance, especially temperature. This work enabled us to demonstrate that richness and species diversity indices of dung beetle assemblages did not reflect the great difference in environmental quality of the habitats, since through them it was not possible to verify differences between the communities of different habitats. This way, the use of these indices alone would not be sufficient to assess dung beetles indication. However, in beta diversity partition we were able to perceive the differences in the structure of communities, with specialist species from each habitat. Furthermore, we can state that the transit of beetles between one habitat and another shows that the structuring of local communities is also a product of dispersion between areas, with interaction between populations.

Keywords: Bioindicators. Biodiversity conservation. Ecology. Dispersion. Niche.

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

APRESENTAÇÃO GERAL

Há séculos os ambientes naturais vêm sendo modificados pelo ser humano com o objetivo de obtenção de recursos, transformando-os em agroecossistemas ou áreas urbanas. Contudo, a partir de meados do século XX a grande maioria dos sistemas agropecuários, de média e larga escala, tem se caracterizado pela monocultura e práticas intensivas com grande aporte de insumos externos (NICHOLLS *et al.*, 1999). O plantio de monoculturas arbóreas, apesar de importante economicamente, resulta em efeitos negativos devido à perda de diversidade (VALLEJO *et al.*, 1987). Além disso, as monoculturas afetam a integridade dos ambientes naturais, pois a substituição de grandes áreas de vegetação natural por ecossistemas diferentes, leva à criação de fragmentos isolados, imersos em uma matriz antropizada (FORMAN & GODRON, 1986; FRANKLIN, 1993).

No Brasil, o plantio em escala comercial das espécies de *Pinus* iniciou a partir da década de 1960, principalmente nas regiões Sul e Sudeste do País e sua utilização envolve produção de celulose, laminados, extração de resina e madeira serrada (MACHADO & SCOLFARO, 1988; AGUIAR *et al.*, 2011). No entanto, a introdução de espécies de *Pinus* empobrece o solo no que diz respeito ao complexo de troca e teor de micronutrientes (DICK *et al.*, 2007), causando sérios impactos em áreas de Mata Atlântica, tanto na fauna edáfica, quanto na qualidade do solo e nos processos de sucessão por inibição das espécies vegetais (CÓRDOVA *et al.*, 2009). As alterações do solo, bem como a inibição das espécies vegetais, se devem ao fato das acículas possuírem ceras cuticulares e compostos polifenólicos, os quais dificultam a decomposição da serapilheira interferindo nas características do solo, bem como nos organismos vivos ali presentes (STURGES & ATKINSON, 1993). Estes compostos são aleloquímicos conhecidos pela alta solubilidade em água e por inibirem o crescimento de outras espécies de vegetais (INDERJIT, 1996; GRAÇA *et al.*, 2002). Esta inibição sobre espécies vegetais continua até mesmo após o corte e retirada das árvores dos locais, dificultando os processos sucessionais e interferindo assim na resiliência das comunidades biológicas. Além disso, características como rápido crescimento e maturação, as quais tornam o *Pinus* uma boa escolha para silvicultura, também facilitam sua expansão fora das áreas de plantio, sendo invasor de áreas naturais (PAUCHARD *et al.*, 2015).

As causas da variação espacial e temporal na distribuição dos organismos é o principal objeto de investigação da ecologia de comunidades (BEGON *et al.*, 2006). A conservação da diversidade passa pela compreensão do uso que as diferentes espécies fazem destes ambientes heterogêneos na paisagem antropizada. As espécies que originalmente viviam nos ambientes naturais podem ou não conseguir habitar as áreas que vêm sofrendo as modificações ambientais, devido aos recursos disponíveis e às interações entre os mesmos (LAWTON, 1999; BEGON *et al.*, 2006). Desta forma, as comunidades se estruturam de forma diferente em cada tipo de ambiente. Assim sendo, certas características no habitat são importantes preditoras relacionadas à estruturação de comunidades biológicas, podendo explicar a distribuição e a abundância de certas espécies (PERES-NETO *et al.*, 2006). No entanto, os diversos organismos podem se encontrar em habitats pouco adequados, provindo de outras comunidades locais através da dispersão, formando metacomunidades (LEIBOLD *et al.*, 2004). Dentro dos modelos descritos para caracterização de uma metacomunidade, a alocação de espécies ou *species sorting* enfatiza que o habitat e as interações entre as espécies são determinantes na estruturação das comunidades (LEIBOLD *et al.*, 2004). Por outro lado, o modelo de efeito de massa ou *mass effect* é marcado pelo resgate de espécies da exclusão competitiva via dispersão de indivíduos entre áreas com diferentes qualidades ambientais (LEIBOLD *et al.*, 2004). Neste caso, ocorre uma saída de indivíduos de sítios considerados de melhor qualidade para sítios de pior qualidade de recursos, resultando em ambientes funcionando como fontes e outros como sumidouros. O efeito de massa pode ser mais significativo em espécies com grande capacidade de dispersão ou em extensões espaciais menores devido à maior proximidade dos habitats, independentemente da qualidade ambiental (HEINO *et al.*, 2015).

Assim, a importância de se estudar as diversas formas de estruturação de comunidades em ambientes heterogêneos (naturais e antropizados) reside no fato de que a resposta dos organismos encontrados nestas áreas pode levar ao entendimento de fatores ecológicos que determinam a distribuição geográfica e espacial destas espécies, assim como os possíveis efeitos da antropização das paisagens. Observa-se também uma necessidade de práticas com melhor aproveitamento dos recursos e minimização dos impactos, visando formas mais sustentáveis de uso. A avaliação dos efeitos da implantação de monoculturas pode ser efetuada através da análise de organismos utilizados como indicadores ecológicos (SILVEIRA NETO *et al.*, 1995; THOMAZINI & THOMAZINI, 2000).

Os besouros detritívoros da subfamília Scarabaeinae são considerados bons indicadores de qualidade e perturbações ambientais, já que as espécies se vêm afetadas em ambientes alterados pela ação humana, tendo sido utilizados em vários estudos que investigaram os efeitos de perturbação ambiental na diversidade (HALFFTER *et al.*, 1992;

HALFFTER & FAVILA, 1993; DURÃES *et al.*, 2005, NICHOLS *et al.*, 2007; GARDNER *et al.*, 2008; HERNÁNDEZ *et al.*, 2014).

Os coleópteros da subfamília Scarabaeinae são besouros coprófagos, necrófagos e saprófagos que, devido a este comportamento, atuam em diversos serviços ecossistêmicos, como processadores de matéria orgânica em decomposição (NICHOLS *et al.*, 2008). Esses besouros são comumente chamados de “rola-bostas” e se caracterizam por usarem fezes ou outros detritos orgânicos, como carcaças e frutos em decomposição como recurso alimentar, tanto no estágio adulto como de larva (HALFFTER & MATTHEWS, 1966). O comportamento reprodutivo inclui a construção de ninhos dentro do recurso (residentes ou endocoprídeos), na forma de túneis com galerias onde enterram o alimento logo abaixo do recurso (tuneleiros ou paracoprídeos) ou enterrando bolas de alimento mais afastadas do recurso (roladores ou telecoprideos) (HALFFTER & MATTHEWS, 1966; HALFFTER & EDMONDS, 1982). Com a remoção e reentrada de matéria orgânica morta no ciclo de nutrientes, estes insetos acabam promovendo e aumentando a fertilidade e aeração dos solos, prolongando sua capacidade produtiva (HALFFTER & MATTHEWS, 1966; MITTAL, 1993; SHEPHERD & CHAPMAN, 1998).

Como seus recursos alimentares são relativamente escassos e efêmeros, a competição interespecífica é forte dentro das comunidades de escarabeíneos, o que tem levado a uma evolução adaptativa dentro do grupo permitindo a ocupação de determinados habitats, existindo espécies que utilizam exclusivamente áreas florestais e outras espécies que são tipicamente de áreas abertas, como savanas ou campos (HANSKI & CAMBEFORT, 1991). Desta forma, a dispersão na procura de recursos pode ser um fator importante na sobrevivência dos indivíduos, variando entre espécies e entre sexos, mas sendo frequentemente pequena (ARELLANO *et al.*, 2008; DA SILVA & HERNÁNDEZ, 2015) e muito rara entre habitats diferentes, tendo as espécies um alto grau de fidelidade por um biótopo ou fitofisionomia em particular (KLEIN, 1989; DRISCOLL & WEIR, 2005). A movimentação dentro de um mesmo habitat varia entre espécies e entre sexos, mas frequentemente é pequena, entre 300 e 1500 metros (ARELLANO *et al.*, 2008; DA SILVA & HERNÁNDEZ, 2015). Portanto, as espécies de escarabeíneos que compõem uma comunidade local podem incluir tanto as espécies residentes como algumas que estejam vindo de outros habitats. Assim, a teoria de metacomunidades vem auxiliar na compreensão da estruturação das comunidades que se encontram em uma paisagem em mosaico, com áreas de monocultura de *Pinus* e de mata nativa.

Nossa hipótese é de que as comunidades locais de besouros escarabeíneos nas monoculturas de *Pinus* e nas matas nativas em seu redor estão conectadas por dispersão, constituindo metacomunidades. Os fatores que permitiriam aos escarabeíneos habitarem tanto as áreas de monocultura de *Pinus* como as de mata nativa seria a presença de recursos alimentares como produto da presença de mamíferos, somada às condições microclimáticas adequadas à permanência dos besouros.

OBJETIVOS

OBJETIVO GERAL

Analisar e descrever a estrutura das metacomunidades de coleópteros da subfamília Scarabaeinae que habitam áreas de monoculturas de *Pinus* e de mata nativa.

OBJETIVOS ESPECÍFICOS

1 - Verificar a fidelidade das espécies ao habitat, observando o uso do ambiente na construção de ninhos e descrever a capacidade de dispersão das espécies entre os habitats, avaliando se há diferença entre áreas de monoculturas de *Pinus* e de mata nativa contíguas e isoladas;

2 - Descrever a metacomunidade de escarabeíneos que habitam áreas de monoculturas de *Pinus* e de mata nativa e classificar as espécies em especialistas e generalistas de acordo com a preferência de habitat;

3 - Analisar a influência do habitat sobre as metacomunidades, incluindo a disponibilidade de recursos alimentares, variáveis microclimáticas e da estrutura da vegetação.

CAPÍTULO 1 – DUNG BEETLE METACOMMUNITIES IN NATIVE FORESTS AND *PINUS* MONOCULTURES RAISE QUESTIONS ABOUT METRICS USED FOR ECOLOGICAL INDICATION

ABSTRACT

Beetles of the subfamily Scarabaeinae are commonly used as ecological indicators in studies about the effects of environmental changes. There are few studies about the composition and dynamics of dung beetle communities in *Pinus* monocultures. It is possible that some environmental features of *Pinus* monocultures do not show such discrepant microclimatic changes when compared to native forest areas. In those cases, it would be of great importance understand which variables (habitat type, vegetation or environmental conditions) have more influence in the metacommunities. For that, we analyzed dung beetle metacommunities in native forest and in *Pinus* monocultures and then evaluated the factors driving them. In the summer of 2018/2019, we had 12 sampling areas in Southern Brazil, six *Pinus* monocultures and six native forests. We performed a dispersal test with traps to attract live beetles, applying a marking-recapture method, obtaining 18 recaptured individuals. Three of those recaptures occurred in different habitats, showing low dispersal between habitats. We recorded behavioral activities confirming the use of both native forest and *Pinus* areas. We also collected 3222 dung beetles from 41 species in pitfall traps. When comparing species richness and diversity in different habitats, the metrics did not reflect the difference in the environmental quality of the areas. This shows that these metrics are not the best when using dung beetles' communities as ecological indicators of biodiversity lost resulting from land-use changes, having a need to complement the analysis with composition analysis methods. However, when we partitioned beta diversity between habitats, we observed a dissimilarity between the communities of *Pinus* monocultures and native forest, due to species substitution, with 24 species contributing to the dissimilarity between habitats. In our structural equation models, the influence of environmental factors on metacommunities did not show any predictor related to dung beetle richness, but several variables influenced their abundance, especially the temperature.

INTRODUCTION

The beetles of the subfamily Scarabaeinae, commonly called dung beetles, have been used in several studies as ecological indicators since their first proposal by Halffter & Favila in 1993 (DAVIS & SUTTON, 1998; DAVIS *et al*., 2001; GARDNER *et al*., 2008; AUDINO *et al*., 2014; SARMIENTO-GARCÉS & HERNÁNDEZ, 2021). The advantages of using this taxon are many since they are abundant in a wide range of terrestrial ecosystems (MCGEOCH *et al*., 2002; DAVIS *et al*., 2004; HERNÁNDEZ *et al*., 2014), easy to sample and quick response to environmental disturbance (GARDNER *et al*., 2008), and mainly because of their species specificity to different habitats (HANSKI & CAMBEFORT, 1991; SCHOLTZ *et al*., 2009). They also can be used to explore species-functioning relationships (SARMIENTO-GARCÉS & HERNÁNDEZ, 2021), as they provide ecosystem services actively participating in nutrient cycling, promoting soil aeration and removal of decaying organic matter (HALFFTER & MATTHEWS, 1966; NICHOLS *et al*, 2008).

We can interpret the narrow ability of dung beetles to change habitat as an evolutionary response to the high interspecific competition for resources, which are often limited and ephemeral (HANSKI & CAMBEFORT, 1991). These beetles use dung or other organic debris, such as carcasses and some decaying fruits, as food resources and high competition has great influence in their community structure (SIMMONS & RIDSDILL-SMITH, 2011). Furthermore, there is also a high correlation between dung beetles' richness and mammals because of the amount and diversity of available resources (HALFFTER & MATTHEWS, 1966; ESTRADA *et al*., 1999; DAVIS *et al*., 2002; ANDRESEN & LAURANCE, 2007; NICHOLS *et al*., 2009; BARLOW *et al*., 2010; BOGONI *et al*. 2016). Dung beetles have developed foraging techniques by using their olfactory cues to be able to rapidly locate and choose resources, depending on the type, distance and nutritional quality of each resource (HANSKI & CAMBEFORT, 1991). Nevertheless, most species of this group are generalist in feeding and breeding strategies (LARSEN *et al*., 2008; FRANK *et al*., 2018; GIMÉNEZ GÓMEZ *et al*., 2018).

