Mariah Wuerges

A DISPERSÃO COMO PROCESSO: UMA ABORDAGEM SOBRE UMA METACOMUNIDADE DE BESOUROS ESCARABEÍNEOS

Dissertação submetida ao Programa de Pós-Graduação em Ecologia, da Universidade Federal de Santa Catarina para a obtenção do Grau de Mestre em Ecologia.
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Esta Dissertação foi julgada adequada para obtenção do Título de "Mestre em Ecologia" e aprovada em sua forma final pelo Programa de Pós-Graduação em Ecologia.

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Este trabalho é dedicado às trabalhadoras e trabalhadores da sociedade brasileira, que lutam por uma Universidade Pública, gratuita e de qualidade, a serviço do povo.

AGRADECIMENTOS

(...)
Que vivan los estudiantes
que rugen como los vientos
cuando les meten al oído
sotanas o regimientos,
pajarillos libertarios
igual que los elementos.
Caramba y zamba la cosa,
vivan los experimentos.
(...)
Me gustan los estudiantes
que con muy clara elocuencia
a la bolsa negra sacra
le bajó las indulgencias.
Porque, ¿hasta cuándo nos dura,
señores, la penitencia?
Caramba y zamba la cosa,
que viva toda la ciencia.

Violeta Parra

RESUMO

Em Ecologia, estamos constantemente buscando padrões e, consequentemente, tentando inferir os processos que os explicam. No entanto, traçar estas relações é uma tarefa complicada, ilustrando um dos maiores desafios da ecologia em geral. A dispersão é um destes processos que atuam sobre os padrões de distribuição espacial das espécies na natureza, influenciando fortemente a dinâmica das populações e comunidades naturais em escalas locais e regionais. Regionalmente, a dispersão pode estruturar metacomunidades, que são comunidades conectadas por dispersão, por meio de diferentes processos. Considerando os besouros escarabeíneos, existem espécies específicas de áreas abertas e outras de áreas florestais, o que pode ser consequência de processos de alocação de espécies ou de efeito de massa. Neste sentido, nosso objetivo é descrever a força da dispersão em uma metacomunidade de escarabeíneos em uma paisagem heterogênea, respondendo a questões desde o nível populacional, passando pela comunidade e chegando à metacomunidade. Para tanto, este estudo foi realizado em um local onde campos e pastagens formam uma matriz junto a fragmentos de Floresta Ombrófila Mista, no Sul do Brasil, resultando em três tipos distintos de ambientes: áreas abertas, bosques e florestas. Para caracterizar os ambientes, uma avaliação da estrutura vegetacional foi realizada, e os diferentes habitats foram classificados por meio de uma análise de componentes principais. Para esboçar os padrões de dispersão das espécies, além de descrever composição, riqueza, diversidade e dissimilaridade entre as assembleias dos ambientes distintos foram dispostos 36 pontos de amostragem distribuídos nos três ambientes (além de 20 pontos a maiores distâncias), e realizado um experimento de marcação e recaptura (MRR), juntamente com amostragem de besouros rola bosta. Para traçar um caminho entre os padrões e processos envolvidos na estruturação da metacomunidade, os dados de abundância relativa das espécies da metacomunidade foram relacionados aos dados ambientais e espaciais relativos aos sítios de amostragem. Além disso, testamos nosso método de marcação em um experimento anterior em laboratório, comparando indivíduos marcados com indivíduos não marcados. Nossos resultados laboratoriais demonstraram que a marcação não afetou o comportamento, a fertilidade e a sobrevivência, sendo que é permanente e fácil de identificar. No campo, marcamos 2032 besouros de cinco espécies. Para *Canthon rutilans* recapturamos 5,53% dos indivíduos marcados (n=524)

e para *Canthon angularis* recapturamos 2,36% dos marcados (n=1270), enquanto para as outras três espécies tivemos apenas uma recaptura. Os escarabeíneos moveram-se principalmente, mas não exclusivamente, dentro de seus ambientes específicos, em média 13 metros por dia. A diversidade de espécies foi maior nos bosques, seguida de áreas abertas e de floresta, com menor diversidade, embora a riqueza fosse igual em todos os três ambientes. Houve grande dissimilaridade entre as assembleias de ambientes estruturalmente distintos, predominantemente liderada por substituição de espécies e variação balanceada na abundância das espécies. A maior parte da variação dos dados de abundância relativa da metacomunidade foi explicada pela variação estrutural da paisagem. Estas são evidências de forte influência do nicho e baixas taxas de movimento, inferindo a presença de um forte efeito de alocação de espécies sobre a estruturação desta metacomunidade.

Palavras-chave: Ecologia, Marcação e recaptura, Scarabaeinae, Alocação de espécies.

ABSTRACT

In Ecology, we are constantly seeking patterns and, consequently, trying to infer the processes that explain them. However, tracing such relationships is a complicated task, illustrating one of the major challenges of ecology in general. The dispersal is one of these processes acting on the patterns of species spatial distribution in nature, strongly influencing the dynamics of natural populations and communities at local and regional scales. Regionally, dispersion can structure metacommunities, which are communities connected by dispersion, following different processes. Considering dung beetles, there are species of open and forested areas, which might be consequence of species sorting or a mass effect. Our goal is to describe the dispersal strength in a metacommunity of dung beetles in a heterogeneous landscape, by answering to questions across population, community, and metacommunity levels. Accordingly, this study was carried out in a place where fields and pastures form a matrix nearby fragments of Mixed Ombrophilous Forest in southern Brazil, resulting in three distinct types of environments: open areas, woodlands and forests. To characterize the environments, an evaluation of the vegetation structure was carried out, and different habitats were classified with a principal component analysis. In addition to describing composition, richness, diversity and dissimilarity between the assemblages fom the different environments, 36 sampling points in the three environments (with an addition of 20 extra points at greater distances) were arranged to perform a mark-release (MRR) experiment and scarabaeinae sampling. To draw a path between patterns and processes involved in structuring the metacommunity, data from the relative abundance of species of the metacommunity were related to the environmental and spatial data relative to the sampling sites. In addition, the marking method was tested earlier in a laboratory experiment by comparing marked with unmarked individuals. Our laboratory results showed that marking did not affect behavior, fertility and survival, and it is permanent and easy to identify. In the field, we marked 2032 beetles from five species. For *Canthon rutilans rutilans* we recaptured 5.53% of the marked individuals (n = 524) and for *Canthon angularis* we recaptured 2.36% of the marked ones (n = 1270), whereas for the other three species we had only one recapture. The beetles moved mainly, but not exclusively, within their specific environments, averaging 13 meters per day. Species diversity was higher in the woodlands, followed by open areas and then

by forests, with smaller diversity indexes, although the richness was the same in all three environments. There was great dissimilarity between assemblages of structurally distinct environments, predominantly led by species turn over and balanced variation in species abundance. Most of the variation of the metacommunity relative abundance data was explained by the structural variation of the landscape. These are evidences of strong niche influence and low movement rates, inferring the presence of a strong species sorting effect on the structuring of this metacommunity.

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APRESENTAÇÃO

Em estudos de ecologia, buscamos encontrar padrões de diversidade, abundância e composição das espécies na natureza, além de tentar entender quais processos podem gerar estes padrões. Vellend (2010) propôs quatro categorias básicas de processos que podem resultar nos padrões que encontramos nas comunidades: deriva, especiação, dispersão e seleção. No entanto, relacionar tais processos e padrões é uma tarefa bastante complicada, já que os processos podem ocorrer em escalas temporais e espaciais difíceis de serem estudadas, sendo que, além disso, certos padrões podem ser explicados por mais de um processo. Consequentemente, existe uma caixa "preta" em ecologia de comunidades, ilustrando possivelmente um dos maiores desafios da ecologia em geral, que é traçar uma relação entre os padrões e processos (Vellend, 2010).

A dispersão é um fator determinante de padrões de distribuição espacial das espécies na natureza, influenciando fortemente na dinâmica de populações e comunidades naturais (Vellend, 2010; Silva e Hernández, 2015). Assim, a dispersão dos indivíduos pode modificar a composição das espécies em uma comunidade, já que os indivíduos que se movimentam por locais compostos por diferentes habitats podem ter características distintas daqueles que não realizam dispersão (Townsend et al, 2006). Além disso, os padrões de uma comunidade em uma escala local, podem estar sendo influenciados por outras comunidades inseridas na escala regional, principalmente através da dispersão dos indivíduos entre comunidades distintas (Chase e Bengtsson, 2010). Desta maneira, diferentes comunidades podem estar conectadas através da dispersão das espécies, resultando em metacomunidades (Leibold et al, 2004). O estudo de metacomunidades, nos permite entender os padrões das comunidades naturais, em uma escala espacial regional (Leibold et al, 2004), incluindo um conjunto de comunidades locais que estão conectadas por dispersão de espécies que podem potencialmente interagir (Wilson, 1992).

