Pedro Giovâni da Silva

EFEITO AMBIENTAL, ESPACIAL E TEMPORAL NA ESTRUTURAÇÃO DAS ASSEMBLEIAS DE SCARABAEINAE (COLEOPTERA: SCARABAEIDAE) NA MATA ATLÂNTICA DO SUL DO BRASIL

Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Doutor em Ecologia.
Orientadora: Prof.ª Dr.ª Malva Isabel Medina Hernández

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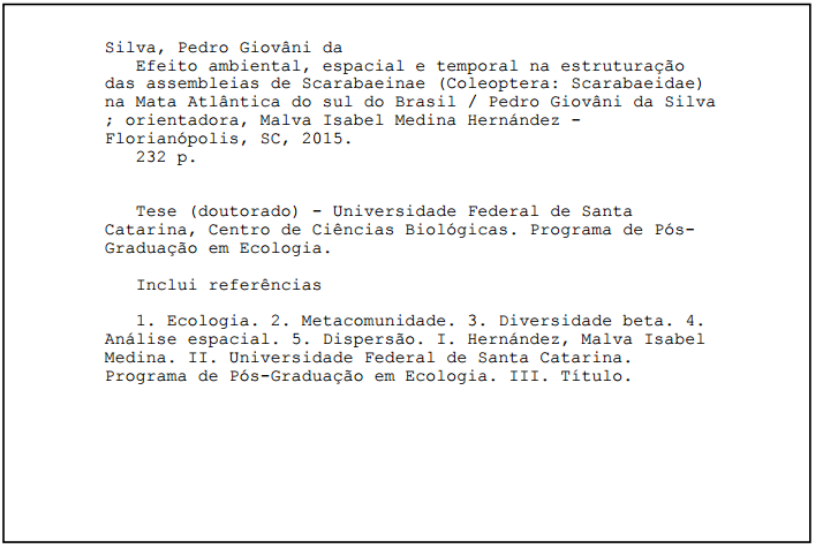

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“Efeito ambiental, espacial e temporal na estruturação das assembleias de Scarabaeinae (Coleoptera: Scarabaeidae) na Mata Atlântica do sul do Brasil”

Por

Pedro Giovâni da Silva

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Este trabalho é dedicado à minha esposa, pais e irmãs.

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RESUMO

Entender os processos pelos quais a diversidade beta é gerada é um dos principais objetivos da ecologia de comunidades. A teoria de metacomunidades trouxe novas formas de pensar sobre a estruturação das comunidades locais, incluindo processos presentes em diferentes escalas espaciais. Além de novas teorias, foram desenvolvidas novas técnicas que permitem identificar o padrão de distribuição de diversidade beta entre diferentes escalas, particionar a contribuição individual e compartilhada de efeitos ambientais, espaciais e temporais na estruturação das comunidades, e identificar locais e espécies que possuem relativa importância na geração da diversidade beta ao longo de gradientes ecológicos. Estas técnicas têm sido utilizadas com diferentes abordagens, como a diversidade funcional e a desconstrução das comunidades em grupos de espécies com traços relacionados. A distribuição espacial de comunidades de escarabeíneos (Coleoptera: Scarabaeinae) em áreas de Mata Atlântica em um cenário continente-ilha no sul do Brasil foi avaliada com o objetivo geral de identificar os processos que direcionam a distribuição da composição, abundância e biomassa das espécies em três escalas espaciais. A tese está dividida em quatro artigos científicos. O Artigo I tem como objetivo analisar a estrutura e a composição das assembleias de Scarabaeinae relacionando-as com a heterogeneidade ambiental de remanescentes florestais de Mata Atlântica. O Artigo II visa verificar em diferentes escalas espaciais os efeitos espaciais e da heterogeneidade ambiental na composição, abundância e biomassa de Scarabaeinae em remanescentes florestais de Mata Atlântica em um cenário de continente-ilha no sul do Brasil. No Artigo III foi avaliada a movimentação das espécies de Scarabaeinae em área de Mata Atlântica no sul do Brasil testando o protocolo de distância entre armadilhas de queda para estudos de biodiversidade dessa fauna. No Artigo IV investigaram-se em diferentes escalas espaciais os efeitos espaciais, temporais e da heterogeneidade ambiental utilizando as abordagens de diversidade funcional e desconstrução da comunidade. Para os Artigos I, II e IV o estudo foi desenvolvido em 20 sítios amostrais distribuídos em quatro localidades, duas no continente e duas na Ilha de Santa Catarina. A distribuição dos sítios amostrais é hierárquica e as localidades amostradas encontram-se isoladas. Os escarabeíneos foram amostrados através de protocolos padronizados (armadilhas de queda iscadas), durante o verão de 2012 (Artigo I e II) e 2013 (Artigo IV). O Artigo III foi desenvolvido na Unidade de Conservação Ambiental Desterro, uma área de proteção de Mata