In local communities, high diversity of dung beetles is related to niche differentiation, due to behavior variation according to the type of resource allocation, time of activity, body size, among others intraspecific differences such as sex and age (HANSKI & CAMBEFORT, 1991). The adaptive evolution inside the group allows the occupation and preference of many species for a certain type of habitat, with some being exclusive to forest areas and others typical of open areas, like savannas and meadows (HANSKI & CAMBEFORT, 1991). These features of habitat partition allow dung beetles to occupy a more diverse number of environments, having a high degree of fidelity for a biotope or phytophysiognomy (KLEIN, 1989; DRISCOLL & WEIR, 2005). Some studies show that some forest specialist species do not leave their habitat even with the supply of food resources in open areas nearby (KLEIN, 1989; LARSEN *et al.*, 2008).

The high competition and ephemeral nature of food resources together may suggest that dung beetles are probably good dispersers (ROSLIN & VILJANEN, 2011). However, according to some studies, Scarabaeinae species with different sets of ecological traits have differences in mean movement rate (HOWDEN & NEALIS, 1975; PECK & FORSYTH, 1982), with only a few species traveling longer distances in the same habitat (ARELLANO *et al.*, 2008; DA SILVA & HERNÁNDEZ, 2015). This dung beetles' dispersion ability in the search of resources through poorly suited habitats and the tolerance to remain in sub-optimal environments can be an important factor in their species reproduction. Some species from open areas may even have more tolerance to microclimatic changes, being able to enter and inhabit degraded forests and vice versa, changing the community composition of these areas. As a result, forested areas adjacent to open habitats can present a high turnover of species composition, where open habitat specialists increase the alpha diversity of these disturbed places (ARELLANO & HALFFTER, 2003; GARDNER *et al.*, 2008). Although remnants of native forests allow forest-associated dung beetles and other animals to survive in patchy landscapes (HALFFTER & ARELLANO, 2002; ARELLANO & HALFFTER, 2003; ANDRESEN, 2005), the modification of the habitat is often related to species loss, especially the ones with larger body size (GARDNER *et al.*, 2008; BATILANI-FILHO & HERNÁNDEZ, 2017; SARMIENTO-GARCÉS & HERNÁNDEZ, 2021).

When using dung beetles as ecological indicators we hope to obtain by their presence and abundances in a particular area reliable measurements and interpretations regarding changes in environmental conditions (NICHOLS & GARDNER, 2011). For that, richness and diversity indexes are often used as measures to assess communities' changes, considering most of the time different species as equal in their contribution to the functioning of ecosystems (BARRAGÁN et al., 2011). However, when we try to understand how dung beetle communities vary between habitats (such as natural and anthropogenic), it is possible to obtain better understanding of biological diversity and the extent to which human actions can transform its dynamics, structure and behavior (BALVANERA et al., 2006).

We also point here to the importance of considering the spatial scale when using dung beetles as ecological indicators since they have the ability to disperse between different areas. In this study, we try to look beyond the diversity of each location, seeking a better understanding on the dynamics of these communities as well as the metacommunities formed between them. That is because in metacommunity ecology not only local scale matters, but a combination of local and regional processes to understand patterns of species abundance, occurrence, composition, and diversity in different scales of space and time (CHASE *et al*., 2020). The formation of dung beetle metacommunities is strongly marked by the habitat (model known as species sorting), but can also follow the mass effect model, where the rescue of species from competitive exclusion is marked by dispersal of individuals between areas with different environmental qualities (LEIBOLD *et al*., 2004). In this case, there is a departure of individuals from sites considered to be of better quality to areas of worse resource quality, resulting in some environments working as sources and others as sinks. The mass effect can be more significant in species with high dispersal capacity or in smaller spatial extensions due to habitat proximity, regardless of environmental quality (HEINO *et al*., 2015).

Many studies point out the exotic trees from the genus *Pinus* as invaders and the potential to inhibit the growth of other plant species, negatively affecting local and regional biodiversity (BREWER, 1998; REJMÁNEK & RICHARDSON, 1996; LEDGARD, 2001; ESSL *et al*., 2011; BUCKLEY *et al*., 2005; RICHARDSON, 2006; GUNDALE *et al*., 2014). There are not many information and studies related to the composition and dynamics of dung beetle communities in *Pinus* monocultures. However, it could be possible that certain aspects of the environmental characteristics of *Pinus* monocultures as temperature and canopy cover percentage may not show such discrepant microclimatic changes when compared to native forest areas, as it happens in open fields. There are studies that showed high diversity and abundance of dung beetles in land-uses that preserve tree canopy (BUSTAMANTE-SÁNCHEZ *et al*., 2004; BRAGA *et al*., 2012; GÓMEZ-CIFUENTES *et al*., 2017; GIMÉNEZ GÓMEZ *et al*., 2018). Therefore, in cases where habitats modified for forestry use present similar microclimatic conditions to native habitats, it would be of great importance to understand under which conditions dung beetles can be used as ecological indicators.

In this paper, our hypothesis is that the local communities of dung beetles in *Pinus* monocultures and in the native forest remnants around are connected by dispersion constituting metacommunities. The factors that allow dung beetles to inhabit both *Pinus* monocultures and native forest areas would be the presence of food resources, as a product of the transit of mammals and attendance of domestic animals, in addition to similar microclimatic conditions suitable for their occurrence. Our aim is therefore to understand if the structuring of local dung beetle communities in *Pinus* monocultures resembles or not the nearby native forest dung beetle communities. We first checked the species dispersal and their fidelity to the different habitat, and then we looked for the factors that may drive them, relating dung beetle communities to factors known to influence their ecology, such as food resources availability, microclimate conditions, and vegetation structure variables (HALFFTER & ARELLANO, 2002).

METHODS

Study area

We developed this study in the microregion of Tabuleiro in Santa Catarina state, south of Brazil, which includes the counties of Anitápolis, Rancho Queimado, Alfredo Wagner, Águas Mornas and São Bonifácio (27°54’25.25”S, 49°10’48.3”W). This region has a rugged topography, with elevation ranging between 440-1,000 m a.s.l. and native vegetation mainly composed by dense ombrophilous forest. The landscape is a heterogeneous mosaic composed by forest patches that vary in size, density and connectivity, immersed in a matrix of forestry, pastures and small crop fields. The climate is Cfa according to the Köppen-Geiger classification, with rainfall well distribute during all year, with the average annual rainfall of 1,700 mm, and temperatures can vary strongly across the year, between 0-40ºC, with the annual average being 19ºC (PELL *et al*., 2007).

In this region, we select six sample sites that presented two landscape components each, a *Pinus* monocultures and a native forest area (**Fig. 1**). Thus, sampling was performed in six areas, with *Pinus* monocultures (P1, P2, P3, P4, P5, P6) each one paired with six native forest areas (F1, F2, F3, F4, F5, F6), totalizing 12 sampling areas. We select the sites based on their accessibility and degree of isolation of the *Pinus* monocultures in relation to the forest fragments. Thereby, three of the *Pinus* monocultures (P1, P2, and P3) were connected to the native forest and the other three monocultures (P4, P5, P6) were at least 60 meters away from the native forest areas. Between all three areas that were apart, we had open fields with small bushes. All six areas were at least 1 km apart from each other. We carry out the fieldwork during the months of November-December of 2018 and January-February of 2019, the season with the greatest abundance of dung beetles in southern Brazil (HERNÁNDEZ & VAZ-DE-MELLO, 2009; DA SILVA *et al.*, 2013).

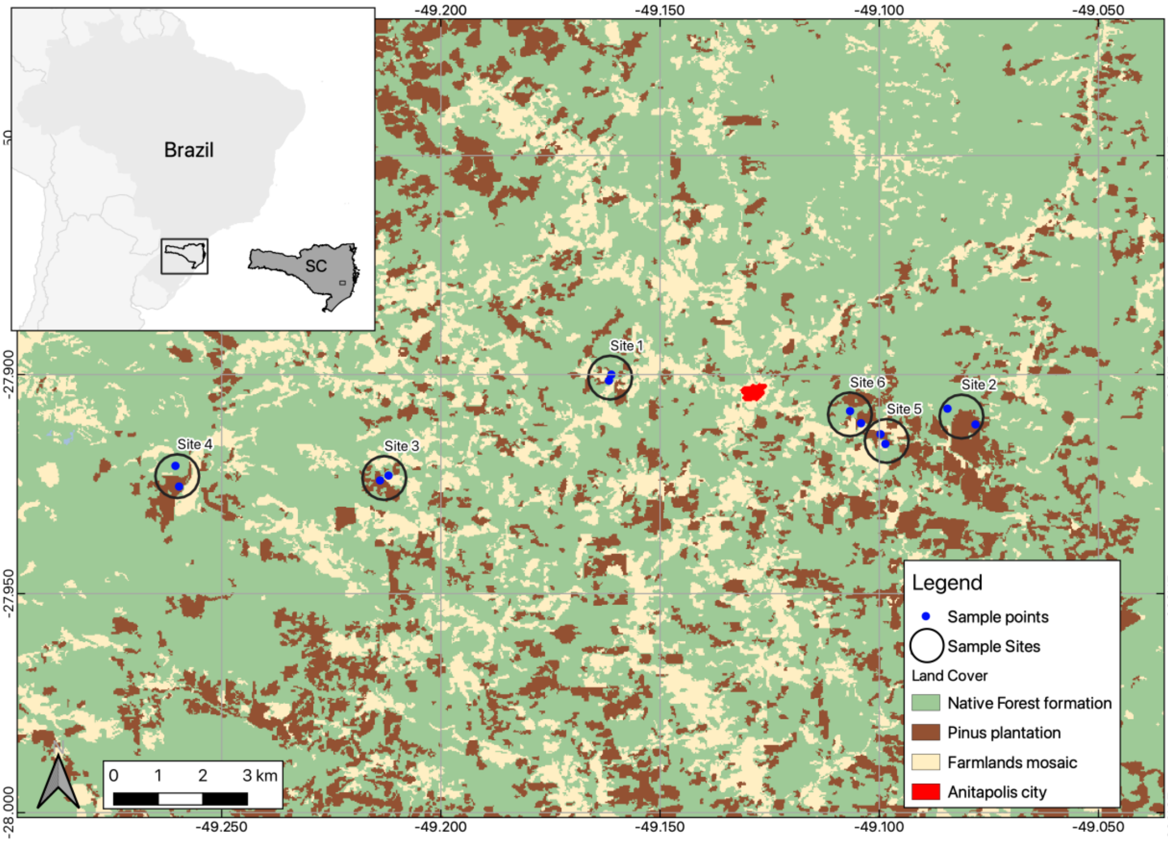


Fig. 1 General view of the landscape and the six sample sites, each one with their two areas of different habitat (one of *Pinus* monocultures and one of native forest), in Santa Catarina state, south of Brazil.

Habitat use and dung beetle dispersal: sampling and analysis

In order to test if dung beetles build nests for reproduction in both habitats and the dispersion between different habitat (*Pinus* monocultures and native forest), we placed in each area 10 attraction traps for dung beetles. Those traps, named "nesting houses", consist of PVC pipes buried vertically on the ground, with an opening on top for dung beetles' free access, filled with soil and containing dog feces as food resource. The nesting houses were placed 10 meters from each other at a distance of 10 meters from the edge of the area (**APPENDIX A**). After 48 hours of exposure, we applied the following marking and release protocol: first we cleaned and identified the collected Scarabaeinae, then we marked them with a scarification on the pronotum with the help of a dental drill added to a small battery and released near the trap in the same areas of their capture. The identification of the species was by comparison using a reference collection of regional species from the Entomological Collection Mítia Heusi-Silveira of the Universidade Federal de Santa Catarina. The scarification marking technique that we used is considered noninvasive and does not have the risk to be lost by the insect as some paints (WUERGES & HERNÁNDEZ, 2020). The mark had the shape of a line and allowed us to identify the habitat the beetle was first found, *Pinus* monocultures if in left side of the pronotum and native forest if right. We marked only species with body length 4 mm or higher. We replicate the marking-release protocol once after a month from the first sampling. After 3 weeks from that second sampling, we had one last attempt to recapture marked individuals.

With the nesting houses data, firstly, we confirmed the use of the different habitats (*Pinus* monocultures and native forest) by the dung beetle species found there. Afterwards, we calculate recapture rates for each species who had one or more recaptured individual. We then analyze the recaptures that occurred outside the original marking habitats to observe the dispersion of the dung beetles between the different habitats (*Pinus* monocultures and native forests).