As abordagens teóricas em metacomunidades que incluem ambientes heterogêneos e discutem a importância da dispersão entre eles incluem dois modelos: alocação de espécies ("species sorting") e efeito de massa ("mass effect"). Quando consideramos que as espécies estão separadas espacialmente em diferentes habitats por possuírem nichos distintos e que a dispersão não é suficiente para ampliar suas

distribuições, é possível que essas metacomunidades estejam sendo estruturadas por alocação de espécies ("species sorting") e o nicho tenha maior efeito do que a dispersão das espécies. Neste caso, considera-se que existem variações ambientais entre as diferentes manchas de habitat e o que viria determinar os padrões de distribuição de espécies nas manchas, seriam os diferentes *trade offs* entre os atributos das espécies, que permitem que elas se especializem em diferentes tipos de manchas e diferenciem seus nichos. Portanto, neste caso existe dispersão, mas a coexistência de espécies dentro de um nível regional ocorre devido à diferenciação de nicho entre elas provocando alta diversidade beta, ou seja, o nicho seria um fator estruturante destas metacomunidades por possuir um papel mais importante que a dispersão (Leibold et al, 2004).

Por outro lado, se a estrutura da metacomunidade é determinada principalmente por uma forte dispersão entre as espécies, é possível que o processo determinante seja o efeito de massa ("mass effect"), com uma fonte constantemente fornecendo espécies para um habitat sumidouro. Neste sentido, em contraponto ao processo de alocação de espécies, o efeito de massa possui a dispersão das espécies como importante fator estruturante da metacomunidade. No efeito de massa também consideramos manchas estruturalmente distintas em relação às suas condições ambientais, mas estas manchas devem estar suficientemente conectadas para que a dispersão possa resultar em uma relação de fontes e sumidouros entre comunidades de manchas distintas. Neste sentido, a força da dispersão tem uma importante influência nos padrões regionais destas comunidades, provocando baixa diversidade beta, já que mesmo que haja extinção local em um ambiente que atua como sumidouro de espécies, a existência de uma fonte pode permitir constante fluxo de indivíduos, renovando constantemente os padrões locais (Leibold et al, 2004).

Além disso, as taxas de dispersão podem estar ocorrendo em diferentes escalas espaciais (Roslin, 2000), sendo que pode existir uma série de fatores influenciando na capacidade de dispersão dos indivíduos nos ambientes naturais: condições abióticas, como luminosidade, temperatura, umidade e conectividade estrutural das manchas de habitat em que estas espécies ocorrem, além das questões bióticas, como a estrutura vegetacional do habitat e as capacidades dos indivíduos de se moverem no cenário ambiental, como resposta a estímulos internos e externos (Bell, 1990), além da percepção em relação à detecção dos recursos, qualidade e distribuição do recurso alimentar e limitações relacionadas às capacidades de voo. Além disso, diferenças nos comportamentos de forrageamento podem afetar a capacidade de

dispersão das espécies, sendo que geralmente as espécies que dependem fortemente do voo para a localização do alimento são geralmente as espécies de maior dispersão (Gill, 1991). Ou seja, os padrões de movimentação das espécies podem depender de como os organismos percebem a heterogeneidade ambiental (Wiens et al, 1995).

Os besouros escarabeíneos (Coleoptera: Scarabaeidae: Scarabaeinae), conhecidos como rola-bosta, são majoritariamente animais coprófagos (Halffter e Edmonds, 1982), sendo que ao longo de sua história evolutiva desenvolveram técnicas de forrageamento para localizar rapidamente seu recurso alimentar, já que este frequentemente é efêmero (Hanski e Camberfort, 1991; Roslin e Viljanen, 2011). Devido ao seu comportamento alimentar e de nidificação, estes insetos realizam importantes funções ecológicas dentro dos ecossistemas, já que como consequência da alocação do alimento, eles incorporam matéria orgânica no solo (Batilani-Filho & Hernández, 2017) e realizam funções secundárias como aeração do solo e dispersão de sementes (Nichols et al. 2008). Portanto, as comunidades destes insetos são afetadas pela riqueza de mamíferos em associação com o habitat (Bogoni et al. 2016), o que os torna extremamente suscetíveis a alterações ambientais. Assim, esses insetos são frequentemente usados em estudos como indicadores ecológicos (Halffter e Favila, 1993) já que é comum haver uma diminuição da riqueza de espécies em áreas de florestas degradadas (Hernández e Vaz-de-Mello, 2009).

Neste sentido, a estrutura das comunidades dos escarabeíneos é extremamente influenciada pela competição por alimento (Simmons e Riddill-Smith, 2011), já que eles frequentemente utilizam fezes para nidificação e reprodução (Halffter e Edmonds, 1982). Dentro de comunidades locais, a grande diversidade de espécies de escarabeíneos está relacionada à diferenciação de nichos, já que os comportamentos destes animais podem variar de acordo com diferenças em horários de atividade (Hernández, 2002), forma e tamanho do corpo (Hernández et al., 2011) ou diferenças intraespecíficas como sexo, idade, ou preferências individuais. Além disso, existem diversos comportamentos dependendo do tipo de alocação do recurso realizado pela espécie: paracoprídeos ou "tuneleiros", em que os indivíduos cavam túneis e enterram o alimento logo abaixo da fonte alimentar; telocoprídeos ou "roladores", em que os indivíduos rolam o alimento, formando bolas e o enterram em profundidades menores longe da fonte alimentar; e endocoprídeos ou "residentes", em que os organismos constroem seu ninho na fonte alimentar (Halffter e Edmonds, 1982);

Neste contexto, entre os besouros rola-bosta em ecossistemas tropicais, onde a maioria das espécies são encontradas, existe muita especificidade de habitat, havendo um contraste entre as espécies de áreas abertas e as dependentes de florestas (Hanski e Cambefort, 1991; Gill, 1991). Apesar disso, pouco se sabe como os besouros escarabeíneos se movimentam diante da variação na estrutura do habitat (Arellano et al, 2008). Uma maneira de entender como os organismos se dispersam pode ser a realização de experimentos utilizando marcação e recaptura. Experimentos utilizando esta metodologia com besouros escarabeíneos mostram uma baixa taxa de recaptura, de cerca de 5% a 10% (Escobar e Chacón, 2000; Roslin, 2000; Arellano et al, 2008; Larsen e Forsyth, 2005; Noriega e Acosta, 2011; Silva e Hernández, 2015). Características como tamanho corporal podem afetar a capacidade de dispersão (Peck e Forsyth, 1982) e, dependendo das espécies e dos habitats em questão, pode haver diferenças na velocidade de locomoção entre machos e fêmeas ou de acordo com a idade dos indivíduos (Arellano et al, 2008), ou pelo contrário, não haver diferenças na dispersão entre machos e fêmeas (Silva e Hernández, 2015).

Muitas perguntas sobre a capacidade de dispersão das espécies de escarabeíneos ainda restam, como por exemplo se as observações de Klein (1989) na Amazônia, de que os indivíduos da mata não saem dela à procura de comida, são aplicáveis para todas as espécies. Ainda não é possível dizer se os indivíduos de floresta permanecem na floresta, ou se aqueles de campos abertos permanecem nos campos abertos, mesmo com grande disponibilidade de recurso em locais estruturalmente distintos. Além disso, não se sabe ao certo quais espécies de besouros escarabeíneos possuem especificidade de habitat, e se são verdadeiramente dependentes destes ambientes ou só apresentam preferências, já que é provável que aqueles indivíduos descritos como dependentes de certos tipos de habitat, também se movimentem por outras áreas. Adicionalmente, a movimentação dos indivíduos pode variar de acordo com seu propósito: forrageamento ou nidificação, ou variar de acordo com características interespecíficas ou intraespecíficas.

Devido a um cenário recorrente de fragmentação florestal, entender como os indivíduos se movem nos ambientes naturais é muito importante para o planejamento de estratégias futuras relacionadas à conservação. Uma maneira de entender como os besouros escarabeíneos se dispersam é através de estudos de marcação e recaptura (Peck & Forsyth 1982; Favila 1988; Escobar e Chacón 2000; Roslin 2000; Larsen e Forsyth 2005; Arellano et al. 2008; Noriega e Acosta 2011;

Larsen e Forsyth 2005; Arellano e outros 2008; Martínez-Quintero 2013; Cultid-Medina 2015; Villada-Bedoya e Cultid 2017; da Silva e Hernández 2015). No entanto, no Neotrópico, poucos estudos discutem como os besouros se movimentam entre diferentes coberturas vegetais (Arellano et al., 2008, Cultid-Medina et al., 2015, Villada-Bedoya e Cultid-Medina, 2017) ficando em aberto a importância da dispersão em metacomunidades.

Para tanto, este trabalho está dividido em dois capítulos. O primeiro corresponde a uma nota científica, submetida à revista *The Coleopterists Bulletin*. Esta nota se propõe a testar a metodologia de marcação individual utilizada neste trabalho sobre a sobrevivência, comportamento e fertilidade de uma espécie de besouro escarabeíneo. O segundo capítulo do trabalho corresponde a um artigo científico a ser submetido à revista *PlosOne*, e está vinculado ao objetivo principal deste trabalho: descrever a força da dispersão sobre os processos de estruturação de uma metacomunidade de escarabeíneos em uma paisagem de Mata Atlântica que envolve áreas abertas e florestais, respondendo a questões desde o nível populacional, passando pela comunidade e chegando à metacomunidade.