Atlântica situada na Ilha de Santa Catarina. A movimentação das espécies de Scarabaeinae foi investigada através de experimento de marcação-soltura-recaptura entre novembro de 2013 e março de 2014. Os resultados gerais dos artigos sugerem: (i) várias espécies de Scarabaeinae estiveram associadas a determinadas características ambientais relacionadas à estrutura florestal da Mata Atlântica ou apresentaram associações com determinado sítio ou área de estudo amostrados no continente e na ilha, demonstrando a importância da distribuição espacial de áreas de Mata Atlântica com características ambientais espacialmente estruturadas para a manutenção e conservação da diversidade gama de Scarabaeinae; (ii) a importância relativa dos processos ecológicos envolvidos na estruturação das comunidades de Scarabaeinae amostradas em áreas de Mata Atlântica no sul do Brasil é dependente da escala espacial. A heterogeneidade ambiental é o principal direcionador da diversidade beta na escala local (sítios), enquanto efeitos espaciais (*mass effects* e limitação da dispersão) são mais importantes em largas escalas. O aumento da diversidade beta em escalas maiores parece ser resultante da limitação na capacidade de dispersão das espécies devido à fragmentação do hábitat e à presença de barreiras geográficas, especialmente entre continente-ilha. Em geral, a composição, abundância e biomassa de Scarabaeinae responderam de forma similar aos efeitos ambientais e espaciais; (iii) espécies com diferentes conjuntos de traços ecológicos parecem apresentar diferenças na habilidade de movimentação dentro da Mata Atlântica e, consequentemente, podem afetar de forma distinta a estruturação das comunidades locais de Scarabaeinae devido à maior ou menor limitação de dispersão. Ao investigar a movimentação das espécies de Scarabaeinae foi possível investigar o protocolo de distância entre armadilhas de queda utilizadas para a captura deste grupo. A nova distância de 100 m entre pares de armadilhas de queda iscadas é sugerida para substituir os 50 m anteriormente propostos por outros autores na amostragem padronizada de Scarabaeinae em florestas tropicais utilizando-se tanto fezes humanas como carne em decomposição como isca atrativa; (iv) a diversidade gama de Scarabaeinae foi atribuída principalmente à diversidade beta como consequência do aumento nas diversidades alfa e beta entre áreas quando comparadas as amostragens realizadas em 2012 e 2013. Índices de diversidade funcional podem ser utilizados como método complementar, mas não substitutivo, para investigar os efeitos ambientais, espaciais e temporais na distribuição das espécies. Ao desconstruir a comunidade, foi possível identificar dois grandes grupos de respostas entre 17 grupos funcionais avaliados. Em geral, filtros ambientais foram importantes nas escalas local e regional. Fatores espaciais foram mais importantes na escala intermediária, também suportando a dependência da escala dos processos ambientais, espaciais e temporais na distribuição e organização funcional de Scarabaeinae.

Palavras-chave: Metacomunidade. Ecologia de comunidades. Diversidade beta. Diversidade gama. Floresta ombrófila densa.