Dung beetle metacommunities: sampling and analysis

Parallel to the first experiment, we installed in the same 12 areas 10 pitfall traps for the capture of dung beetles (**APPENDIX A**). We placed those traps 40 meters away from the nesting houses, staying 50 meters from the edge of sampled areas. Sampling design consisted of 10 pitfall traps distributed in pairs into two parallel transects, one pair trap spaced 100 meters apart from the other to avoid pseudoreplication (DA SILVA & HERNÁNDEZ, 2015). Paired traps were spaced 10 meters apart and had different bait types, one with human feces (20 g) and the other with two-day rotten meat (20 g), for the attraction of both coprophagous and necrophagous species, respectively. The pitfall traps consisted of plastic containers (15 cm diameter × 20 cm depth), buried with the top edge leveled to the ground, allowing insects to fall in. All traps contained water (300 ml) and neutral detergent, with a plastic lid supported by wooden sticks for rain protection, placed approximately 10 cm above their opening. The lid prevented overflow and supported the bait. We replicate sampling three times, once a month, during three months (December of 2018 and January – February of 2019) on every one of the 12 areas. All traps remained in the field for 48 hours. After this period, we took the collected material to the Laboratório de Ecologia Terrestre Animal (LECOTA/UFSC). There, we mounted dung beetles individuals on entomological pins, dried in an oven (40°C for 48h), identified and included them in the Coleção Entomológica Mítia Heusi-Silveira from the Centro de Ciências Biológicas of the Universidade Federal de Santa Catarina. The expert Dr. Fernando Vaz-de-Mello, from the Universidade Federal de Mato Grosso, Brazil, confirmed the identifications.

We classified species into generalists and specialists of the two different habitats with the help of a multinomial classification model based on an iterative program (CLAM). The program estimated species relative abundance in the two habitats types (*Pinus* monocultures and native forest) allowing a robust statistical classification of habitat specialists and generalists, without excluding rare species from start (CHAZDON *et al*., 2011). We used the R package "vegan" for this analysis (OKSANEN *et al*., 2020).

We used rarefaction and extrapolation curves with the effective number of species to compare and estimate species richness, diversity and sample sufficiency between different habitats of each site. This method is based on Hill numbers and sets up confidence intervals around species richness ($q = 0$), Shannon entropy ($q = 1$) and Simpson dominance ($q = 2$) (CHAO *et al.*, 2014; HSIEH *et al*., 2016). The baseline sample size was the highest or double of the lowest sample size, confidence intervals were 95% and the analysis were performed using the R package "iNEXT".

To check for differences in composition among communities of native forest and *Pinus* monocultures we used the Bray-Curtis index of dissimilarity, partitioned in two components: balanced variation in abundance and abundance gradients. The first related to individuals of some species in one site substituted by the same number of individuals of different species in another site, and the second about the loss of individuals from one site to the other (BASELGA, 2013). We used the R package "betapart" for this analysis. After that, we compared the dissimilarities between the sites that had adjacent habitats and the ones with habitats apart, with a t-test to see if there were major differences among the areas.

Finally, we partitioned total beta diversity into species contributions to beta diversity (SCBD), which is the degree of variation of individual species across the study area, to test the relative importance of each species in affecting beta diversity patterns per site; the analysis was based on abundance data (LEGENDRE & DE CÁCERES, 2013). All analyses were performed in R 3.6.3 program (R Core Team, 2020).

Environmental influence in the metacommunities

For dung beetle resource availability, we used camera traps to record mammalian presence inside the areas. We placed one camera trap in the central point of each area during dung beetle sampling and checked batteries every 20 days. The cameras were active for a minimum of 30 days and maximum of 60 days, then, we only considered the records made during the period of 1 month for all locations. After that period, we identified the mammals from the photographs. The mammalogist Dr. Mauricio E. Graipel from the Universidade Federal de Santa Catarina, Brazil, confirmed the species identification. To make an approximation on the amount of excrement, we considered only records of mammals from the same species that had at least one-hour difference each, as well as the number of individuals of the same species in each record when in groups.

Variation in tree features and physical structure of the forest floor can change conditions that may affect dung beetles (FEER, 2013; NICHOLS *et al*., 2013; DA SILVA & HERNÁNDEZ, 2016). This been said, we measured environmental variables on each area related to vegetation using an adapted point-centered quarter method (COTTAM & CURTIS, 1956). In each study area, we placed a plastic pipe cross in the center of every two sampling points dividing them into four quadrants: northwest, southwest, southeast and northeast. Then, we measured for each quadrant: distance of the nearest tree and distance of the nearest shrub and their height. Besides that, we estimated visually in 1m^2 plots in each quadrant percentage cover of vegetation and bare ground. For shrubs, we considered those with minimum height of one meter and for trees height over one meter and the diameter at breast height over five centimeters. We measure the circumferences and distances with a tape measure.

Temperatures (in ^{o}C) were measured throughout the experiment with the use of an environmental thermometer (datalogger) installed in the central point of each sampling site, buried in the ground. Geographical coordinate data (UTM) of each site as well as the sampled points were obtained using a manual GPS. We use Google Earth Path software to measure the altitude and size of the sites, along with the distance between the isolated sites of *Pinus* monocultures and native forest.

We used structural equation models (SEM) to evaluate the relationships of environmental factors on dung beetle communities (GRACE, 2006; SHIPLEY, 2016). This way, we build a conceptual model, where we decide to put dung beetle richness and abundance as response variables. For the explanatory variables we had the habitat type, temperature, vegetation structure (trees for tall vegetation structure, shrubs for middle vegetation structure and herb cover for the ground level), and the number of times mammals were recorded (as a way to measure the amount of food resources available to dung beetles). In this model, we could observe which explanatory variables would influence other variables, with hierarchical submodels that influence the final result. The regressions between variables were performed by Piecewise SEM in R 3.6.3 program (R Core Team, 2020). All variables with probability below 0.05 were included in a structural frame, where we estimate the coefficient for each equation in the model. Then, we highlight the positive and negative relationships using arrows, which their sizes were according to coefficient value of each variable relationships.

RESULTS

Habitat use and dung beetle dispersal

We marked and released 883 alive individuals belonging to 19 species, all captured in the nesting houses (**APPENDIX B**). We register feeding balls from telecoprids and tunnels with paracoprids inside the traps, showing that dung beetles utilize both native forests and *Pinus* monocultures to feed and bury resources for nesting. The species with the highest number of marked and released individuals were *Dichotomius sericeus* (236), *Canthon rutilans cyanescens* (133), *Coprophanaeus saphirinus* (122) and *Dichotomius assifer* (102). During a period of 20 to 76 days, we recaptured 18 individuals from three species only: *Canthon rutilans cyanescens*, *Dichotomius sericeus* and *Dichotomius assifer*, with an overall recapture rate of 3.82 (**Table 1**).

Table 1 Number of marked (Mk), recaptured (Rc) individuals and total recapture rate (% Rc) per species. Number of individuals recaptured in the same marking area (Sm) and area of recapture (Rc Areas). Number of individuals recaptured in different areas (Diff) and areas from where the individuals dispersed and were recaptured (Disp), P = *Pinus* monocultures and F = native forest.

Species	Mk	Rc	% Rc	Sm	Rc Areas	Time	Diff	Disp	Time
Canthon rutilans cyanescens	133	5	3.76	4	3 in P1 and 1 in F4	20 to 58 days	1	P4 – F4	65 days
Dichotomius assifer	102	4	3.92	4	3 in P1 and 1 in P5	20 to 39 days	0	-	-
Dichotomius sericeus	236	9	3.81	7	4 in P6, 2 in F3 and 1 in P3	37 to 76 days	2	P5 – F5 P3 – F3	29 to 76 days
Total	**471**	**18**	**3.82**	**15**			**3**		

Of those individuals, 15 were recaptured in the same marking areas, 12 in *Pinus* monocultures and three inside native forests. Three individuals from two species were found in different areas from where they were marked, showing their ability to move between habitats, having been marked on *Pinus* monocultures and found afterwards in native forests (**Table 1**). From the species *Canthon rutilans cyanescens*, 133 individuals were marked and we recaptured five of them. Among these, 3 were recaptured in the same marking area (*Pinus* monocultures P1) and one was found in a different habitat, being marked in the *Pinus* monocultures area and recaptured 2 months after at a distance of 180 meters in the native forest (from P4 to F4, Table 2). For *D. assifer*, 102 individuals were marked and four were recaptured, all in the same marking areas: inside *Pinus* monocultures (three in P1 and one in P5), of which one was recaptured in 20 days, another in 36 and the last two in 58 days. *D. sericeus* had the highest number of individuals marked (236) and recaptured (9). From those, we found seven individuals in the same marking areas, both in *Pinus* monocultures and native forests (four in P6, one in P3 and two in F3). The other two individuals were found in different areas from where they were first captured and marked, going from *Pinus* monocultures to native forest (from P3 to F3 at a distance of 60 meters and from P5 to F5, at 130 meters). These results show the species dispersion capacity inside and between both habitats.

Dung beetle metacommunities

We collected 3222 dung beetles belonging to 41 species (**APPENDIX C**). The three most abundant species were *Dichotomius sericeus* (19.11%), *Eurysternus inflexus* (14.83%) and *Deltochilum morbillosum* (13.22%), which together represented 47.16% of the total individuals captured. The rare species, with only one individual collected were *Canthidium* aff. *taurinum*, *Canthidium femorale* and *Canthon oliverioi*, *Scatonomus fasciculatus* and *Sulcophanaeus radamanthus* had two individuals captured each.

From the species collected, seven of them were found in all sampled areas: *Deltochilum morbillosum*, *Dichotomius assifer*, *Dichotomius sericeus*, *Canthidium* aff. *trinodosum*, *Coprophanaeus saphirinus*, *Eurysternus inflexus* and *Phanaeus splendidulus*. In contrast, we collected six species in only one of the 12 areas: *Dichotomius opalescens* (P4), *Canthidium* aff. *taurinum* (F3), *Canthidium dispar* (F2), *Canthidium femorale* (F2), *Canthon oliverioi* (F2) and *Sulcophanaeus radamanthus* (F2).

According to the multinomial classification analyses, only four species were native forest specialists: *Canthidium* aff. *trinodosum*, *Canthon angularis*, *Paracanthon* aff. *rosinae* and *Uroxys terminalis* and seven were *Pinus* monocultures specialists: *Canthidium* sp.1, *Canthon lividus seminitens*, *Canthon rutilans cyanescens*, *Deltochilum multicolor*, *Deltochilum rubripenne*, *Eurysternus inflexus* and *Onthophagus tristis*. This analysis showed 16 habitat generalist species, inhabiting both *Pinus* monocultures and native forest habitats, reaffirming that many species are occupying both habitats. Fourteen species were considered too rare to be classified with confidence (**Fig. 2**).

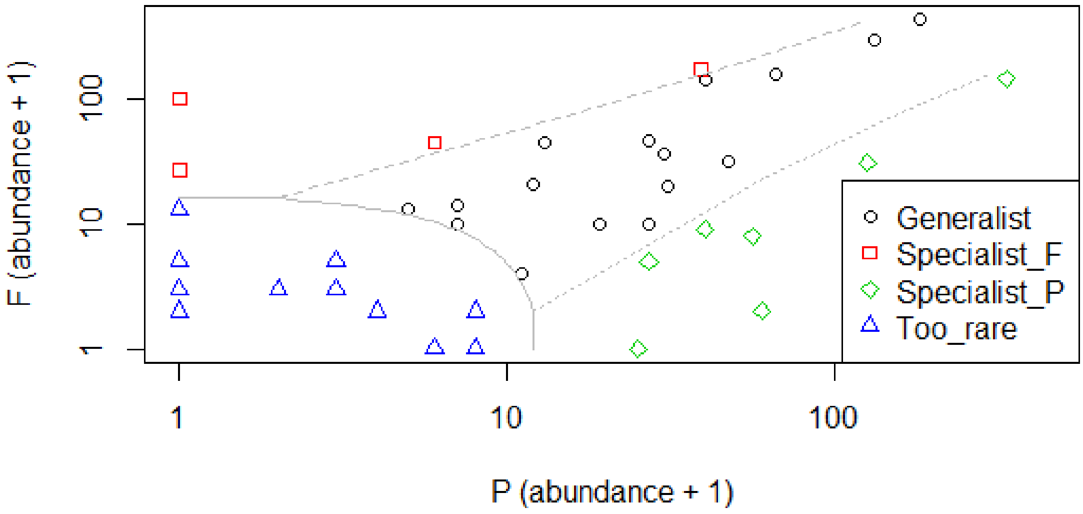


Fig. 2 Species classification with data collected in habitats of native forest and *Pinus* monocultures in Santa Catarina state, south of Brazil. Specialist_F: native forest specialist, Specialist_P: *Pinus* monocultures specialist.

Pitfall traps baited with feces attracted 70.1% of dung beetles caught in all areas, showing preference for this resource. In native forest areas, we captured 1,274 individuals in feces-baited traps and 578 in meat traps. In *Pinus* monocultures, we also caught more individuals in feces-baited traps, with 985 dung beetles against 386 in meat traps.

The abundance of dung beetles found per type of habitat was 1,351 individuals from 32 species in the *Pinus* monocultures and 1,844 dung beetles from 38 species in the native forest areas (**APPENDIX C**). The extrapolated species accumulation curves for each area showed sampling sufficiency, since all curves reached the asymptote (sample coverage over 95% for all the sampling areas). In all six sites, species richness ($q = 0$) was similar between *Pinus* monocultures and native forests, with confidence intervals overlapped (**Fig. 3**).