CAPÍTULO 1. Nota Científica submetida à revista *The Coleopterists Bulletin*

MARKING DUNG BEETLES: RETROSPECTIVE AND A RELIABLE STARDARIZED "SCARIFICATION" METHOD

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Scarabaeinae (Coleoptera: Scarabaeidae), with over 6200 species described (Tarasov and Génier 2015), are widely studied insects, often used as ecological indicators in diversity studies (Halffter and Favila 1993), and with important ecological role in nutrient cycling, soil aeration, secondary seed dispersal, and control of parasites (review in Nichols *et al.* 2008). However, some aspects of the basic biology of these species are poorly investigated, such as life span, dispersal capacity and other population parameters (Hanski and Cambefort 1991). One way to access this information is through mark, release and recapture studies (MRR) via permanent marks with the least possible effect on individuals' behavior and survival (Martínez-Quintero *et al.* 2013).

The first published MRR study with dung beetles was carried out by Peck and Forsyth (1982), which sought to estimate population size for some species by marking them with enamel paint spots on pronotum and elytra, with a five color-code. Following jut one recapture event, with a recapture rate of 0.02%, they described distances covered by some species. After that, Favila (1988) presented an individual marking method for laboratory and field studies, using paint and glue on top, to protect the marking from soil friction, highlighting the pronotum as the best part of the insect's body to mark. Using mark release methods in fieldworks, Escobar and Chacón (2000) described the use of different habitat for some species, marking individuals of species greater than 10mm, for 5 months, using different colors of painting. Their results provided information about movement patterns and distances covered for *Sulcophanaeus velutinus* e *Dichotomius* cf. *quinquedens*. Roslin (2000) provided results about distances covered by Aphodinae beetles, another Scarabaeidae subfamily, carrying out a mark which

consisted of two small holes in different positions in the elytra, using the tip of the thinnest available insect pin, and could only be seen under a microscope. Larsen and Forsyth (2005) performed a mark-release study with *Canthon acutus*, a small diurnal ball-rolling beetle (body width=4.1 mm) using a silver pen. Every group was identified with a unique dots' combination in the elytra and pronotum and released once, performing recaptures at every 24 hours for four days, which allowed them to propose a spatial design to avoid pseudo replicates in ecological studies of biodiversity. Arellano and collaborators (2008), to understand the effects of landscape structure on patterns of abundance and movement and the differences between males and females movement, painted individuals of *Canthon cyanellus cyanellus* (a diurnal, necrophagous, and roller scarab); *Phanaeus pyrois* (a diurnal, necrophagous, and burrower scarab) and *Dichotomius amplicollis* (a nocturnal, coprophagous, and burrower scarab), using silver pens making a unique combination of dots on the elytra and/or pronotum. Based in Favila (2008), every mark was covered with a fine layer of glue with cyanocrilate. Noriega and Acosta (2011), did a mark-release experiment, over three months with Sulcop*hanaeus leander*, marking the ventral surface of the metasternum of this large body size species using a fast-drying latex paint. The same mark was used for all individuals. They observed high fidelity to the habitat and dispersal between different environments and answered questions such as daily activity and sex ratio.

Recently, Martínez-Quintero and collaborators (2013) proposed a novel standard method for marking dung beetles, which consisted of a permanent and individual scarification mark. They used a Mototol Stylus 1100 Dremel® to perform a scraping on the back of the elytra and pronotum, with an emerald 84922 Dremel® stone, which allowed a clean brand on the insect body. This mark was applied on individuals from 10 to 35 mm because it was difficult to perform in individuals smaller than 10mm, although they report that they have been able to mark individuals up to 6 mm as well. They reported none ecological, biomechanical and reproductive implications on individuals, but, like previous studies, they did not test for it. Cultid-Medina and collaborators (2015), based on the same method, carried out a populational study of two species: *Oxysternon conspicillatum* and *Dichotomius* cf. *alyattes*, chosen for being abundant large species (10 to 35 mm of body length), and with different habitat preferences. They performed a general marking in the elytra and pronotum, which allowed them to identify sex, site and type of vegetation in which individuals

were captured. They obtained answers regarding the distance covered by the species, patterns of movement between areas, and estimated population sizes, with an extremely high recapture rate of about 18%. They proposed that this fact was consequence of the permanent mark that does not affect individuals. Using a similar permanent marking technique, da Silva and Hernández (2015) redesigned the trap spacing protocol proposed by Larsen and Forsyth (2005). They used a broken tip of a needle, performing a scarification and removing part of the cuticle present in the pronotum and elytra with a dot scheme resulting in an individual mark. Villada-Bedoya and Cultid-Medina (2017) also used the scarification method (Martínez-Quintero *et al*. 2013) and carried out a population study for 7 months with *Dichotomius* cf. *satanas* and *Dichotomius* cf. *alyattes* obtaining a recapture rate of 0.04%. They demonstrated distances traveled by individuals was equal between sexes for both species.

Therefore, the use of permanent and individual markings has been an important tool in the study of the biology and ecology of dung beetles. Accordingly, our aim was to check whether the scarification technique affects any component of individual fitness, by assessing survival, behavior and reproduction of marked and unmarked dung beetles. In addition, we assessed whether markings could be applied individually and permanently on species of different sizes, and thus whether this technique can be used in laboratory experiments and in the field without harming these insects. To do so, we conducted a laboratory experiment with 26 couples of *Canthon rutilans cyanescens*, a neotropical species with about 0.4 mm length, with 13 marked couples and 13 unmarked couples to verify if markings affect survival, behavior and reproduction. The marking was performed with a dental micromotor (Beltec LB100) with a 0.5mm spherical drill and the aid of a magnifying glass or a stereoscope. We performed a scraping in the elytra of the individuals drawing a scheme of points and lines resulting in a number to be used as an individual identifier (Figure 1). Each point represented a unit, and each line corresponded to the number 5. The right elytra correspond to the units, the left elytra to the decimals, the right part of the pronotum to the hundreds and the left part to the thousands. We can visualize a mark corresponding to the numbers 8 (Fig 1A), which resulted from one line and three points in the right elytra, adding 8; and 13 (Fig 1B) in which a point was made in the left elytra, and three points in the right one, adding 13.

The individuals were collected early in the spring, in September 2017, at the Serra do Tabuleiro State Park (27°43'S, 48°48'W), an area

of Atlantic rain forest located in southern Brazil, and then taken to the Laboratory of Terrestrial Animal Ecology at Federal University of Santa Catarina (UFSC). To avoid weight and age confounding effects on the experiment, we formed couples of similar weight and age, and distributed them in two treatments systematically allocating similarly pairs of different ages and sizes between treatments. Age categorization was performed according to the opacity of the elytra and the wear of the tarsal spur of the anterior tibia, classifying individuals as new, mature and old. Very old or damaged individuals were not used. All 26 couples were placed in pots (8 x 11 x 6 cm) with 400g of soil from the same collection site, which was heated in a microwave for 5m to avoid contamination, especially by mites. Weekly, the beetles were fed with 10g of resource (feces of domestic dog bred with animal feed at the Laboratory Animal House of the University). The experiment started in November 2017 and lasted until the beginning of March 2018, completing four months. During this period the beetles were kept in the laboratory under controled temperature and luminosity (12 hours of light and 12 hours of darkness). Every week the deaths and births were counted, and twice (December 2017 and once in January 2018), the number of nest balls produced by the couples was counted.

Markings did not affect the survival of individuals, neither between sexes (t=0.51, df=48.63, p=0.61), as males lived 62.0 days in mean and females lived 67.8 days, nor between treatments (t=0.33, df=50, p=0.74) with marked individuals living 66.8 days and unmarked 63.10 days. Moreover, the mark did not affect behavior, when measured by the production of nesting balls: marked couples produced a mean of 2.33 nest balls, and unmarked ones produced on average 1.58 nest balls, with no difference between treatments (t=1.25, df=34.98, p=0.22). The reproduction was also not affected on the marked couples, since the counting of offspring per couple was the same in both treatments (z=1.48, df=11, p=0.77). The total counting of offspring was ten females and six males for all marked couples, and 4 females and 3 males for all the unmarked couples. Furthermore, the life cycle of the larva was the same (F=0.55, df=1, p=0.46), with an average of 86.62 days and 78.71 days with and without the mark on the parental, respectively. The fertility rate (calculated by the ratio between the number of individuals emerged per couple divided by the maximum number of nest balls produced by that couple) among the marked couples was 0.53 and 0.54 of the unmarked couples, with no difference (F=0.001, df=1, p=0.97).

MRR experiments with insects are a quite challenging task, improving according to technological advances, although requiring

creativity and dexterity of the one who proposes to carry them out. Beyond the difficulties of application, mainly because of the great abundance and small size of these animals, an ideal marking must be durable, cheap, non-toxic, easy to apply and to check (Hagler and Jackson 2001). Paintings and tattoos have been a common technique for dung beetles (Peck and Forsyth 1982; Favila 1988; Escobar and Chacón 2000; Larsen and Forsyth 2005; Arellano *et al.* 2008; Noriega and Acosta 2011), although some studies managed to apply it on small insects (<10 mm) (Larsen and Forsyth 2005; Arellano *et al.* 2008) this method is mainly used on large insects because of the logistic difficulties in applying the mark on small insects (Hagler and Jackson 2001). Moreover, the use of ink makes it possible to recapture the individuals only over short periods, since their habit of burial, markings have a limited life time due to the friction with the soil (Martínez-Quintero 2013). Although Favila (1988) and Arellano and collaborators (2008) applied a drop of glue to fix the paint, this technique is difficult to perform because of the waxy material present in the elastin cover of most beetlesand the small of size of some species. Furthermore, Roslin (2000), performing perforations on the elytra, only visualized with a microscope, was able to mark small individuals. Even though it was a permanent mark, perforations in the elytra can expose individuals to parasites (Martínez-Quintero 2013), and solar radiation, and it needs to be tested regarding individual fitness.

Scarification marks, more recently performed, are durable, cheap, non-toxic, and easy to identify. This method has been mostly applied on large individuals (> 10mm length) (Martínez-Quintero 2013; Cultid-Medina 2015; Villada-Bedoya and Cultid 2017), and more rarely applied to small individuals (<10 mm length) (da Silva and Hernández 2015), although it was not tested according to the possible negative effect it might cause on individuals. Here, we have shown that labeling with a "scarification mark" has no influence on survival, behavior and fertility of individuals, being permanent and easy to see and identify (it can be identified with the naked eye) and this method can be applied in field works and in species of different sizes or shape (Fig 2). Therefore, we can infer that scarification can be a reliable method for field and laboratory MRR studies, because it does not interfere in the survival, behavior and reproduction and it allows us to achieve an individual, durable, cheap and non-toxic mark, plus being easy both to apply and check.

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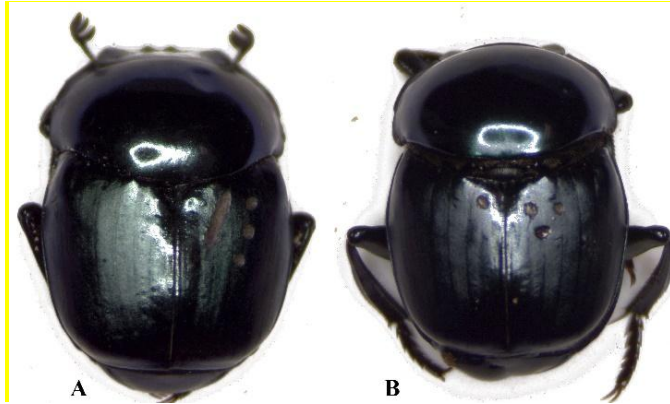
Fig 1. Scarification mark made on *Canthon rutilans cyanescens*. A) Mark corresponding to the number 8, in which was made one line and three dots in the right elytra, adding eight; B) Mark for number 13, in which a point was made in the left elytra, and three points in the right one, adding 13.

Fig 2. A) Marking procedure on a male of *Coprophanaeus saphirinus*, with the use of a stereoscope and a dental micromotor with a 0.5 mm spherical drill. B) Mark in an individual of *Canthon rutilans rutilans,* corresponding to the number 1428, in which was carried out one point at the left pronotum (thousands), 4 points in the right pronotum (hundreds), 2 points at the left elytra (decimals) and one risk and three points in the right elytra (units).

CAPÍTULO 2. Artigo Científico a ser submetido à revista *PlosOne*

UNVEILING DISPERSAL STRENGTH ON A

METACOMMUNITY OF DUNG BEETLES IN A

HETEROGENEOUS LANDSCAPE

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Abstract

Dispersal strongly influences species distributional patterns in nature, and it can structure metacommunities through different processes in a regional scale. Species of dung beetlescan be specialized for either openor forested areas, which might be a consequence of species sorting or mass effect. We aim to describe the dispersal strength in a metacommunity of dung beetles in a heterogeneous landscape, by answering questions on population, community and metacommunity levels. To characterize the environments, an evaluation of vegetational structure was performed, and the different habitats were classified through a principal component analysis. To describe composition, richness, diversity and dissimilarity between assemblages from the distinct environments, 36 sampling points were placed in the three environments, with additional 20 points located at greater distances and used to perform a mark-release experiment combined with Scarabaeinae sampling. To investigate processes behind the metacommunity structure, species relative abundance data of the metacommunity were related to the environmental and spatial data of the sampling sites. For *Canthon rutilans* we recaptured 5.53% of the marked individuals (n=524) and, for *Canthon angularis* we recaptured 2.36% of marked ones (n=1270), whereas other three species were recaptured only once. Dung beetles moved mainly, but not exclusively, in their specific environments, on average, for 13 meters a day. Species diversity, considering the total pool of species, was higher in woodlands, followed by open areas and forest as less diverse, although richness was equal in all three environments. There was a great dissimilarity between assemblages from structurally distinct environments, predominantly lead by turnover of species and balanced abundance variation. Most of the variation of the relative abundance data of the metacommunity was explained by the vegetational structural variation of the landscape. Those are evidences of strong niche influence, and low movement rates, inferring a species sorting effect on this metacommunity.

Introduction

In ecology, we are constantly seeking patterns and consequently trying to infer the processes that explain them. However, to draw a relationship between such processes and patterns is a rather complicated task, illustrating one of the major challenges of ecology in general [41]. Dispersal is one of those determinant processes acting over the patterns of species spatial distribution in nature, strongly influencing the dynamics of natural populations and communities [41]. However, under its most traditional perspective, community ecologyfocuses on a single spatial and local scale, as well as assuming closed and isolated communities, although species may interact through a regional scale among distinct communities [33], which might have large consequences on local patterns.

Accordingly, dispersal can modify the species composition in a community, since individuals moving through different habitats may have different characteristics from those that do not disperse [40]. Moreover, community patterns on a local scale may be influenced by other communities on a regional scale, mainly through individual's dispersal among distinct communities [10] resulting in a metacommunity connected by species dispersal [33]. This perspective

allows us to understand the patterns of natural communities on a regional spatial scale [33], including a set of local communities that are connected by dispersal of many species that may potentially interact [43].

Thus, a metacommunity approach can be a way to relate patterns and processes, expanding our spatial study scale to a regional scale, and considering dispersal as an important process in structuring communities and metacommunities. Several processes may be acting on these metacommunities structure. In heterogeneous landscapes, these processes can be exemplified thought two paradigms: species sorting and mass effect. When we consider that species are spatially separated by distinct niches and dispersal is not strong enough to alter their distributions, it is possible that these metacommunities are being structured by species sorting and the niche has greater effect than the species dispersal. On the other hand, if the structure of metacommunity is determined mainly by a strong dispersal between species, it is possible that the main process behind it is a mass effect, in which there is a source constantly supplying species to a sinking habitat [33].

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae), are mostly coprophagous insects [23], with great behavioural variation, such as daily activity [26] and a great variety of body shape and size [27]. In

addition, their nesting and feeding behaviour depends on the type of resource allocation performed by the species, such as: paracoprids or "tunellers", in which individuals dig tunnels and bury the food just below the food source; telecoprid or "ball-rollers" in which individuals roll the food, constructing balls and burying it in smaller depths away from the food source; and endocoprids or "residents", in which organisms build their nest inside the food source [23].

These insects are specific to certain habitats, resulting in a contrast between species from opened and forested areas [22, 24], a possible consequence of a niche differentiation process, allocating species in structurally distinct environments, structuring a metacommunity. Yet, little is known about how dung beetles react to habitat structure variation [3]and it is difficult to say whether individuals remain in the forest, as stated by Klein's (1989) observations in the Amazon forest, or in the open areas, even though their food is normally available on both. Movement may also vary by its purpose: foraging or nesting, or by characteristics related to behaviour, flight ability, sex or age. In addition, open and forest areas can be sources and sinks for species according to their habitat preferences.

One way to understand how dung beetles move and disperse is through mark, release and recapture studies (MRR)

[3,12,14,20,21,32,35,36,38,42]. However, for the Neotropics, few studies discuss how dung beetles move in different vegetation coverages [3, 12, 42], and even less how to quantify dispersal and relate it to community and metacommunity levels. Thus, we aim to describe the strength of dispersal over a metacommunity of dung beetles in an Atlantic Forest landscape with open and forest areas through the dispersal dynamics of species that inhabit distinct environments. We intended to answer the following questions: 1) In a population level: what are the patterns of species movement through a heterogeneous landscape? Does movement differ according to age or sex? Do individuals move to habitats different from those their niche corresponds to? How do intermediate environments fit into this context? 2) In a community level: What are communities' composition, richness, diversity and dissimilarity on a heterogeneous landscape scenario? Which species are typical of each community or which ones are result of a source and sink effect from distinct communities? 3) In a metacommunity level: Are the communities related by species dispersal resulting in a metacommunity? How strong is dispersal and niche influence over those patterns?

Materials and Methods

Environmental Characterization of the Study Area

The experiment was carried out in the São Joaquim National Park, Urubici (28°08 '28.4"S, 49°38'05.7"W), at an altitude of about 1300 meters, where open areas of natural fields, such as grasslands of altitude with shrub and herbaceous structure [9], and pastures formerly used for livestock conform a matrix beside forests fragments in different stages of Mixed Ombrophilous Forest. According to that, our experimental design was distributed along a gradient of three basic structural types of environments: Open Areas, which are a mixture between natural fields and sites previously used for livestock; Forest Fragments in different stages of Mixed Ombrophilous Forest; and Woodlands, which are open areas with scattered araucaria trees (Araucaria angustifolia) and without dense shrub vegetation.