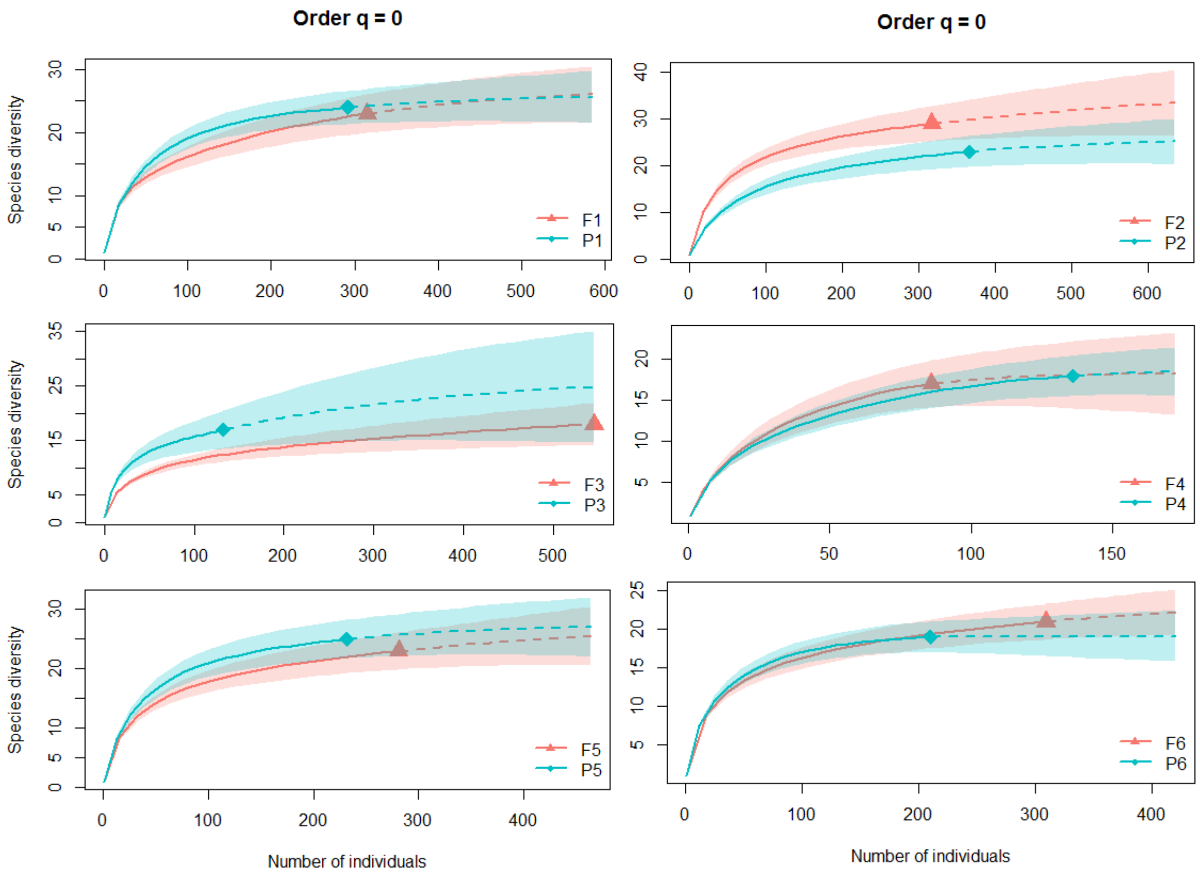


Fig. 3 Individual-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the smallest sample size) of dung beetles' species richness for Hill number (q = 0) for each site, where F represents native forests and P represents *Pinus* monocultures.

Including abundance data in the analyses (Shannon entropy exponential, q = 1), we can see that the number of typical species were the same in four of the six sites, with the same diversity measure between *Pinus* monocultures and native forest. Only the Sites 2 and 3 had opposite patterns, with the first having higher diversity in the forest (F2 with 15.12 typical species and P2 with 6.24) and the second in *Pinus* monocultures (P3 with 10.45 typical species and F3 with 5.51) (**Fig. 4**).

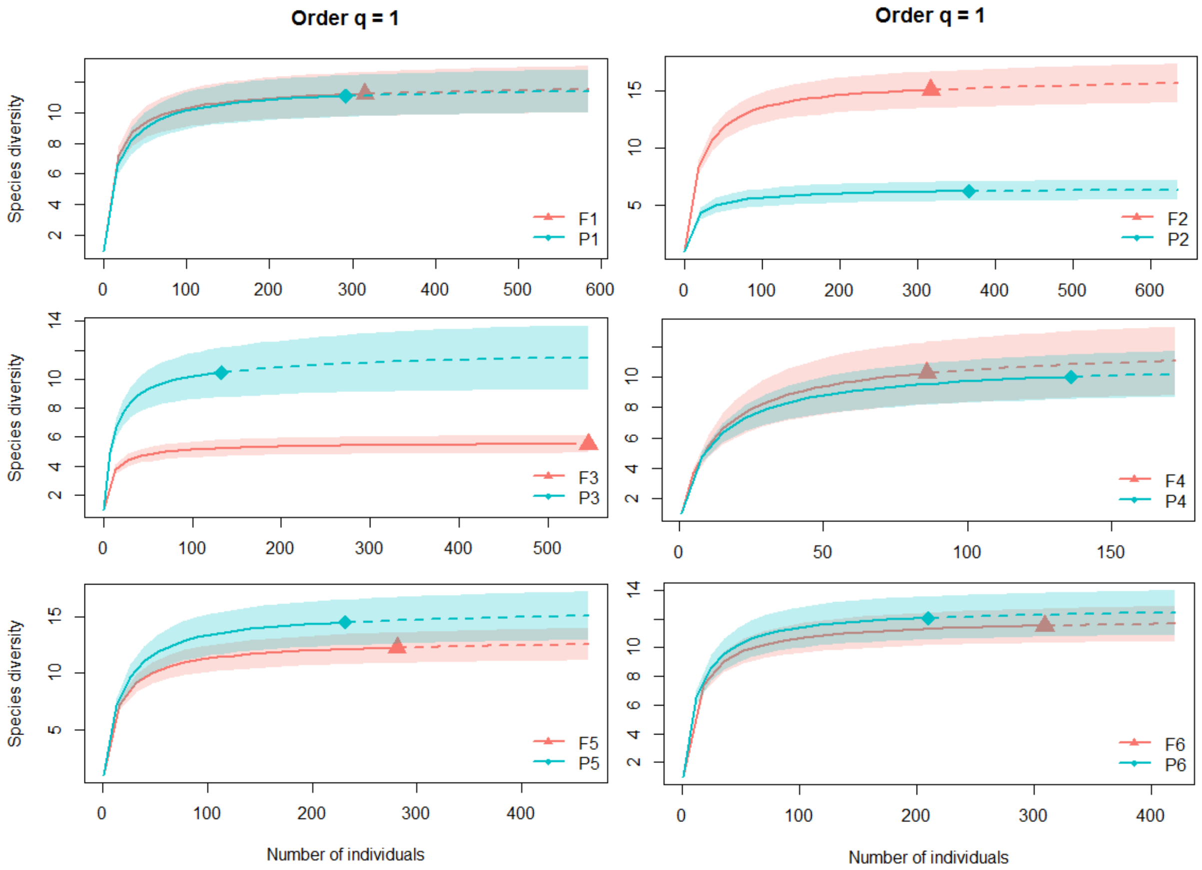


Fig. 4 Individual-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the sample size) of Dung beetles' diversity for Hill numbers (q = 1) for each site, where F represents native forests and P represents *Pinus* monocultures.

In Simpson's dominance analyses (q = 2) (abundant species) the areas of *Pinus* monocultures and native forest statistically had the same number of dominant species in four of the six sites from this study (Site 1, 4, 5 and 6). Site 2 presented more dominant species in the native forest habitat (F2 with 9.82 and P2 with 3.15) and Site 3 had more dominant species in the *Pinus* monocultures (F3 with 3.28 dominant species and P3 with 7.93) (**Fig. 5**).

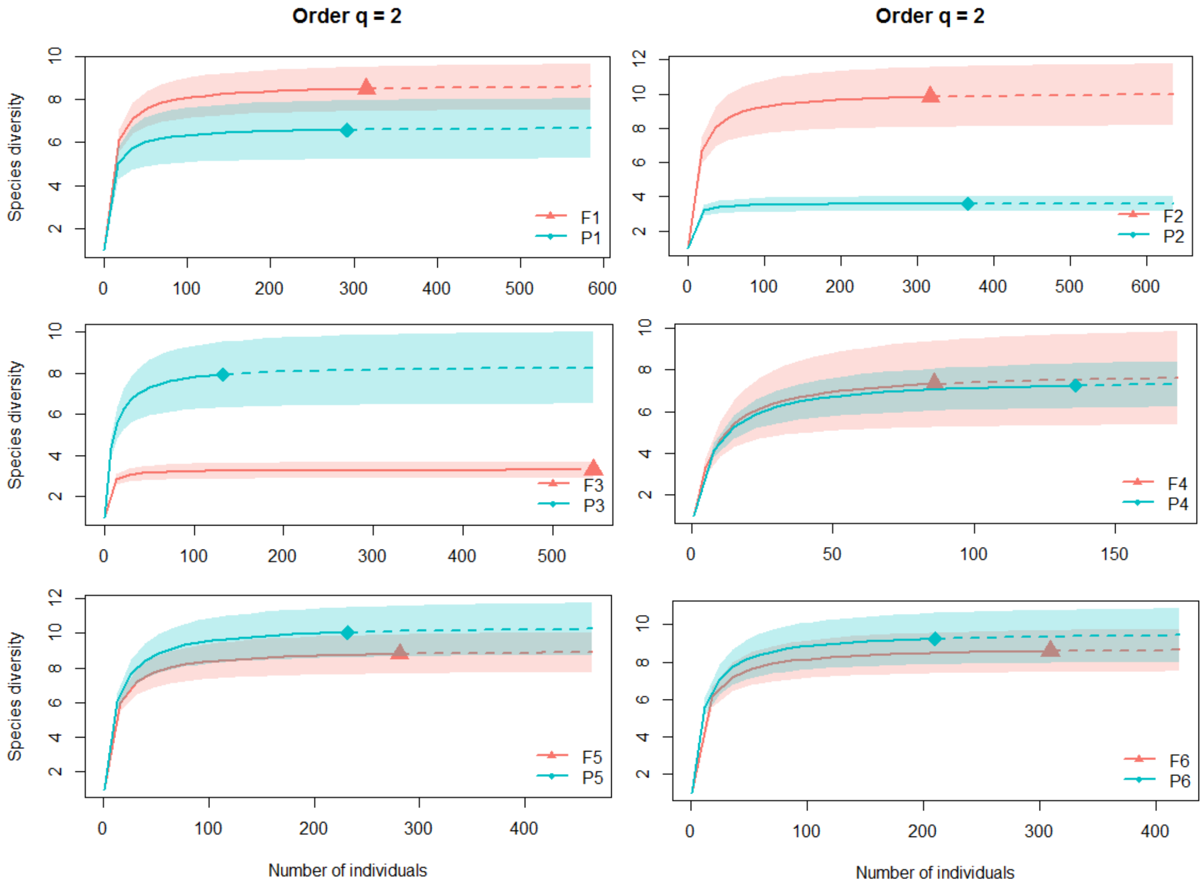


Fig. 5 Individual-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the sample size) of Dung beetles' diversity for Hill numbers (q = 2) for each site, where F represents native forests and P represents *Pinus* monocultures.

As opposed to diversity analysis, which shows the two habitats with similar richness, beta diversity was very high between them. The Bray-Curtis index of dissimilarity pointed out a greater difference between the communities that inhabit *Pinus* monocultures and native forests, varying between 47% and 72% of dissimilarity (**Table 2**). The partitioning of beta diversity showed that the dissimilarity due to balanced variation in abundance is higher in all areas (except in Site 3) showing that species composition and relative abundance of the communities in native forest areas are different from *Pinus* monocultures.

The dissimilarity did not vary according to the native forest and *Pinus* monocultures proximity, since both adjacent areas (Mean: 0.563, Sites 1, 2 and 3) and areas apart (Mean: 0.574, Sites 4, 5 and 6) had the same dissimilarity values, when compared using a t-test (t = 0.104, df = 3.99, p-value = 0.92).

Table 2 Bray-Curtis index (BC - index) and its balanced variation in abundance (BC - balanced) and abundance gradients (BC - gradient) components between native forest (F) and *Pinus* monocultures (P).

Dissimilarity	**Site 1** **F1 – P1**	**Site 2** **F2 - P2**	**Site 3** **F3 - P3**	**Site 4** **F4 - P4**	**Site 5** **F5 - P5**	**Site 6** **F6 - P6**
BC – balanced	0.452	0.476	0.241	0.64	0.461	0.367
BC – gradient	0.021	0.038	0.461	0.081	0.051	0.121
BC – index	0.473	0.514	0.702	0.721	0.513	0.487

The analysis of species contribution to beta diversity (SCBD) pointed out that 24 species are important contributors to beta diversity whether for just one site or more (**Table 3**). All SCBD values ranged between 0.035 to 0.299, and 14 species contributed above the overall mean (0.102) to beta diversity. The species that most contributed to beta diversity were *Eurysternus inflexus* and *Onthophagus tristis*, being more abundant in *Pinus* monocultures than in native forests, and *Canthidium* aff. *trinodosum* and *Paracanthon* aff. *rosinae* more abundant in native forest habitat (**Table 3)**. Reinforcing the multinomial classification analysis previously carried out (**Fig. 4**), all 11 species classified as specialists are present in the SCBD results. However, the SCBD analysis had 13 more species contributing to overall beta diversity, which were identified as generalists or too rare in the multinomial classification analysis.

Table 3 Species contributions to beta diversity (SCBD) and their values for degree of relative importance in affecting beta diversity patterns per site. HC or habitat contributor: habitats where the species had more overall abundance, P represents *Pinus* monocultures and F native forests.