Firstly, we differentiated the environments through a visual characterisation. At each point contained in our experimental design we made an evaluation of the vegetation structure to measure the structural differentiation between environments. Environmental measurements were performed using the point-centered quarter method [11] and included the distance to the first tree and the first shrub (as measures of

density) and the DAP and height of those (calculating a volume value), and the relative amount of litter soil and canopy coverage.

Sampling design: Spatial patterns of dung beetle's movement

Dung beetles were sampled with attraction traps at the summer of 2017 and 2018 (December to March). Beetles were collected using plastic containers (15 cm diameter; 8 cm deep) filled with soil in the background and baited once with 10 g of domestic dog faeces. Traps were buried at ground level and had an opening for individuals to enter. Moreover an "umbrella" was installed to avoid trap inundation. Thirty-six traps were arranged in seven sites in an area of 600 m in diameter, including three forest environments and three open area environments, as well as intermediate environments which were called as woodlands. Beside those, 20 additional traps were placed 1 km away (Fig 3).

Seven species were previously chosen to perform the experiment in the field due to their great abundance and biomass within the dung beetles' communities in the study area, according to previous studies [17], and following behaviour and morphology variations: *Dichotomius opalescens* (diurnal, paracoprid, 12mm length); *Canthon angularis* (diurnal, telecoprid, 6 mm length); *Dichotomius* aff. *acuticornis* (nocturnal, paracoprid, 13mm length); *Homocopris* sp. (nocturnal, paracoprid, 15mm length); *Canthon rutilans rutilans*

(diurnal, telecoprid, 9 mm length); *Coprophanaeus saphirinus* (diurnal, paracoprid, 17 mm length); *Deltochilum brasiliense* (crepuscular/nocturnal, telecoprid, 20 mm length).

After 24 hours, the insects were captured, identified, sexed, classified by age and marked. Later they were released in the same place where collected. This protocol was performed six times from December (2017) to March (2018), totalling five recapture events. The marking was performed with a dental micromotor (Beltec LB100) with a 0.5 mm spherical drill and the aid of a magnifying glass. We performed a scraping in the elytra of the individuals drawing a scheme of dots and lines resulting in a number as an individual mark. Each point represents a unit, and each line corresponds to the number 5. The right elytra correspond to the units, the left elytra to the decimals, the right part of the pronotum to the hundreds and the left part to the thousands (for mark method see Wuerges and Hernández, in press). To verify if the species were nesting, a nesting house was placed nearby every four traps.

Sampling design: Describing Communities

Thirty-six attraction traps, as described above, were used to collect the number of records of each species per point to describe the communities, as well as it was noted the geographical coordinates at each one of those sites (Fig 3). The individuals collected in each trap

were identified in the field with the aid of an identification guide from a reference from Entomological Collection of the Universidade Federal de Santa Catarina and put back to nature in the same place. The species not identified in the field were conserved in 70% alcohol and sent to Dr. Fernando Vaz-de-Mello (Universidade Federal de Mato Grosso, Brazil) to be identified. A total of six sampling events were performed, from December (2017) to March (2018).
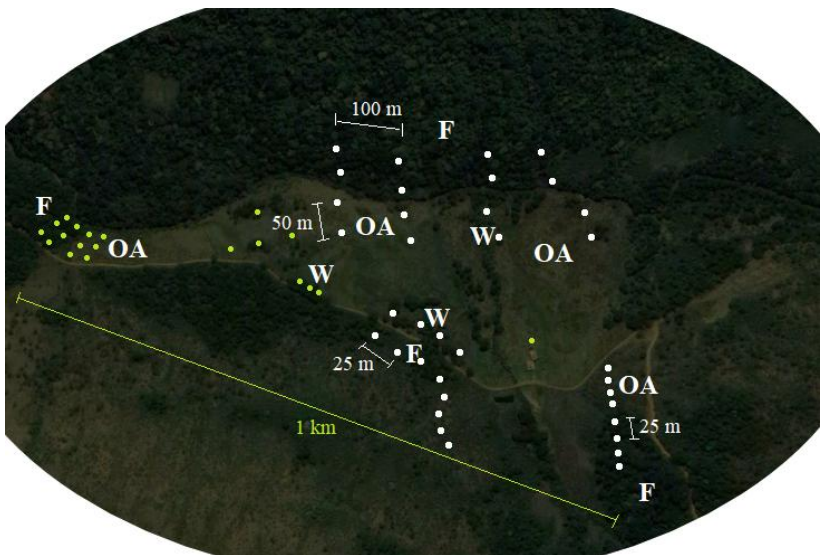
Fig 3. Representation of the experimental design containing three types of environments (OA: open areas, W: woodlands and F: forests) sampled in São Joaquim National Park, Urubici, highlands in Santa Catarina state, Brazil. The map shows a total of 56 sampling points: 36 sites for the communities' description (white circles ○), and 20 extra points (green circles ●) at larger distances for the mark-release and recapture (MRR) experiment. Image extracted from Google Earth.

Data analysis: Environmental Characterization of the Study Area

In order to distinguish and characterize the 36 sampling points within the three different environments we used the data from environmental characterization of the areas to separate the study sites according to their vegetative structure. We removed highly correlated variables, keeping only: distance from the first tree, volume of the tree, volume of shrub, percentage of litter, of naked soil and canopy cover. Then, we performed a PCA (Principal Components Analysis), based on the Euclidean distances of the environmental variables using a correlation matrix with the vegan package in R Studio. To select the number of axis, we applied the Kaiser-Guttman criterion, which reveals eigenvalues greater tha one [8].

The principal component analysis revealed two axes with eigenvalue> 1. These two components accounted for 81% of the total data variation. The first component explained 48% of the data variation and was positively associated with the distance of the first tree (DTRE), thus differentiating close from open areas (Fig 4, in brown). In addition, negative values of the first compenent were associated with canopy cover (CANO), indicating higher canopy coverage sites, representing forest areas (Fig 4, in green). The second component, which represented 33% of the data variation, is positively associated to the volume of the

first tree (VTRE), distinguishing a group of points representing an area with big trees nearby (negatively related to DTRE), such as araucaria trees, and absent shrub vegetation (negatively related to VSRH), named as woodlands (Fig 4, yellow square). According to that, the experimental design was categorized in the total of 13 sites of open area, nine of woodland and 14 sites of forest (Fig 4).
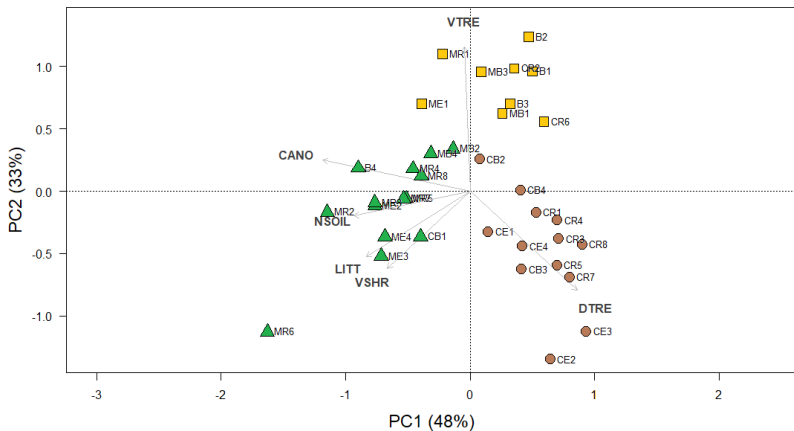
Fig 4. Principal Components Analysis (PCA), of the environmental variables measured on the 36 sampling sites. The brown circles correspond to open areas (●), related positively with DTRE (distance of the first tree); the green triangles correspond to forest areas (▲) related positively to CANO (canopy cover percentage), NSOIL (naked soil percentage), LITT (percentage of litter in the soil) and VSHR (volume of the first shrub); the yellow squares correspond to intermediate areas (▢) related with VTRE (volume of the first tree) in the second principal component.

Data analysis: Spatial patterns of dung beetle's movement

Only one recapture event was included in the analysis, and individuals recaptured at the same sites in the same sampling event were excluded from the analysis. We calculated a recapture rate per species as the number of recaptures / total number of marked individuals. Based on the Euclidean distance traveled by each species, we calculated the mean, median and maximum distance traveled. We calculate a "speed" of dispersal: MMR (Mean Movement Rate), which was the ratio between average distance and average time, by each species. We verified whether the distances differed by both sex through a t-test and age using a generalized linear model (with Poisson distribution).

Data analysis: Describing Communities

Following the results from previous analysis, we compared the dung beetles' communities between the three habitats: open area, woodland and forest, with an individual-based rarefaction and extrapolation of diversity for Hill numbers (q = 0, 1, 2) for each of the three communities. The 95% confidence intervals were obtained by a bootstrap method based on 50 replications. The baseline sample size was of 1820 individuals, being the double of the smaller reference sample size. Sample coverage and species accumulation curves for all three environments were calculated with the "iNEXT" R package [29].

To check for differences in composition among communities, we used a dissimilarity matrix accounting for beta diversity, measured as Jaccard pair-wise dissimilarity (a monotonic transformation of beta diversity), partitioned in turnover, measured as the turnover-fraction of Jaccard pair-wise dissimilarity, and nestedness, measured as the nestedness-fraction of Jaccard pair-wise dissimilarity. Besides that, including abundance data, it was used a dissimilarity matrix accounting for total abundance-based dissimilarity between sites, measured as the Bray-Curtis index, partitioned in the dissimilarity derived from balanced variation in abundance between sites and the dissimilarity derived from unidirectional abundance gradients. We used the package betapart in RStudio, to calculate Jaccard dissimilarity [4,5], and Bray Curtis dissimilarity [6].