Species	**HC**	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**
Eurysternus inflexus	P	0.061 P	0.299 P	0.115 P		0.099 P	0.042 F
Canthidium aff. *trinodosum*	F	0.073 F	0.108 F	0.138 F	0.052 F		
Onthophagus tristis	P	0.048 P			0.137 P	0.086 P	0.068 P
Paracanthon aff. *rosinae*	F		0.063 F	0.152 F		0.165 F	0.158 F
Dichotomius fissus	P		0.038 F	0.050 P			0.056 P
Canthidium sp.1	P					0.139 P	0.307 P
Canthidium sp.2	F/P		0.069 F	0.134 P			
Canthon angularis	F	0.068 F			0.110 F		
Coprophanaeus saphirinus	F		0.047 F				0.064 F
Dichotomius sericeus	F			0.101 F		0.180 F	
Phanaeus splendidulus	F	0.107 F		0.054 F			
Uroxys terminalis	F		0.076 F			0.100 F	
Ateuchus aff. *carbonarius*	P					0.044 P	
Canthon lividus seminitens	P				0.168 P		
Canthon luctuosus	F		0.057 F				
Canthon rutilans cyanescens	P	0.140 P					
Deltochilum brasiliensis	F						0.076 F
Deltochilum dentipes	P					0.043 P	
Deltochilum morbillosum	F				0.115 F		
Deltochilum multicolor	P				0.160 P		
Deltochilum rubripenne	P						0.067 P
Eurysternus parallelus	P	0.044 P					
Ontherus sulcator	P	0.035 P					
Uroxys sp.1	F	0.163 F					

Environmental influence in the metacommunities

As a result of camera trap records, we got 92 records of mammals belonging to 13 species (**Table 4**). Nine species were native, with few records, occurring mainly in native forests. Three exotic species showed a large occurrence in *Pinus* areas, demonstrating the large supply of food resources that these habitats offer to dung beetles. These are: *Bos taurus*, *Equus caballus* and *Canis lupus familiaris,* the first two considered to be of large size.

From the result obtained in the measurement of environmental variables, temperature, altitude and tree density assessment (calculated as the average distance between trees) were very similar between *Pinus* monoculture and native forests of each site (**Table 5**). In the shrubs density assessment, we got lower values of distance between shrubs in the native forests when compared to *Pinus* monocultures, showing greater density of shrubs in those areas (understory). Lastly, the green cover percentage of the soil varied widely between areas, without following any apparent pattern.

Table 4 Records of mammals species in six native forests (F) and six *Pinus* monocultures (P) areas in Santa Catarina State, south of Brazil in the summer of 2018/2019. Species marked with * are exotic.

Species	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Site 5**		**Site 6**		**Total**
	F1	**P1**	**F2**	**P2**	**F3**	**P3**	**F4**	**P4**	**F5**	**P5**	**F6**	**P6**	
*Bos taurus**	0	0	0	8	0	8	4	66	0	10	0	1	97
Cerdocyon thous	1	21	0	1	0	5	0	0	0	0	0	0	28
*Equus caballus**	0	0	0	0	0	0	0	21	0	0	0	0	21
*Canis lupus familiaris**	0	12	0	0	0	0	0	5	0	0	0	0	17
Nasua nasua	0	0	8	0	0	0	0	0	0	0	0	0	8
Dasypus novemcinctus	0	1	4	0	1	0	0	0	0	0	0	0	6
Dasypus sp.	0	0	0	0	2	0	0	0	2	0	0	0	4
Leopardus guttulus	0	0	1	0	0	1	0	0	2	0	0	0	4
Didelphis sp.	0	0	3	0	0	0	0	0	0	0	0	0	3
*Lepus europaeus**	0	0	0	0	0	0	0	0	0	1	0	0	1
Procyon cancrivorus	0	0	1	0	0	0	0	0	0	0	0	0	1
Guerlinguetus brasiliensis	0	0	0	0	0	1	0	0	0	0	0	0	1
Didelphis aurita	0	0	0	0	0	1	0	0	0	0	0	0	1
Abundance	**1**	**34**	**17**	**9**	**3**	**16**	**4**	**92**	**4**	**11**	**0**	**1**	**192**
Richness	**1**	**3**	**5**	**2**	**2**	**5**	**1**	**3**	**2**	**2**	**0**	**1**	

Table 5 Environmental characteristics in six native forests (F) and six *Pinus* monocultures (P) in Santa Catarina State, south of Brazil. Trees: trees density assessment; Shrubs: shrubs density assessment; Herbs: green cover percentage, TH: average height of trees; SH: average height of shrubs; Temperature: soil average temperature; Altitude: average altitude of the sampled areas.

Environmental Survey	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Site 5**		**Site 6**	
	F1	**P1**	**F2**	**P2**	**F3**	**P3**	**F4**	**P4**	**F5**	**P5**	**F6**	**P6**
Trees (m)	2.0	2.5	2.2	2.3	1.5	1.6	1.8	1.8	2.0	2.4	2.3	2.1
Shrubs (m)	5.6	9.4	1.4	3.1	1.3	6.5	1.4	20.2	1.4	5.0	2.0	9.9
Herbs (%)	60.6	31.5	31.2	47.5	43.1	33.1	35.0	17.5	29.4	46.9	16.2	10.0
TH (m)	12.4	13.7	9.7	23.2	7.4	11.0	7.6	9.3	8.2	15.0	9.0	15.0
SH (m)	1.5	1.1	1.6	1.8	2.1	1.1	1.8	1.0	2.0	1.6	1.9	2.3
Temperature (ºC)	18.9	19.2	20.0	20.1	20.0	20.2	18.6	19.1	19.3	19.4	19.9	19.9
Altitude (m a.s.l.)	779.5	782.0	704.5	627.0	637.5	640	948.5	935.5	740.0	748.0	720.0	666.0

In the overall SEM model, none of the environmental factors has a significant effect on dung beetle richness, but several influence dung beetle abundances (**Fig. 6**). The variables habitat type, temperature, vegetation structure (trees and herbs) and resource amount have a positive influence upon the abundance of dung beetles. Temperature, which had the major relationship with dung beetles' abundance, with a strong positive influence, had also a negative relation with resource amount. Vegetation and mammal richness also influenced the amount of resources, but in a positive way.

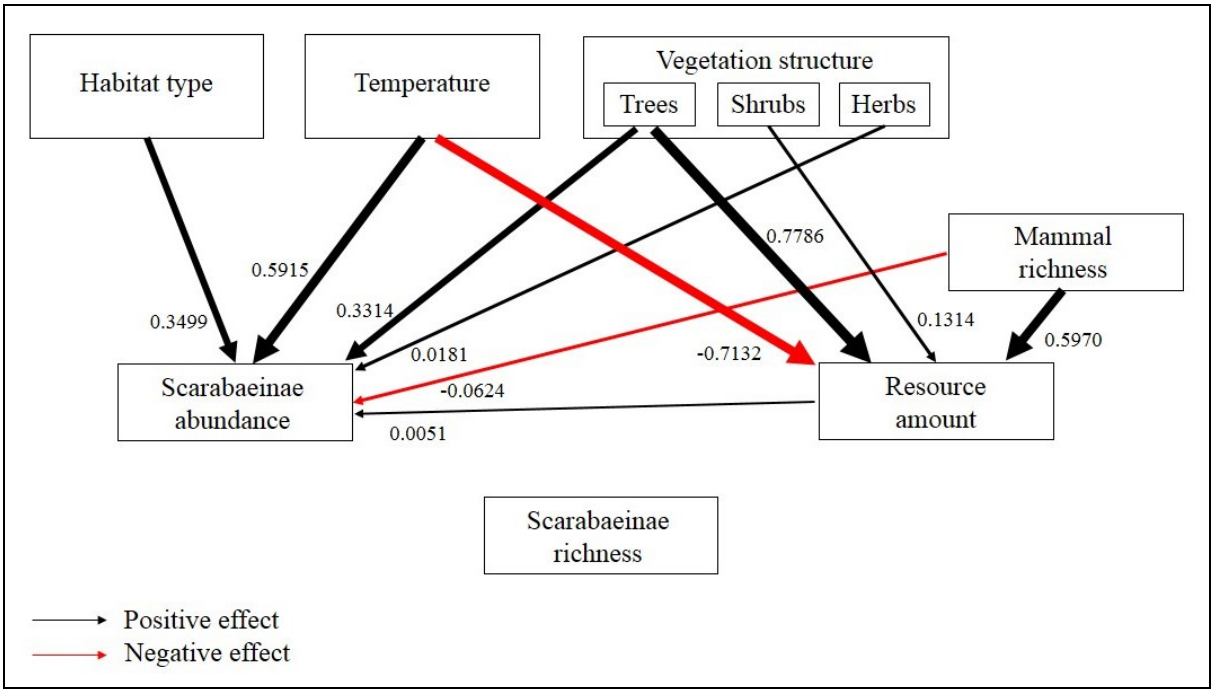


Fig. 6 Structural equation model for dung beetle richness and abundance. The arrows indicate the significant influence of environmental factors and resources (with their respective coefficients) on dung beetle abundance. Black arrows denote positive relationships and red arrows denote negative relationships.

DISCUSSION

The results from the marking-recapture experiment show a species sorting effect in dung beetle metacommunities, in which niche has more influence than dispersal, with low movement rates. We observed some movement of individuals between the habitats, but most dispersion were inside the same habitat, showing that dung beetle dispersal was not sufficient to expand strongly their distributions, but was enough for the individuals to track the alternative resources present in the *Pinus* monocultures. Although we have a low rate of individuals' recaptures, the recapture rate was similar to results presented in other studies (ARELLANO, 2008; NORIEGA, 2011; DA SILVA & HERNÁNDEZ, 2015). In addition to the dispersal between areas, the species found inside the nesting houses were effectively using the habitats, since we registered the presence of feeding balls and tunnels in the interior of those traps in both habitats (*Pinus* monocultures and native forest).

The transit of dung beetles between one habitat and the other shows that they move through areas of *Pinus* monocultures and native forest, having interaction and connectivity between those communities. We can state that the coexistence of species within a regional level occurred due to the niche differentiation between them causing high beta diversity (LEIBOLD et al., 2004), differences that were not pointed out by richness and diversity indices. The species richness and diversity of dung beetles had close values in both *Pinus* monocultures and native forest habitats. A study in areas close to those of the present work, related to dung beetle's taxonomic and functional diversity among native forests and altered subtropical habitats, also showed that forests and *Pinus* monocultures have similar richness values, different from open habitats (fields), which presented great decrease of species richness and individuals abundance (SARMIENTO-GARCÉS & HERNÁNDEZ, 2021). These results contrast with the severe decline in biodiversity observed in other studies areas that suffered higher alteration levels (NICHOLS et al., 2007).

Then, considering species abundance and richness, as shown in the analysis of extrapolation curves, it is not possible to observe significant differences between communities of different habitats, not being a reliable and sufficient approach. Moreover, even in cases where these measures serve the purpose of assessing changing patterns of diversity, they remain limited in describing which species are lost and how this loss can alter ecosystem dynamics (CARDINALE *et al.*, 2007). That's because the purpose of ecological indicators should be to provide reliable and interpretable information on the ecological consequences of human activities for a measured component of biodiversity (NICHOLS & GARDNER, 2011). In the diversity partitioning analysis, we are able to see that there are in fact differences in both communities, which are mainly due to the species variation in abundance. Considering the Bray-Curtis index analysis we see that part of the dissimilarity between the areas of *Pinus* monocultures and native forests is due to the abundance of some species, which prefer one or another habitat. This occurs because of the balance or shift of species between the areas. The composition of the communities is similar to a certain point, where some species become more specific to forest areas and others more linked to *Pinus* monocultures sites. These species, presented in the multinominal classification analyzes as habitat-specific, are few when compared to the ones considered generalists or too rare to be classified.

Furthermore, the structural equation models showed no influence of environmental factors or even of resource availability on dung beetle richness, with very close averages among habitats. On the other hand, many factors like habitat type, temperature, vegetation structure (trees and herbs) and resource amount had positive influence on dung beetle abundance, with more emphasis on temperature. Then, we can see features that are important for the maintenance of the dung beetles, such as proper temperature and presence of resources. It is interesting to reflect on the presence of exotic animals, such as cattle, horses and dogs, which greatly contributed to the occurrence and richness of mammals, especially in the *Pinus* monocultures. These domestic animals can have a major effect on dung beetles communities, being an alternative as a potential source of resources, reflecting the amount of resource in altered habitats. In this way, dung beetle community in the *Pinus* monocultures areas is affected by the mammal composition found there, jointly with the habitat structure and spatial distance (BARLOW *et al*., 2010; BOGONI *et al*., 2016).

The presence of exotic domestic mammal species mainly in monoculture areas reaffirms the anthropization of these areas. In addition, among all species recorded, two are large, contributing even more to the supply of resources (*Bos taurus* and *Equus caballus*). Although, it has been shown in several studies that there is a positive relationship between dung beetles and richness of omnivorous mammals, where the majority of the individuals being attracted by the feces of mammals from this trophic group (ESTRADA *et al*., 1993; FILGUEIRAS *et al*., 2009, BOGONI *et al*., 2016). We took the opportunity to reflect on the limitations we found when analyzing and calculating the amount of resources available because we know that the size of identified mammals is not standard, with species of large, medium and small size. Other points that was not included are the different trophic groups of mammals present in the areas (herbivores, carnivores and omnivores), as well as necrophagous dung beetles preference for arthropod carcasses (BOGONI *et al.*, 2016; GIMENÉZ GÓMEZ *et al*., 2020).

Some studies suggests that very few forest dung beetles can extend their activity into strongly altered forests or natural open habitats (NUMMELIN & HANSKI, 1989; HALFFTER & ARELLANO, 2002; GARDNER *et al*., 2008; GRIES & LOUZADA, 2011), but our results suggest that *Pinus* monocultures provide habitat for forest dung beetles. Canopy openness is an influential variable structuring dung beetle community, both across all habitats and within plantation types (HERNÁNDEZ & VAZ-DE-MELO, 2009; BARLOW *et al.*, 2010; GARDNER *et al.*, 2011; DA SILVA *et al.*, 2016). Canopy cover can influence both humidity and soil surface temperature, which might affect the survival and reproduction of dung beetles, as well as food availability and attractiveness (GRIES & LOUZADA, 2011). Thus, the conservation of either native or exotic canopy can determinate whether highly diverse dung beetle assemblages and their ecological functions are preserved or not (GIMÉNEZ GÓMEZ *et al*., 2018).

We remember the risk that *Pinus* monocultures pose to biodiversity in Brazil, who has more than seven million hectares in homogeneous reforestation, with *Pinus* being one of the most representative in the southern region of the country (ANUÁRIO ESTATÍSTICO DE BASE FLORESTAL PARA O ESTADO DE SANTA CATARINA, 2019). In addition to being exotic, the species has a high invasive potential, being well documented across the planet (RICHARDSON, 2006). In addition, some of its features, such as short juvenile period and numerous small winged seeds, which characterize them as pioneers in their native range, are also responsible for their invasiveness (RICHARDSON, 2006; REJMÁNEK, 1996). This way, *Pinus* trees are able to bring severe impacts on the local biota and ecosystem processes such as changes in water and fire regimes (SIMBERLOFF *et al.*, 2010).

CONCLUSION

Through this work, we were able to observe the lack of indication of the approach of dung beetles richness and diversity in *Pinus* monocultures and native forest, and to reflect about the need to complement the method with other composition analysis when using dung beetles as ecological indicators. This is due the differences in the composition of the communities (species that prefer different types of habitats) being demonstrated only when we calculate beta diversity. We must consider that when using dung beetles as ecological indicators, since we found similar indices in very different areas in terms of biodiversity. Thus, our results demonstrate that the use of species richness and diversity indices alone may not show real differences between communities in areas with distinct habitats, not reflecting the real environmental quality of the sites. Therefore, we must take in account the differences in species composition of the communities between habitats. In this case, analyses like the ones of dissimilarity, SCBD and multinomial classification complement each other, contributing to better understanding the dung beetle metacommunities. Still according to these results, our structural model overall SEM shows that dung beetle richness in both types of habitats is not influenced by environmental factors, although dung beetle abundance is. We also conclude that there is no relation between composition and abundance of dung beetle communities in monocultures to the distance of the native forest areas. However, the presence of native forests and other habitats very likely provides individuals to the *Pinus* monocultures. These monocultures, on the other hand, have characteristics similar to the native forests, such as temperature, humidity, canopy cover and alternative food resources, which allow the permanence of the beetles. We also emphasize that even though the *Pinus* monocultures allow the permanence of dung beetle communities with richness similar to those found in areas of native forests, we should take on consideration the invasive potential of this exotic species and the inhibitory effect on native plants, as well as other possible negative impacts on animal species in the region. Also, the high availability of food resources in *Pinus* monoculture areas with the presence of domestic animals is not an exclusive feature of all monocultures. The monocultures areas in this study belong to small farmers, with some presence of shrubs of other plant species (understory) and are used for purposes other than logging (such as resin extraction, cattle raising). Thus, we can consider that other *Pinus* monoculture areas, which are larger, more isolated and aimed only in the use of logging, with high plantation turnover, can provide a much less suitable environment for dung beetles. In this case, most likely, the richness and diversity indexes would be more effective.

ACKNOWLEDGMENTS

We are grateful to the farmers and landowners for allowing the entry in their areas for the fieldwork. We thank the members of Laboratório de Ecologia Terrestre e Animal for help and support, Dr. Fernando Vaz-de-Mello (UFMT) for confirming dung beetle identifications and Dr. Maurício Graipel (UFSC) for help with mammals' identifications. We also thank the financial support of the Programa de Pós Graduação em Ecologia (POSECO/UFSC), the Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina (FAPESC) for the scholarship awarded to TROSC and the Conselho Nacional de Desenvolvimento Científico e Tecnológico, Ministério da Ciência, Tecnologia e Inovação, Brazil (CNPq) for a Productivity Grant awarded to MIMH (Process: 307437/2017-5).

REFERENCES

ANUÁRIO ESTATÍSTICO DE BASE FLORESTAL PARA O ESTADO DE SANTA CATARINA. Lages, 3ª edição, p. 28-34, 2019.

AUDINO, L. D.; LOUZADA, J.; COMITA, L. Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity? **Biological Conservation,** v. 169, p. 248-257, 2014.

ANDRESEN, E. Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. **Biotropica**, v. 37, p. 291-300, 2005.

ANDRESEN, E. & LAURANCE, S. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. **Biotropica**, v. 39, p. 141-146, 2007.

ARELLANO, L. & HALFFTER, G. Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. **Acta Zoológica Mexicana**, v. 90, p. 27-76, 2003.

ARELLANO, L.; LEÓN-CORTÉS, J. L.; OVASKAINEN, O. Patterns of abundance and movement in relation to landscape structure: a study of a common scarab (*Canthon cyanellus cyanellus*) in Southern Mexico. **Landscape Ecology**, v. 23, p. 69-78, 2008.

BARLOW, J.; LOUZADA, J.; PARRY, L.; HERNÁNDEZ, M. I. M.; HAWES, J.; PERES, C. A.; HAWES, J.; PERES, C. A.; VAZ-DE-MELLO, F. Z.; GARDNER, T. A. Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. **Journal of Applied Ecology**, v. 47, p. 779-788, 2010.

BASELGA, A. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. **Methods in Ecology and Evolution**, v. 4, p. 552-557, 2013. DOI: 10.1111/2041-210X.12029.

BATILANI-FILHO, M. & HERNÁNDEZ, M. I. M. Decline of ecological functions performed by dung beetles in areas of Atlantic Forest and contribution of rollers and tunnellers in organic matter removal. **Environmental Entomology**, v. 46, n. 4, p. 784-793, Aug. 2017. DOI: 10.1093/ee/nvx091.

BRAGA, R. F.; KORASAKI, V.; AUDINO, L. D.; LOUZADA, J. Are dung beetles driving dung-fly abundance in traditional agricultural areas in the Amazon? **Ecosystems**, v. 15, p. 1173-1181, 2012.

BREWER, J. Patterns of plant species richness in a wet slash-pine (*Pinus elliottii*) savanna. **The Journal of the Torrey Botanical Society**, v. 125, p. 216-224, 1998.

BOGONI, J. A.; GRAIPEL, M. E.; DE CASTILHO, P. V.; FANTACINI, F. M.; KUHNEN, V. V.; LUIZ, M. R.; MACCARINI, T. B.; MARCON, C. B.; DE SOUZA PIMENTEL TEIXEIRA, C.; TORTATO, M. A.; VAZ-DE-MELLO, F. Z.; HERNÁNDEZ, M. I. M. Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. **Biodiversity and Conservation**, v. 25, p. 1661-1675, May 2016. DOI: 10.1007/s10531-016-1147-1

BUCKLEY, Y. M.; BROCKERHOFF, E.; LANGER, L.; LEDGARD, N.; NORTH, H.; REES, M. Slowing down a pine invasion despite uncertainty in demography and dispersal. **Journal of Applied Ecology**, v. 42, p. 1020-1030, 2005.

BUSTAMANTE-SÁNCHEZ, M. A.; GREZ, A. A.; SIMONETTI, J. Descomposición de heces y sus coleópteros asociados en un bosque templado fragmentado. **Revista Chilena de Historia Natural**, v. 77, p. 107-120, 2004.

CAMPOS, R. & HERNÁNDEZ, M. I. M. The Importance of Maize Management on Dung Beetle Communities in Atlantic Forest Fragments. **PLOS ONE**, v. 10, 2015.

CHAO, A.; GOTELLI, N. J.; HSIEH, T. C.; SANDER, E. L.; MA, K. H.; COLWELL, R. K.; ELLISON, A. M. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. **Ecological Monographs**, v. 84, p. 45-67, 2014.

CHASE, J. M.; JELIAZKOV, A.; LADOUCEUR, E.; VIANA, D. S. Biodiversity conservation through the lens of metacommunity ecology. **Annals of the New York Academy of Sciences**, v. 1469, n. 1, p. 86-104, 2020.

CHAZDON, R. L.; CHAO, A.; COLWELL, R. K.; LIN, S.; NORDEN, N.; LETCHER, S. G.; CLARK, D. B.; FINEGAN, B.; ARROYO, J. B. A novel statistical method for classifying habitat generalists and specialists. **Ecology**, v. 92, n. 6, p. 1332-1343, 2011.

COTTAM, G. & CURTIS, J. T. The use of distance measures in phytosociological sampling. **Ecology**, v. 37, n. 3, p. 451-460, 1956.

DA SILVA, P. G.; VAZ-DE-MELLO, F. Z.; DI MARE, R. A. Diversity and seasonality of Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in Santa Maria, Rio Grande do Sul, Brazil. **Anais da Academia Brasileira de Ciências**, v. 85, p. 679-697, 2013.

DA SILVA, P. G. & HERNÁNDEZ, M. I. M. Spatial variation of dung beetle assemblages associated with forest structure in remnants of southern Brazilian Atlantic Forest. **Revista Brasileira de Entomologia**, v. 60, p. 73-81, 2016. DOI: 10.1016/j.rbe.2015.11.001.

DA SILVA, P. G. & HERNÁNDEZ, M. I. M. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. **PLoS ONE**, v. 10, n. 5, p. 1-18, 2015. DOI: 10.1371/journal.pone.0126112

DA SILVA, P.; LOBO, J.; HENSEN, M.; VAZ-DE-MELLO, F.; HERNÁNDEZ, M. I. M. Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. **Diversity and Distributions**, v. 24, p. 1277-1290, 2018.

DAVIS, A. J. & SUTTON, S. L. The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. **Diversity and Distributions**, v. 4, p. 167-173, 1998.

DAVIS, A. L. V.; SCHOLTZ, C. H.; PHILIPS, T. K. Historical biogeography of Scarabaeinae dung beetle. **Journal of Biogeography**, v. 29, n. 9, p. 1217-1256, 2002.

DAVIS, A.; HOLLOWAY, J.; HUIJBREGTS, H.; KRIKKEN, J.; KIRK-SPRIGGS, A.; SUTTON, S. Dung beetles as indicators of change in the forest of northern Borneo. **Journal of Applied Ecology**, v. 38, p. 593-616, 2001.

DAVIS, A. L. V.; SCHOLTZ, C. H.; DOOLEY, P. W.; BHAM, N.; KRYGER, U. Scarabaeine dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. **South African Journal of Science**, v. 100, p. 415-424, September/October 2004.

DRISCOLL, D. A. & WEIR, T. Beetle response to habitat fragmentation depends on ecological traits, habitat conditions and remnant size. **Conservation Biology**, v. 19, p. 182-194, 2005.

ESSL, F.; MANG, T.; DULLINGER, S.; MOSER, D.; HULME, P. Macroecological drivers of alien conifer naturalizations worldwide. **Ecography**, v. 34, p. 1076-1084, 2011.

ESTRADA, A.; ANZURES, A. D.; COATES-ESTRADA, R. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*) and dung beetles at Los Tuxtlas, Mexico. **American Journal of Primatology**, v. 48, n. 4, p. 253-262, 1999.

FEER, F. Variations in dung beetles assemblages (Coleoptera: Scarabaeidae) within two rain forest habitats in French Guiana. **Revista de Biologia Tropical**, v. 61, n. 2, p. 753-768, 2013.

FRANK, K.; KRELL, F. -T.; SLADE, E. M.; RAINE, E. H.; CHIEW, L. Y.; SCHMITT, T.; VAIRAPPAN, C. S.; WALTER, P.; BLÜTHGEN, N. Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient. **Ecology Letters**, v. 21, n. 8, p. 1229-1236, 2018.

GARDNER, T. A.; HERNÁNDEZ, M. I. M.; BARLOW, J.; PERES, C. A. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. **Journal of Applied Ecology**, v. 45, n. 3, p. 883-893, 2008.

GIMÉNEZ GÓMEZ, V. C.; VERDÚ, J. R.; VAZ-DE-MELLO, F. Z.; ZURITA, G. A. Influence of land use on the trophic niche overlap of dung beetles in the semideciduous Atlantic forest of Argentina. **Insect Conservation and Diversity**, v. 11, p. 554-564, 2018.

GIMÉNEZ GOMÉZ, V. C.; VERDÚ, J. R.; VELAZCO, S.; ZURITA, G. A. Dung beetle trophic ecology: are we misunderstanding resources attraction? **Ecological Entomology:** v. 46, n. 3, 2020.

GÓMEZ-CIFUENTES, A.; MUNEVA, A.; GIMÉNEZ, V. C.; GATTI, M. G.; ZURITA, G. A. Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina. **Journal of Insect Conservation**, v. 21, n. 1, p. 147-156, 2017.

GRACE, J. B. **Structural equation modeling and natural systems.** England: Cambridge University Press, 2006.

GRIES, R.; LOUZADA, J.; ALMEIDA, S.; MACEDO, R.; BARLOW, J. Evaluating the impacts and conservation value of exotic and native tree afforestation in Cerrado grasslands using dung beetles. **Insect Conservation and Diversity**, v. 5, n. 3, p. 175-185, 2011.

GUNDALE, M. J., PAUCHARD, A., LANGDON, B., PELTZER, D. A.; MAXWELL, B. D.; NUÑEZ, M. A. Can model species be used to advance the field of invasion ecology? **Biological Invasions**, v. 16, n. 3, p. 591-607, 2014.

HALFFTER, G. & ARELLANO, L. Response of dung beetle diversity to human-induced changes in a tropical landscape. **Biotropica**, v. 34, p. 144-154, 2002.

HALFFTER, G. & FAVILA, M. E. The Scarabaeinae an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. **Biology International**, v. 27, p. 15-21, 1993.

HALFFTER, G. & MATTHEWS, E. G. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). **Folia Entomológica Mexicana**, n. 12/14, p. 1-312, 1966.

HANSKI, I. & CAMBEFORT, Y. **Dung beetle ecology**. Princeton: Princeton University Press, 1991.

HEINO, J.; MELO, A. S.; BINI, L. M. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. **Freshwater Biology**, v. 60, n. 2, p. 223-235, 2015.