Data analysis: Metacommunity level processes

To understand the processes acting over the metacommunity, we performed a redundancy analysis (RDA) with the relative abundance of species matrix data, transformed with the "Hellinger" method, combining it with the standardized environmental data matrix. After that, we performed an ANOVA-like permutation test for significant axis and environmental variables. Finally, we partitioned the variance through a partial RDA, by separating the effects of the significant

environmental variables (distance of the first tree, percentage of litter in the soil and percentage of canopy cover) and spatial matrix (with the geographical coordinates by point) over the explanatory matrix of relative abundance of species [7]. We used the packages vegan of the environment R to perform the analysis.

Results

Population level: Spatial patterns of movement

Were marked 2,032 individuals from seven species and recaptured 62 individuals from five species (Table 1). There were no recaptures of the species *Coprophanaeus saphirinus* (five marked individuals, one in open area, one in woodland and three in forest) and *Dichotomius* aff. a*cuticornis* (22 marked individuals, four in woodland and 18 in forest). For *Homocopris* spp. three individuals were marked in the forest and only one female was recaptured at the same site 11 days later. Of the species *Dichotomius opalescens* 148 individuals were marked: 28 in open areas, 69 in woodland and 51 in forest. Only one individual was recaptured (recapture rate = 0.68%), and it transited from forest to woodland travelling 76 m in 15 days. For *Deltochilum brasiliense*, 60 individuals were marked, one in open area, eight in woodland and 51 in forest; only one individual (rate = 1.67%) was

recaptured, transiting from woodland to forest crossing an open area and travelling 195 m in 22 days.

Canthon rutilans rutilans and Canthon angularis were the species with the greatest number of recaptures (Table 1). The covered distances did not differ according to sex for Canthon rutilans rutilans (t=1.49; d.f.=6.05, p=0.19), since females travelled 11±9 m/day and males tracked 57±81 m/day, and for Canthon angularis, (t=1.72, d.f.=24.05, p=0.10), since females travelled 9±12 m/day and males tracked 18±16 m/day. Young individuals of C. rutilans travelled longer distances (F=4.27, d.f.=2, p=0.02), since young ones travelled 77±109 m/day; mature 13±14 m/day, and old ones 16±15 m/day. Distance travelled did not differ according to age for C. angularis (F=0.43, d.f.=2, p=0.65) (young = 12±15 m/day; mature = 12±13 m/day; old = 18±17 m/day).

Table 1. Marked (Mark) and recaptured (Rec) individuals by species, sex and age categories, with movement values and time between recaptures for Scarabaeinae species in a fieldwork experiment performed in South Brazil. %: recapture rate. Sex: female (F) and male (M). Age categories: immature (I), young mature (Y), and old (O). Movement: mean movement rate (MMR [m/d]), number of individuals recaptured at the same trap (same), mean, median (med) and maximum (max) movement distance and time (range) in days.

Species	Individuals			Sex		Age			Movement (meters/days)					
	Mark	Rec	%	F	M	I	Y	O	MMR	same	mean	med	max	time
Homocopris sp.	3	1	3.33	1	0	-	-	-	0	1	0	0	0	11
D. opalescens	148	1	0.68	1	0	-	-	-	5	0	76	76	76	15
D. brasilense	60	1	1.67	-	-	-	-	-	9	0	195	195	195	22
C. angularis	**1270**	**30**	**2.36**	**14**	**14**	**8**	**13**	**9**	**14**	**5**	**208**	**103**	**954**	**15(9-39)**
C. rutilans	**524**	**29**	**5.53**	**20**	**7**	**4**	**12**	**13**	**13**	**4**	**250**	**237**	**675**	**19(1-63)**

Of *Canthon angularis*, 1270 individuals were marked. From those, 4 in open areas, 167 in woodlands and 1099 in forest and a total of 30 individuals were recaptured (rate = 2.36%). From those, 16 remained in the forest tracking an average of 105 m in 12 days (two individuals crossed woodland), and 8 individuals transited between forest and woodland, travelling on average 462 m in 22 days; and 4 individuals remained in the woodland travelling 21 m in 11 days (Fig 5A). Moreover, 2 individuals of *C. angularis* traveled between forest and open area, in an average of 390 meters in 15 days. Thus, they moved mainly around forests, tracking 14 meters/day and a maximum of 954 meters, and those individuals which might have crossed larger distances between areas, did it by crossing intermediate areas of woodland, or along forest fragments (Fig 5A). Besides that, in the nidification house, individuals only produced feeding balls in the forest and in the woodland.

Of *Canthon rutilans rutilans*, a total of 524 individuals were marked: 292 in open area, 180 in woodland and 52 in forest and a total of 29 individuals were recaptured (rate = 5.53%). From those, 15 remained in open areas, averaging 235 meters in 16 days; 5 remained in the woodlands, travelling on average 50 m in 14 days; seven moved between open area and woodland, travelling an average of 312 m in 23

days; and 4 individuals transited between open area and forest, averaging 322 m in 21 days. Thus, they mainly moved around open areas, travelling on average 13 meters/day and a maximum of 675 meters, but also moved around woodland, and on a smaller proportion, around forest areas (Fig 5B). Additionally, it was observed in the nidification houses that individuals constructed balls in all three areas.
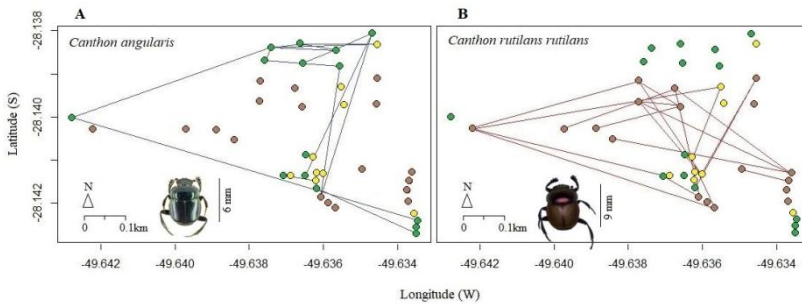
Fig 5. Movement patterns of dung beetle species. A) *Canthon angularis*. B) *Canthon rutilans* rutilans. Circles depict the trap design. Brown circles represent open areas sites (●); yellow circles represent woodland sites (●); green circles represent forests sites (●). Each line segment depicts a dung beetle movement between two traps. Time between recaptures ranged from 1 to 63 days.

Revealing community-level patterns

A total of 3,518 dung beetles from 23 species were sampled from the 36 sampling traps design, 1,585 in the forest, 1,021 in woodland and 910 in open area (Table 2). The five most abundant species (totalling over 90% from the total number of individuals) were

C. angularis, *Uroxys terminalis*, *C. rutilans rutilans, Canthon seminitens* and *Dichotomius opalescens*. Furthermore, *C. angularis* was the most abundant species in the forest, representing 72% of the total abundance of this environment. The most abundant species in the woodlands was *U. terminalis* followed by *C. rutilans*, *C. angularis* and *Canthon seminitens*, representing 36%, 18%, 17% and 17% from the total abundance respectively. Finally, *U. terminalis* was also the most abundant in open area, with 43% of the abundance, followed by *C. rutilans,* with 36% of the area abundance (Table 2).

Table 2. Abundance of dung beetles (Coleoptera: Scarabaeinae) according to three types of environments: Forest, Woodlands and Open Areas, sampled from December (2017) to March (2018) in the São Joaquim National Park, Urubici, Santa Catarina, southern Brazil

Species	Forest	Woodland	Open Area	Total
Canthon angularis	1146	174	5	1325
Uroxys terminalis	162	366	389	917
Canthon rutilans rutilans	58	184	327	569
Canthon seminitens	19	173	85	277
Dichotomius opalescens	50	63	25	138
Onthophagus tristis	36	19	1	56
Deltochilum brasiliense	38	6	1	45
Canthon aff. *coeruleicollis*	3	3	27	33
Dichotomius aff. *acuticornis*	26	6		32
Canthidium aff. *trinodosum* sp. 2	7	5	13	25
Canthidium aff. *lucidum*	18	3		21
Deltochilum morbillosum	1	5	6	12
Canthidium aff. *trinodosum* sp. 1	5	1	5	11
Uroxys dilaticollis	2	3	6	11
Canthidium moestum			10	10
Canthon aff. *luctuosus*	7	2		9
Onthophagus aff. *hirculus*	1	1	5	7
Canthon lividus	1	4	1	6
Coprophanaeus saphirinus	3	1	1	5
Canthon unicolor		1	2	3
Homocopris sp.	2			2
Ateuchus apicalis		1		1
Canthidium sp.			1	1
Total	1585	1021	910	3516

Sample coverage was of 99% in all three areas, demonstrating a proper sampling effortto register the species occurring in the region. Species richness (q=0) was similar in all three areas: forest had 19 observed species and 21 estimated richness (with lower and upper confidence level from 19 to 38); the woodlands had an observed richness of 20 species and 32 of estimated richness (confidence level from 22 to 114); and open areas had an observed richness of 18 species and 30 of estimated richness (confidence level from 20 to 112) (Fig 6A).