HERNÁNDEZ, M. I. M. & VAZ-DE-MELLO, F. Z. Seasonal and spatial species richness variation of dung beetle (Coleoptera, Scarabaeidae *s. str.*) in the Atlantic Forest of southeastern Brazil. **Revista Brasileira de Entomologia**, v. 53, n. 4, p. 607-613, 2009.

HERNÁNDEZ, M. I. M.; BARRETO, P. S. C. S.; COSTA, V. H.; CREÃO-DUARTE, A. J.; FAVILA, M. E. Response of a dung beetle assemblage along a reforestation gradient in Restinga forest. **Journal of Insect Conservation**, v. 18, p. 539-546, 2014. DOI: 10.1007/s10841-014-9645-5

HERNÁNDEZ, M. I. M.; DA SILVA, P. G.; NIERO, M. M.; ALVES, V. M.; BOGONI, J. A.; BRANDL, A. L.; BUGONI, A.; CAMPOS, R. C.; CONDÉ, P. A.; MARCON, C. B.; SIMÕES-CLIVATTI, T. R. O.; TERHORST, L. H.; VAZ-DE-MELLO, F. Z. Ecological characteristics of Atlantic Forest dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in the State of Santa Catarina, Southern Brazil. **The Coleopterists Bulletin**, v. 73, n. 3, p. 693-709, 2019.

HOWDEN, H. F. & NEALIS, V. G. Effects of clearing in a tropical rain forest on the composition of the coprophagous Scarab beetle fauna (Coleoptera). **Biotropica**, v.7, p. 77-83, 1975.

HSIEH, T. C.; MA, K. H.; CHAO, A.; MCINERNY, G. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). **Methods in Ecology and Evolution**, v. 7, p. 1451-1456, 2016.
KLEIN, B. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. **Ecology**, v. 70, p. 1715-1725, 1989.

LEDGARD, N. The spread of lodgepole pine (*Pinus contorta* Dougl.) in New Zealand. **Forest Ecology and Management** v. 141, p. 43-57, 2001.

LEGENDRE, P. & DE CÁCERES, M. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. **Ecology Letters**, v. 16, p. 951-963, 2013. DOI: 10.1111/ele.12141

LEIBOLD, M. A.; HOLYOAK, M.; MOUQUET, N.; AMARASEKARE, P.; CHASE, J. M.; HOOPES, M. F.; HOLT, R. D.; SHURIN, J. B.; LAW, R.; TILMAN, D. & LOREAU, M. The metacommunity concept: a framework for multi-scale community ecology. **Ecology Letters**, v. 7, n. 7, p. 601-613, 2004.

MCGEOCH, M. A.; RENSBURG, B. J.; BOTES, A. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. **Journal of Applied Ecology**, v. 39, p. 661-672, 2002.

NICHOLS, E.; LARSEN, T.; SPECTOR, S.; DAVIS, A. L.; ESCOBAR, F.; DAVILA, M.; VULINEC, K.; THE SCARABAEINAE RESEARCH NETWORK. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. **Biological Conservation**, v. 137, p. 1-19, 2007.

NICHOLS, E; SPECTOR, S.; LOUZADA, J.; LARSEN, T.; AMEZQUITA, S.; FAVILA, M. E. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. **Biological Conservation**, v. 141, p. 1461-1474, 2008.

NICHOLS, E.; GARDNER, T. A.; PERES, C. A.; SPECTOR, S. Co-declining mammals and dung beetles: an impending ecological cascade. **Oikos**, v. 118, p. 481-487, 2009.

NICHOLS, E. & GARDNER, T. A. Dung beetles as a candidate study taxon in applied biodiversity conservation research. In: SIMMONS, L. W. & RIDSDILL-SMITH, T. J. (Eds.). **Ecology and Evolution of Dung Beetles**. Oxford: Wiley-Blackwell, 2011. p. 267-291.

NICHOLS, E.; URIARTE, M.; BUNKER, D. E.; FAVILA, M. E.; SLADE, E. M.; VULINEC, K.; LARSEN, T.; VAZ-DE-MELLO, F. Z.; LOUZADA, J.; NAEEM, S.; SPECTOR, S. H. Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. **Ecology**, v. 94, p. 180-189, 2013.

NORIEGA, J. A. & ACOSTA, A. Population size and dispersal of *Sulcophanaeus leander* (Coleoptera: Scarabaeidae) on riverine beaches in the Amazonian region. **Journal of Tropical Ecology**, v. 27, p. 111-114, 2011.

NUMMELIN, M. & HANSKI, I. Dung beetles of the Kibale Forest, Uganda: comparison between virgin and managed forests. **Journal of Tropical Ecology**, v. 5, p. 349-352, 1989.

OKSANEN, J.; BLANCHET, F. G.; FRIENDLY, M.; KINDT, R.; LEGENDRE, P.; MCGLINN, D.; MINCHIN, P. R.; O'HARA, R. B.; SIMPSON, G. L; SOLYMOS, P.; STEVENS, M. H. H.; SZOECS, E.; WAGNER, H. **vegan**: Community Ecology Package. R package version 2.5-7, 2020. https://CRAN.R-project.org/package=vegan

PECK, S. B. & FORSYTH, A. Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera; Scarabaeidae). **Canadian Journal of Zoology**, v. 60, p. 1624-1634, 1982.

PEEL, M. C.; FINLAYSON, B. L.; MCMAHON, T. A. Updated world map of the Köppen-Geiger climate classification. **Hydrology and earth system sciences discussions**, v. 4, p. 439-473, 2007.

R CORE TEAM. **R: A language and environment for statistical computing.** R Foundation for Statistical Computing, Vienna, Austria, 2020. https://www.R-project.org/

REJMÁNEK, M. & RICHARDSON, D. M. What attributes make some plant species more invasive? **Ecology**, v. 77, p. 1655-1661, 1996.

REJMÁNEK, M. A theory of seed plant invasiveness: the first sketch. **Biological Conservation**, v. 78, p. 171-181, 1996.

RICHARDSON, D. M. Pinus: a model group for unlocking the secrets of alien plant invasions? **Preslia**, v. 78, p. 375-388, 2006.

ROSLIN, T. & VILJANEN, H. Dung beetle populations: structure and consequences. In: SIMMONS, L. W. & RIDSDILL-SMITH, T. J. (Eds.). **Ecology and Evolution of Dung Beetles**. Oxford: Wiley-Blackwell, 2011. p. 221-244.

SARMIENTO-GARCÉS, R.; HERNÁNDEZ, M. I. M. A decrease in taxonomic and functional diversity of dung beetles impacts the ecosystem function of manure removal in altered subtropical habitats. **PLoS One**, v. 16, n. 1, e0244783, Jan. 2021. DOI: 10.1371/journal.pone.0244783.

SCHOLTZ, C. H.; DAVIS, A. L. V.; KRYGER, U. **Evolutionary biology and conservation of dung beetles**. Moscow: Pensoft Publishers, 2009.

SHIPLEY, B. **Cause and correlation in biology**: a user's guide to path analysis, structural equations and causal inference with R 2nd edition (2nd edition, Vol. 314). England: Oxford University Press, 2016.

SIMBERLOFF, D.; NUÑEZ, M. A.; LEDGARD, N. J.; PAUCHARD, A.; RICHARDSON, D. M.; SARASOLA, M.; VAN WILGEN, B. W.; ZALBA, S. M.; ZENNI, R. D.; BUSTAMANTE, R.; PEÑA, E.; ZILLER, S. R. Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. **Austral Ecology**, v. 35, p. 489-504, 2010.

SIMMONS, L. W.; RIDSDILL-SMITH, T. J. **Ecology and Evolution of Dung Beetles**. Oxford: Wiley-Blackwell, 2011.

WUERGES, M. & HERNÁNDEZ, M. I. M. Marking dung beetles (Coleoptera: Scarabaeidae): Retrospective and a reliable "scarification" method**. The Coleopterists Bulletin**, v. 74, n. 1, p. 168-171, 2020.

CONCLUSÕES GERAIS

Este trabalho nos possibilitou refletir sobre a influência das monoculturas de *Pinus* nas metacomunidades de besouros escarabeíneos, pensando no potencial invasor da espécie e o efeito inibitório sobre outras espécies vegetais nativas, bem como seus possíveis impactos negativos às demais espécies animais da região. Foi possível demonstrar que os besouros escarabeíneos utilizam os ambientes de monocultura de *Pinus* e de mata nativa, levantando questionamentos sobre o fato destes besouros serem considerados bons indicadores ecológicos. Entretanto, isto ocorre devido a presença de recursos alternativos para os rola-bostas, com a presença de animais domésticos, como também devido ao processo de dispersão entre os diferentes habitats. Pontuamos aqui a importância de utilizar diferentes abordagens ao se trabalhar com estes besouros e a não utilizar somente índices de riqueza e diversidade de espécies, pois estes podem não apontar diferenças reais entre comunidades, não refletindo a qualidade ambiental dos habitats. Concluímos também que a composição e abundância da comunidade de besouros escarabeíneos nas monoculturas não está relacionada diretamente com a distância das áreas de mata nativa. Entretanto, a presença das matas nativas muito provavelmente provê indivíduos às áreas de monocultura de *Pinus*, reforçando a importância do manejo correto das monoculturas e da preservação dos fragmentos de matas nativas e seus corredores ecológicos.

REFERÊNCIAS

AGUIAR, A. V.; SOUSA, V. A.; SHIMIZU, J. Y. **Cultivo de *Pinus*.** Embrapa Florestas, Sistemas de Produção, 2 ª edição, 2011.

ARELLANO, L.; LEÓN-CORTES, J. L.; OVASKAINEN, O. Patterns of abundance and movement in relation to landscape structure: a study of a common scarab (*Canthon cyanellus cyanellus*) in Southern Mexico. **Landscape Ecology**, v. 23, p. 69-78, 2008.

BEGON, M.; TOWNSEND, C. R. & HARPER, J. **Ecologia: de Indivíduos a Ecossistemas.** Oxford: Blackwell, 2006.

CÓRDOVA, M.; CHAVES, C. L.; MANFREDI-COIMBRA, S. Fauna do solo x vegetação: estudo comparativo da diversidade edáfica em áreas de vegetação nativa e povoamentos de *Pinus sp.* **Revista Eletrônica do Curso de Geografia**, Jataí, n. 12, p. 1-12, 2009.

DA SILVA, P. G. & HERNÁNDEZ, M. I. M. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. **PLoS ONE**, v. 10, n. 5, e0126112, 2015. DOI:10.1371/journal.pone.0126112

DICK, D. P.; DALMOLIN, R. S. D.; LEITE, S. B. Impacto da introdução de *Pinus* nas características químicas e na composição da matéria orgânica de neossolos de campos de cima da serra, RS. In: Anais Congresso Brasileiro de Ciência do Solo, Gramado, 2007.

DRISCOLL, D. A. & WEIR, T. Beetle response to habitat fragmentation depends on ecological traits, habitat conditions and remnant size. **Conservation Biology**, v. 19, p. 182-194, 2005.

DURÃES, R.; MARTINS, W. P.; VAZ-DE-MELLO, F. Z. Dung beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-Cerrado ecotone in Minas Gerais, Brazil. **Neotropical Entomology**, v. 34, n. 5, p. 721-731, 2005.

FORMAN, R. T. T. & GODRON, M. **Landscape Ecology**. New York: Wiley & Sons, 1986.

FRANKLIN, J. F. Preserving biodiversity: species, ecosystems, or landscapes? **Ecological Applications**, v. 3, p. 202-205, 1993.

GARDNER, T. A.; HERNÁNDEZ, M. I. M.; BARLOW, J.; PERES, C. A. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. **Journal of Applied Ecology**, v. 45, n. 3, p. 883-893, 2008.

GRAÇA, M. A. S.; POZO, J.; CANHOTO, C.; ELOSEGI, A. Effects of Eucalyptus plantations on detritus, decomposers, and detritivores in streams. **Science World Journal**, v. 2, n. 4, p.1173-1185, 2002.

HALFFTER, G. & EDMONDS, W. D. The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutive approach. **Journal of the New York Entomological Society**, v. 91, p. 512-515, 1982.

HALFFTER, G. & FAVILA, M. E. The Scarabaeinae an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. **Biology International**, v. 27, p. 15-21, 1993.

HALFFTER, G. & MATHEWS, E. G. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). **Folia Entomológica Mexicana**, v.12/14, p. 1-312, 1966.

HALFFTER, G.; FAVILA, M. E. & HALFFTER, V. A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. **Folia Entomológica Mexicana**, v. 84, p. 131-156, 1992.

HANSKI, I. & CAMBEFORT, Y. **Dung beetle ecology**. New Jersey: Princeton University Press, 1991.

HEINO, J.; MELO, A. S.; BINI, L. M. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. **Freshwater Biology**, v. 60, n. 2, p. 223-235, 2015.

HERNÁNDEZ, M. I. M.; BARRETO, P. S. C. S.; COSTA, V. H.; CREÃO-DUARTE, A. J.; FAVILA, M. E. Response of a dung beetle assemblage along a reforestation gradient in Restinga Forest. **Journal of Insect Conservation**, v. 18, p. 539-546, 2014.

INDERJIT, T. Plant phenolics in allelopathy. **Botanical Reviews**, v. 62, p.186-202, 1996.

KLEIN, B. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. **Ecology**, v. 70, p. 1715-1725, 1989.

LAWTON, J. H. Are there general laws in ecology? **Oikos**, v. 84, n. 2, p. 177-192, 1999.

LEIBOLD, M. A.; HOLYOAK, M.; MOUQUET, N.; AMARASEKARE, P.; CHASE, J. M.; HOOPES, M. F.; HOLT, R. D.; SHURIN, J. B.; LAW, R.; TILMAN, D.; LOREAU, M. The metacommunity concept: a framework for multi-scale community ecology. **Ecology Letters**, v. 7, n. 7, 601-613, 2004.