Including abundance data in the analyses, woodland had greater diversity, followed by open area, and the less diverse was the forest habitat, according to both Shannon and Simpson diversity estimated by Hill numbers, orders q=1 (Fig 6B) and q=2 respectively (Fig 6C). According to q=1, the typical species of woodland summed 5.79 species (with upper confidence level of 6.24), such as *U. terminalis, C. rutilans, C. angularis, C. seminitens, D. opalescens* and *O. tristis.* For the open area there was 4.34 typical species (upper confidence level of 4.76), such as *U. terminalis, C. rutilans, C. seminitens* and *C. coeruleicollis* and/or *D. opalescens*, and for the forest, the habitat with the lowest diversity, with only 3.21 typical species (upper confidence level of 3.46), such as *C. angularis, U. terminalis* and *C. rutilans* (Fig 6B).

Considering q=2 or Simpson metric, woodland had 4.48 abundant species (upper confidence level of 4.77), represented by *U. terminalis*, *C. rutilans*, *C. angularis*, *C. seminitens* and *Dichotomius opalescens.* For the open area, the value was 3.09 (upper confidence level of 3.29), meaning that the community is composed by three abundant species, represented by *Uroxys terminalis, C. rutilans* and *C. seminitens*. Finally, diversity for forest areas had an index of 1.86 (with upper confidence level of 1.97), meaning that the community is dominated by two abundant species, represented by *C. angularis* and *Uroxys terminalis* (Fig 6C and Table 2).
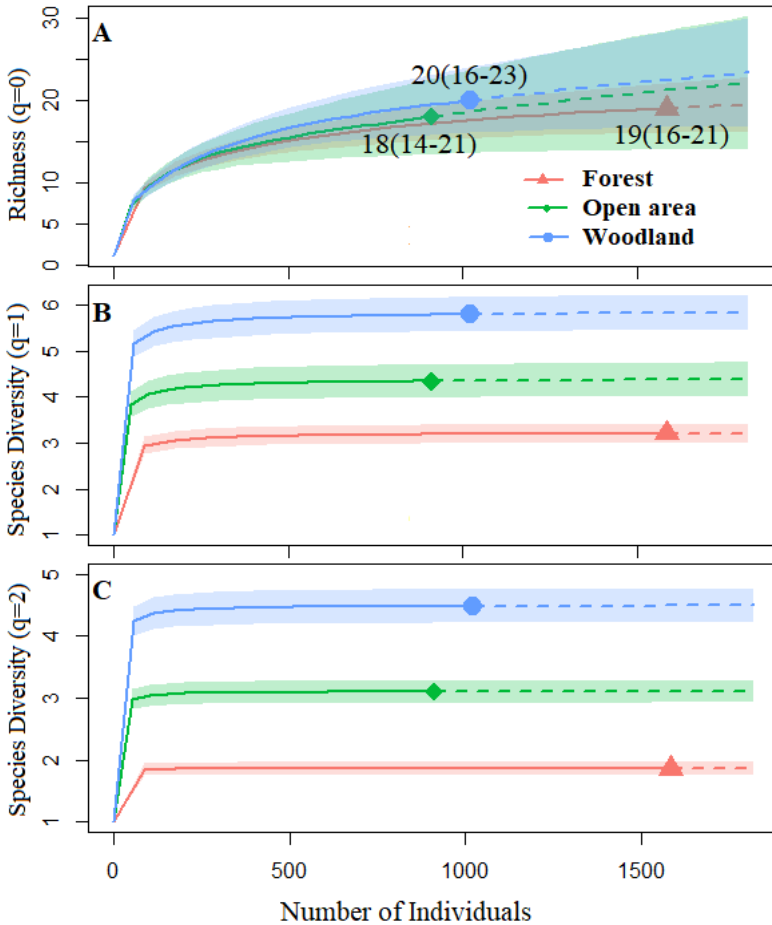
Fig 6. (A, B, C) Individual-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the reference sample size) of Dung beetles' diversity for Hill numbers (q = 0, 1, 2) for each of the three areas, up to the base sample size of 1820 individuals (i.e., double the smaller reference sample size). The 95% confidence intervals were obtained by a bootstrap method based on 50 replications. Reference samples are denoted by solid dots. The numbers in parenthesis are lower and upper limit confidence intervals.

According to the dissimilarity of Jaccard with incidence data, there was 0.35 of dissimilarity between forest and open area, partitioned in 0.29 of turnover and 0.06 of nestedness. Moreover, there was 0.27 of dissimilarity between open area and woodland, partitioned at 0.20 of turnover and 0.07 of nestedness; and 0.18 dissimilarity between woodland and forest, driven by turnover. Thus, dissimilarity in species incidence among communities was mainly driven by a turnover pattern, and it was greater between the most contrasting environments: open area and forest.

By adding abundance data using Bray Curtis dissimilarity, the dissimilarity among communities increased substantially, with 0.77 of dissimilarity between forest and open area, mainly driven by balanced variation (0.68), an equivalent of turnover, and less by unidirectional abundance gradients (0.09), an equivalent of nestedness. There was 0.60 of dissimilarity among forest and woodland, also mainly driven by balanced variation (0.50) and less by unidirectional abundance gradients (0.10). There was a lower Bray Curtis dissimilarity between open area and woodland (0.29), partitioned in 0.24 of balanced variation and 0.04 of unidirectional abundance gradients.

Therefore, when adding the abundance of species, we perceived an increase in dissimilarity between communities of different

environments, demonstrating that the change in abundance of species is an important factor in communities' differences. Most of the dissimilarity between forest and open area is a result of a balanced variation, which means that there is an inverse substitution of the species. This pattern also happens between open area and woodland, and between woodland and forest, demonstrating a great beta diversity among the communities. It evidences that in this heterogeneous landscape, where species richness is not different among habitats, abundant species in a certain site are not the most abundant in another distinct environment. As an example, *C. angularis* is an extremely abundant species in the forest, but much less abundant in open area, demonstrating high habitat fidelity, as well as *C. rutilans* is not abundant in the forest, but it becomes quite numerous in the open area, demonstrating habitat preference (Table 2).

Metacommunity level: Investigating processes

To understand the process behind the metacommunity we combined the species relative abundance data from each community with the environmental and spatial variables, and then one significant axis was extracted according to the ANOVA-like permutation test for redundancy analysis (F=38.4; df=1; p=0.001), as well as three environmental variables: distance of the first tree, percentage of litter in

the soil and canopy cover. According to the partial RDA, descriptors of vegetation structure have an expressive explanation, with 37% of the variation over the relative abundance of species. On the other hand, the geographic matrix, that is the spatial distance, explained only 6% of it. As previously reported, this result mitgh be a consequence from species great habitat fidelity, even if they are willing to fly and the distances are short. There was 14% of the variance shared among environmental and geographical data and the percentage of residuals was 43% (Fig 7).

Therefore, most of the variation of the relative abundance data of the species matrix was explained by the structural variation of the landscape. This is an evidence that niche can be a structuring issue for this metacommunity indicating species sorting as main process acting over these patterns. However, there is dispersal of species among distinct environments, since it was evidenced with our MRR experiment, as well as a small proportion of explanation over the metacommunity comes from the distance's matrix. Due to that, there might be a light source sink effect in the metacommunity, although it is not strong enough to decrease dissimilarity, refusing the idea of mass effect leading this scenario.
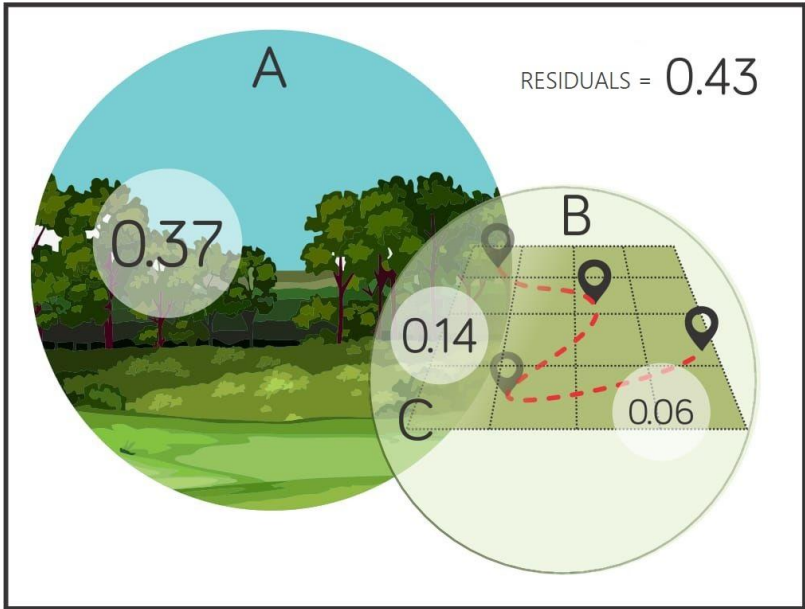
Fig 7. Venn diagram representing the variance partitioning among the explanatory variables over the metacommunity data. A) Explanatory proportion of the environmental variables (distance of the first tree, litter cover in the soil and canopy cover). B) Explanatory proportion of spatial data (geographical coordinates). C) Proportion of shared explanation among environmental and spatial variables.