MACHADO, S. A. & SCOLFARO, J. R. S. Curvas de índice de sítio para plantações de *Pinus elliottii* nos estados do Paraná e Santa Catarina. **Revista Floresta**, Paraná, v. 18, n. 12, p. 140-156, 1988.

MITTAL, I. C. Natural manuring and soil conditioning by dung beetles. **Tropical Ecology**, v. 34, p. 150-159, 1993.

NICHOLLS, C. I.; ALTIERI, M. A.; SANDEZ, E. J. **Manual práctico de control biológico para una agricultura sustentable.** Berkeley: University of California, 1999.

NICHOLS, E.; LARSEN, T.; SPECTOR, S.; DAVIS, A. L.; ESCOBAR, F.; DAVILA, M.; VULINEC, K.; THE SCARABAEINAE RESEARCH NETWORK. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta–analysis. **Biological Conservation**, v. 137, p. 1-19, 2007.

NICHOLS, E.; SPECTOR, S.; LOUZADA, J.; LARSEN, T.; AMEZQUITA, S.; FAVILA, M. E. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. **Biological Conservation**, v. 141, p. 1461-1474, 2008.

PAUCHARD, A.; GARCÍA, R.; ZALBA, S.; SARASOLA, M.; ZENNI, R.; ZILLER, S.; NUÑEZ, M. A. Pine Invasions in South America: Reducing Their Ecological Impacts Through Active Management. In: CANNING-CLODE, J. (Eds.). **Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions**. Warsaw: De Gruyter Open Poland, 2015. p. 318-342. https://doi.org/10.1515/9783110438666-020

PERES-NETO, P. R.; LEGENDRE, P.; DRAY, S.; BORCARD, D. Variation partitioning of species data matrices: Estimation and comparison of fractions. **Ecology**, v. 87, n. 10, p. 2614-2625, 2006.

SHEPHERD, V. E. & CHAPMAN, C. A. Dung beetles as secondary seed dispersers: impact on seed predation and germination. **Tropical Ecology**, v. 14, p. 199-215, 1998.

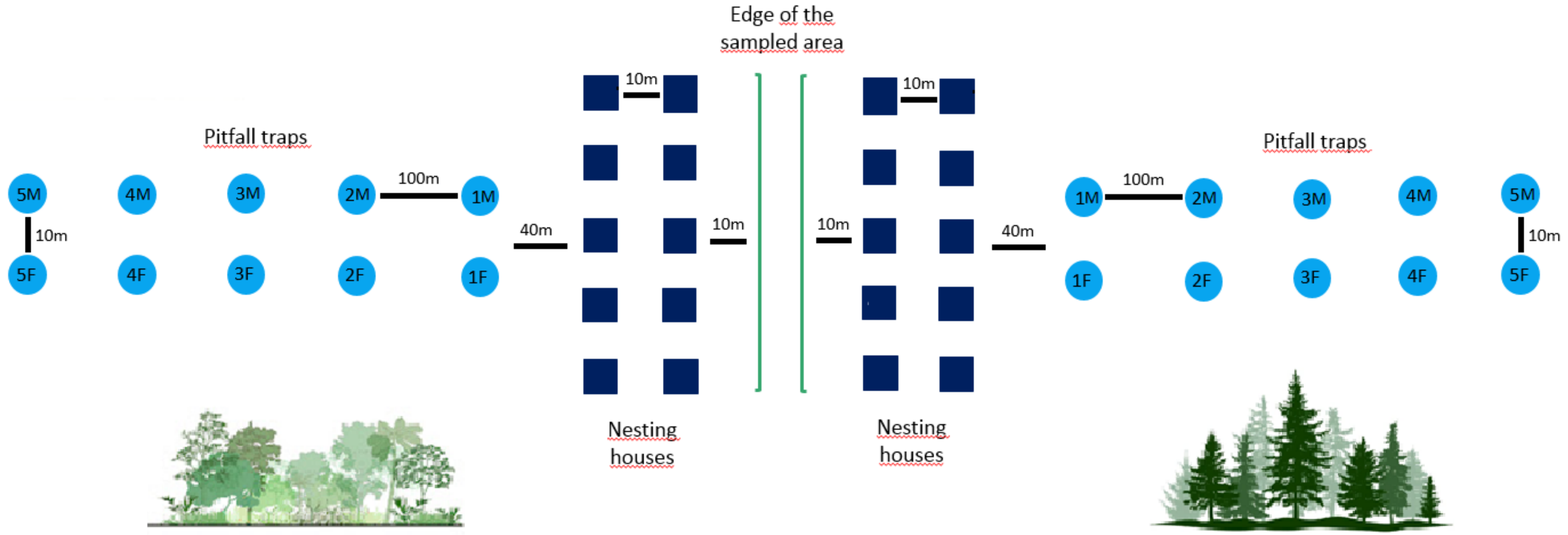
SILVEIRA NETO, S.; MONTEIRO, R. C.; ZUCCHI, R. A.; DE MORAES, R. C. B. Uso da análise faunística de insetos na avaliação do impacto ambiental. **Scientia Agricola**, v. 52, n. 9/15, p. 9-15, 1995.

STURGES, P. & ATKINSON, D. The clear-feeling of sand-dune plantations: Soil and vegetation process in habitat restoration. **Biological Conservation**, v. 66, p. 171-183, 1993.

THOMAZINI, M. J. & THOMAZINI, A. P. B. W. **A fragmentação florestal e a diversidade de insetos nas florestas tropicais úmidas.** Rio Branco: EMBRAPA Acre, 2000. 21 p. Circular Técnica, 57.

VALLEJO, L. R.; DA FONSECA, C. L.; GONÇALVES, D. R. P. Estudo comparativo da mesofauna do solo entre áreas de *Eucalyptus citriodora* e mata secundária heterogênea. **Revista Brasileira de Biologia**, Rio de Janeiro, v. 47, n. 3, p. 363-370, 1987.

APPENDIX A – SAMPLING DESIGN OF PITFALL TRAPS AND NESTING HOUSES INSTALLED IN AREAS OF DIFFERENT HABITATS (NATIVE FORESTS AND *PINUS* MONOCULUTRES) IN ALL SIX SAMPLED SITES.



APPENDIX B - ABUNDANCE AND RICHNESS OF DUNG BEETLES SPECIES WITH 4 MM AND HIGHER IN LENGTH CAPTURED ALIVE IN NESTING HOUSES AND MARKED PER SITE IN NATIVE FORESTS (F) AND *PINUS* MONOCULTURES (P) IN SANTA CATARINA STATE, SOUTH OF BRAZIL.

Species	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Site 5**		**Site 6**		**Total**
	F1	**P1**	**F2**	**P2**	**F3**	**P3**	**F4**	**P4**	**F5**	**P5**	**F6**	**P6**	
Dichotomius sericeus	0	1	83	17	49	30	0	0	19	3	13	21	**236**
Canthon rutilans cyanescens	17	30	2	7	0	0	24	38	6	6	1	2	**133**
Coprophanaeus saphirinus	17	1	26	5	6	2	6	1	45	7	3	3	**122**
Dichotomius assifer	16	25	11	6	8	9	0	2	4	6	9	6	**102**
Eurysternus inflexus	0	0	5	61	0	1	2	0	0	15	2	1	**87**
Phanaeus splendidulus	15	5	9	7	3	7	1	2	7	5	6	6	**73**
Deltochilum morbillosum	13	0	3	1	1	2	1	0	6	1	4	0	**32**
Deltochilum multicolor	0	3	7	1	0	3	0	2	7	0	0	4	**27**
Dichotomius mormom	3	2	5	2	0	0	0	0	0	2	6	4	**24**
Dichotomius fissus	1	0	1	0	3	2	0	0	0	4	1	1	**13**
Dichotomius opalescens	0	0	0	0	1	0	0	6	0	0	0	1	**8**
Dichotomius aff. *acuticornis*	0	0	1	0	3	0	0	0	0	0	0	2	**6**
Homocopris sp.	0	0	0	0	0	0	1	4	0	0	0	0	**5**
Deltochilum rubripenne	0	0	0	0	0	0	0	0	2	0	0	2	**4**
Ontherus sp.	0	2	0	1	0	0	1	0	0	0	0	0	**4**
Eurysternus cyanescens	2	0	0	0	0	1	0	0	0	0	0	0	**3**
Dichotomius aff. *pygidialis*	1	0	0	1	0	0	0	0	0	0	0	0	**2**
Deltochilum brasiliensis	0	0	0	1	0	0	0	0	0	0	0	0	**1**
Dichotomius quadrinodosus	0	0	0	0	0	1	0	0	0	0	0	0	**1**
Abundance	**85**	**67**	**153**	**110**	**74**	**58**	**35**	**55**	**96**	**49**	**45**	**53**	**883**
Richness	**9**	**8**	**11**	**12**	**8**	**10**	**7**	**7**	**8**	**9**	**9**	**12**	**19**

APPENDIX C – ABUNDANCE AND RICHNESS OF DUNG BEETLES (COLEOPTERA: SCARABAEINAE) IN EACH SAMPLED AREA IN SANTA CATARINA STATE, SOUTH OF BRAZIL. F: NATIVE FOREST AND P: *PINUS* MONOCULTURES.

Species	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Site 5**		**Site 6**		**Total**
	F1	**P1**	**F2**	**P2**	**F3**	**P3**	**F4**	**P4**	**F5**	**P5**	**F6**	**P6**	
Dichotomius sericeus	2	6	76	105	280	32	1	8	52	4	24	26	**616**
Eurysternus inflexus	54	95	24	160	15	22	2	2	14	46	36	8	**478**
Deltochilum morbillosum	59	37	17	9	65	9	23	5	59	28	73	42	**426**
Phanaeus splendidulus	50	11	29	13	18	16	10	7	25	12	27	6	**224**
Canthidium aff. *trinodosum*	33	7	36	4	67	1	10	2	9	9	18	15	**211**
Coprophanaeus saphirinus	21	6	25	6	22	10	5	2	28	8	41	7	**181**
Onthophagus tristes	7	24	1	8	5	0	2	35	11	38	4	19	**154**
Paracanthon aff. *rosinae*	0	0	10	0	42	0	0	0	23	0	25	0	**100**
Dichotomius assifer	12	21	5	5	1	5	2	2	4	9	7	4	**77**
Deltochilum brasiliensis	15	8	11	11	0	0	2	1	5	6	12	0	**71**
Canthidium sp.2	0	3	11	0	0	9	2	0	7	6	16	11	**65**
Canthon rutilans cyanescens	3	32	1	4	1	1	2	17	0	1	0	0	**62**
Canthidium sp.1	1	6	0	1	0	3	0	0	0	16	0	33	**60**
Uroxys sp.1	20	0	7	2	0	1	4	2	11	5	2	2	**56**
Dichotomius fissus	2	3	6	0	9	11	0	0	2	10	0	6	**49**
Canthon angularis	19	2	4	1	0	0	14	1	1	1	6	0	**49**
Deltochilum multicolor	2	8	2	2	0	3	0	20	4	4	0	2	**47**
Onthophagus catharinensis	1	3	3	12	2	5	0	0	1	2	2	4	**35**
Dichotomius mórmon	5	3	8	3	1	0	0	0	3	3	3	2	**31**
Deltochilum rubripenne	0	0	1	8	0	0	0	0	0	1	3	17	**30**
Ateuchus aff. *carbonarius*	0	0	0	5	1	1	1	0	1	10	6	2	**27**
Uroxys terminalis	0	0	12	0	0	0	0	0	14	0	0	0	**26**
Canthon lividus seminitens	0	1	0	2	0	0	0	21	0	0	0	0	**24**
Eurysternus cyanescens	2	0	3	1	6	3	1	0	1	2	0	0	**19**

Uroxys dilaticollis	1	1	3	2	7	1	0	0	0	0	1	0	**16**
Uroxys sp.2	3	0	4	1	0	0	0	0	2	2	0	3	**15**
Eurysternus parallelus	0	5	0	1	0	0	0	1	3	3	0	0	**13**
Canthon luctuosus	0	0	9	0	2	0	0	0	0	0	1	0	**12**
Deltochilum dentipes	1	2	0	0	0	0	0	0	0	5	0	0	**8**
Ontherus sulcator	0	4	0	0	0	0	0	3	0	0	0	0	**7**
Homocopris sp.1	0	0	0	0	0	0	4	2	0	0	0	0	**6**
Dichotomius opalescens	0	0	0	0	0	0	0	5	0	0	0	0	**5**
Dichotomius aff. *pygidialis*	0	1	0	0	0	0	1	0	0	0	1	1	**4**
Canthidium díspar	0	0	4	0	0	0	0	0	0	0	0	0	**4**
Ontherus azteca	0	3	1	0	0	0	0	0	0	0	0	0	**4**
Dichotomius quadrinodosus	1	0	0	0	0	0	0	0	1	1	0	0	**3**
Scatonomus fasciculatus	1	0	0	0	0	0	0	0	0	0	1	0	**2**
Sulcophanaeus radamanthus	0	0	2	0	0	0	0	0	0	0	0	0	**2**
Canthidium aff. *taurinum*	0	0	0	0	1	0	0	0	0	0	0	0	**1**
Canthidium femorale	0	0	1	0	0	0	0	0	0	0	0	0	**1**
Canthon oliverioi	0	0	1	0	0	0	0	0	0	0	0	0	**1**
Abundance	**315**	**292**	**317**	**366**	**545**	**133**	**86**	**136**	**281**	**232**	**309**	**210**	**3222**
Richness	**23**	**24**	**29**	**23**	**18**	**17**	**17**	**18**	**23**	**25**	**21**	**19**	**41**