Discussion

Our results demonstrate that dung beetle's species movement rates, measured between different and within the same environments, were quite low, an idea reinforced by other mark-release-recapture experiments as well [3, 14, 35]. Males and females of *Canthon rutilans rutilans* and *C. angularis* move 13 and 14 meter per day respectively, what is a tender difference from dispersal data that have already been

studied for *Canthon rutilans cyanescens*, with 24 meter per day on a homogeneous landcape [14]. Based on that, this research most important result is that spatial distance was not an important variable to explain the metacommunity relative abundance variation, demonstrating that species movement, or dispersal, is not strong enough to drive a mass effect acting over the dung beetles metacommunity structure. Therefore, species niches, represented by the environmental structure, explained most variation in the metacommunity relative abundance, as well as there was great dissimilarity among habitats, illustrating strong evidence of a species sorting effect leading as a process. Evidences related to habitat infuence over species distribution are well known for dung beetles [13, 15], but in naturally heterogeneous landscape, niche influence might increase as a process acting over communities' structure. Thus, the conformation of the metacommunity underwent a niche differentiation process, allocating species in structurally distinct environments, and possibly shaping it according to the species sorting paradigm proposed by Leibold and collaborators (2004).

We assesed species interactions between local and regional scales and laid out general patterns related to distinct communities within a metacommunity, which have both been described as important approaches to investigate metacommunities [37]. Therefore, our results

referring to species dispersal and distribution patterns, state that dung beetles move mainly, but not exclusively, in their specific environments, which reinforces known habitat fidelity descriptions for those insects [24, 25, 31]. Accordingly, in this research it was demonstrated that *Canthon angularis* is a forest specific species, and it moves mainly around forest, not crossing open areas when passing over different forest fragments, but it goes to woodlands, and less often, to open areas as well. This contrasts with Klein's (1989) results, which state that Tropical Forest Scarabaeinae do not leave forests, even when there is food availabe in open areas. Nevertheless, this proposal was in a natural continuous tropical forest context, not considering naturally opened areas such as high-altitude grasslands, such as our research refers to. Therefore, unlike the neotropical lowlands, where dung beetle dispersal studies were traditionally carried out [31, 39, 14], this study was conducted under a natural environmental heterogeneity. Considering that, in a heterogeneous landscape, characterized by open, forest and intermediate areas, species dispersal among distinct communities from distinct environments is an actual process, which evidences that these local communities form a metacommunity [28, 33], increasing beta diversity among habitats [17].

Such results reinforce our statement that different species might presentdiffering habitat fidelity, as well as distinct trade-offs between species attributes, might allow them to specialize in some types of habitat patches, resulting in niche differentiation, suggesting a species sorting scenario for this dung beetle metacommunity in a heterogeneous landscape [33]. Our results show that *Canthon rutilans rutilans*, as an open area predominant species, is typical from woodland and forest as well, even though it is much less abundant in forest. On the other hand, *C. angularis* is much less tolerant to the open areas than *C. rutilans* for the forest. This distinct habitat fidelity is reinforced by the fact that *C. angularis* only produces balls in the forest and woodland, and *C. rutilans* produces balls in all areas. Similar spatial patterns of movement were suggested to have a relationship with a trade-off between species attributes, since one would be a good disperser, such as *Canthon rutilans* and, the other one, a better competitor, such as *Canthon angularis,* within the forest fragment [12, 42]. Dispersal patterns of two *Dichotomius* species in a heterogeneous landcape of forests and coffee plantations exhibit similar results: one of the species was considered more associated to forest areas, since only one individual crossed distinct environments, and the other species, as more generalist one, travelling less than 500 m through different environments [12, 42].

Beyond dispersal patterns, our study embraced the distributional communities' patterns from the distinct environments. In the complete range of environmental heterogeneity addressed by this research, species richness was similar in all communities, which includes forest, woodland and open areas. However, there is a compositional dissimilarity between communities from those environments, predominantly lead by turnover of species, which corroborates previous studies in the same region [17]. Moreover, it was evidenced low nestedness between assemblages, which is an expected pattern in a metacommunity if the predominant process is species sorting [19]. Then, dispersal is not strong enough to result in sources and sinks, and consequently, insufficient to generate subset assemblages from distinct places. Thus, although dispersal happens and generates a light source sink effect between communities, it is low. For instance, our results evidence some individual's movement between structurally distinct environments: *C. angularis* is typical from forest, but it is possible to find it in open areas in a low abundance, and the opposite happens with both *Canthon seminitens* and *C. coeruleicollis*, which are typical from open areas and less abundant in forest ones. Additionally, when we included species abundance in the analysis, dissimilarity was even greater, and mainly driven by a balanced variation between

communities, that is, substitution of the most abundant species among different environments. It became clear with the decrease of some species abundance from the forest to the open area, at the same magnitude that the abundance of other species increased from the forest to the open area [6].

Still addressing the general patterns of the distinct communities in a range of environmental heterogenety, our results show that species diversity is higher in woodlands (intermediate areas), followed by open areas and forest as less diverse. This must be a consequence of great dominance of two very abundant species (*C. angularis* and *U. terminali*s) and less typical species in the forest, when compared to the other environments. It demonstrates that woodland, followed by open areas, has a greater number of typical and abundant species. Greater diversity in opened and intermediate areas can surprise if we consider that fragmentation has negative effects over dung beetle communities, through the change of vegetation from forests to pastures, resulting in loss of species diversity [18]. However, it is necessary to unlink the effects of the processes of fragmentation caused by human action from those processes in natural fragmented scenarios, which are still a challenge for ecology research [16]. It has been observed, by other studies in the same region, similar richness between open and forest

areas, and beyond that, greater richness in open areas than forests [17]. The region of study comprehends high species similarity to open grasslands in Brazilian Pampa as well as to high-altitude grassland in southern Brazil, which is a consequence from their related biogeographic history, resulting in a great range of species tolerant to naturally open areas [15]. Despite this range of species tolerant to open sites within this high-altitude landscape, they may have different abilities to deal with solar radiation in those areas. There is evidence that species appear not to have distinct responses to ultraviolet radiation [1]. For instance, it was demonstrated that *Canthon angularis* when compared to other forest species and with species that inhabit open agriculture areas, showed similar spectrophotometric responses [1]. However, some species may have preferences for open areas to acquire body temperature necessary for their activities [2]. Considering high altitude landscapes and low winter temperatures in our study region, some dung beetles might prefer open environments to forested areas, indicating that thermal tolerance influences their habitat selection [30, 34].

In conclusion, it is undeniable the importance of expanding study scale to metacommunities, since local patterns are strongly influenced by regional processes. In addition, this perspective is a path to relate

patterns and processes, and to address the problems of the "black box" of community ecology [41]. Finally, metacommunities have a great deal to contribute to environmental issues involving conservation measures, mainly considering the importance of the environmental heterogeneity in highland heterogeneous landscapes, since they are environments responsible for maintaining high local and regional diversity.

Acknowledgements

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CONCLUSÕES GERAIS

Com este trabalho demonstramos a importância de ampliar a escala de estudo para metacomunidades, uma vez que os padrões locais são fortemente influenciados pelos processos regionais. Esta perspectiva é um caminho para relacionar padrões e processos e para elucidar questões dentro da ecologia de comunidades. Além disso, o entendimento sobre metacomunidades tem muito a contribuir para as problemáticas ambientais, envolvendo medidas de conservação, principalmente considerando a importância da heterogeneidade ambiental em paisagens heterogêneas, uma vez que são ambientes responsáveis por manter alta diversidade local e regional.

Neste contexto, demonstramos que as espécies de besouros escarabeíneos possuem alta fidelidade de habitat, se movimentam pouco, e habitam principalmente as paisagens ou habitats compatíveis aos seus requerimentos ambientais. Além disso, a distância espacial não foi uma variável importante sobre a estrutura da metacomunidade, sugerindo que a dispersão das espécies não é forte o suficiente para impulsionar um efeito de massa sobre esta metacomunidade. Por outro lado, o nicho das espécies, representado pela estrutura ambiental, explicou a maior parte da variação da abundância relativa da metacomunidade, o que se soma ao fato de haver alta dissimilaridade entre as comunidades dos diferentes habitats, resultado principalmente de substituição de espécies. Estas são evidências da alocação das espécies nos diferentes ambientes como processo fundamental, sendo que existe dispersão, mas a coexistência de espécies dentro de um nível regional ocorre devido à diferenciação de nicho entre elas, ou seja, o nicho das espécies é um fator estruturante da metacomunidade e possui papel mais importante que a dispersão.

Adicionalmente, este trabalho testou uma metologia de marcação de besouros escarabeíneos, chamada de "escarificação", provando que este é um método que não tem influência sobre a sobrevivência, comportamento e fertilidade dos indivíduos, além de ser permanente e de fácil visualização, podendo ser aplicado em campo e em trabalhos com espécies de diferentes tamanhos ou formas. Após validar este método em laboratório e em campo, podemos concluir que a escarificação é um método confiável para estudos de marcação e recaptura, bem como permite prosseguir com estudos em nível individual, populacional ou de comunidades, incluindo dados da dispersão real dos indivíduos dentro dos ambientes naturais, enriquecendo estudos envolvendo metacomunidades.

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