ABSTRACT

Understanding the processes generating beta diversity is a major goal of community ecology. Metacommunity theory brings new ways of thinking about the structure of local communities, including processes occurring at different spatial scales. In addition to new theories, new methods have been developed which allow identification of distribution patterns of beta diversity between spatial scales, partitioning of individual vs. shared contributions of environmental, spatial and temporal effects structuring communities, and for identification of species and sites that generate beta diversity along ecological gradients. These methods have been implemented using different approaches, such as functional diversity and community deconstruction into groups of species-related traits. In the following body of work, areas of Atlantic forest in southern Brazil were investigated within a mainland-island scenario, with the goal of identifying the processes driving composition, abundance and biomass distribution of dung beetle communities (Coleoptera: Scarabaeinae) at three different spatial scales. The thesis is divided into four scientific articles. Article I analyzed the structure and composition of Scarabaeinae assemblages by investigating their relationship with environmental variables in Atlantic forest remnants. Article II aimed to verify spatial and environmental variables effects on composition, abundance and biomass of dung beetles at different spatial scales. Article III evaluated the movement of Atlantic forest dung beetle species via distance between pitfall traps typically used in Scarabaeinae biodiversity studies. Article IV investigated spatial, temporal and environmental heterogeneity effects at different spatial scales using functional diversity and community deconstruction approaches. For Articles I, II and IV, the study was conducted on 20 sampling sites distributed among four areas, two on the mainland and two on the Island of Santa Catarina. The distribution of sampling sites is hierarchical, and the areas are isolated. Dung beetles were sampled using standard protocols (baited pitfall traps) during the summers of 2012 (Article I and II) and 2013 (Article IV). Article III was developed in the Desterro Environmental Conservation Unit, a protected Atlantic Forest area on the Island of Santa Catarina. Movement of dung beetle species was investigated using a mark-release-recapture experiment, performed between November 2013 and March 2014. The main results from articles suggest that: (i) some dung beetle species are associated with structural features of the Atlantic Forest, or with a particular site or study area on the mainland or island, demonstrating the importance of spatial distribution of Atlantic Forest habitats with spatially structured environmental characteristics for the maintenance and conservation of gamma diversity; (ii) the relative importance of ecological processes structuring Scarabaeinae communities in southern Brazilian Atlantic forest depends on spatial scale. Environmental heterogeneity is the main driver of beta diversity at the local scale (sites), while spatial effects (mass effects and limited dispersal) are more important at larger scales. The increase in beta diversity at larger scales seems to result from limitation of species dispersal ability due to habitat fragmentation and geographical barriers, primarily between the mainland and island. In general, the composition, abundance and biomass of dung beetles all respond similarly to environmental and spatial effects; (iii) species with different sets of ecological traits seem to differ in patterns of movement, and consequently may differentially impact local Scarabaeinae community structure due to greater or lesser dispersal limitation. Our study included capture using baited pitfall traps, and the results indicate that 100 m between pairs of traps should replace the 50 m distance proposed by other authors for standardized sampling of dung beetles in tropical forests, using both human feces and rotten meat as bait; (iv) the gamma diversity of Scarabaeinae was primarily attributed to beta diversity, as a result of the increase in alpha and beta diversity between areas when compared the samples collected in 2012 and 2013. Functional diversity can be used as a complementary, but not substitutive, approach to traditional measures of community responses for testing environmental, spatial and temporal effects on species distribution. Community deconstruction yielded two groups of responses from the 17 functional groups evaluated. In general, environmental filters were important at both local and regional scales. Spatial factors were most important at intermediate scales, providing further evidence for scale dependency of environmental, spatial and temporal processes in dung beetle distribution and functional organization.

Keywords: Metacommunity. Community ecology. Beta diversity. Gamma diversity. Dense ombrophilous forest.

SUMÁRIO

INTRODUÇÃO GERAL

PROBLEMA DE ESTUDO

Grande parte do sucesso evolutivo da espécie humana se deve à habilidade de reconhecer padrões. Para os ancestrais do *Homo sapiens* L., 1758 conhecer a distribuição das árvores frutíferas ou cereais comestíveis, presas, fontes de água potável, assim como as rotas de possíveis predadores era fundamental para a sobrevivência (BEGON et al., 2006). Atualmente, essa habilidade tem sido fundamental para identificar as consequências na biodiversidade causados pelos enormes problemas ambientais, principalmente pela atividade antropogênica, para reconhecer os resultados de efetivas estratégias de conservação e para a identificação de processos e mecanismos ecológicos relacionados à geração dos padrões de diversidade. A causa da variação espacial e temporal na distribuição da composição e abundância das espécies de organismos é o principal objeto de investigação da ecologia de comunidades (BEGON et al., 2006; RICKLEFS, 2008b).

O conceito de comunidade é definido como um conjunto de populações de diferentes espécies que ocorrem juntas ao mesmo tempo em determinado espaço (BEGON et al., 2006; MCGILL et al., 2006). Contudo, este conceito foi sofrendo mudanças ao longo de décadas por diferentes autores e sua utilidade dentro da ecologia tem sido debatida recentemente devido à falta de dimensão definida de uma comunidade, à dependência de escala do observador e suas múltiplas aplicações e interpretações (MAGNUSSON, 2013; PRADO & EL-HANI, 2013; MAGNUSSON, 2014).

Uma das principais críticas à ecologia de comunidades é que por muitas décadas os ecólogos devotaram enorme tempo e esforço para entender os processos e mecanismos na estruturação das comunidades localmente, sem levar em consideração a influência de processos que ocorrem em maiores escalas (RICKLEFS, 1987, 2008a). Tais processos foram há muito tempo evidenciados especialmente pelos trabalhos de Whittaker (1960, 1972) sobre diversidade alfa, beta e gama, e também de MacArthur & Wilson (1967) sobre a teoria de biogeografia de ilhas. O conhecimento dos processos locais não é suficiente para entender como as comunidades são estruturadas local e regionalmente (RICKLEFS, 1987, 2008a), uma vez que os processos que atuam em diferentes escalas espaciais podem influenciar de formas distintas o aumento ou diminuição da diversidade de espécies pelas escalas espaciais e temporais (RICKLEFS & SCHLUTER, 1993).

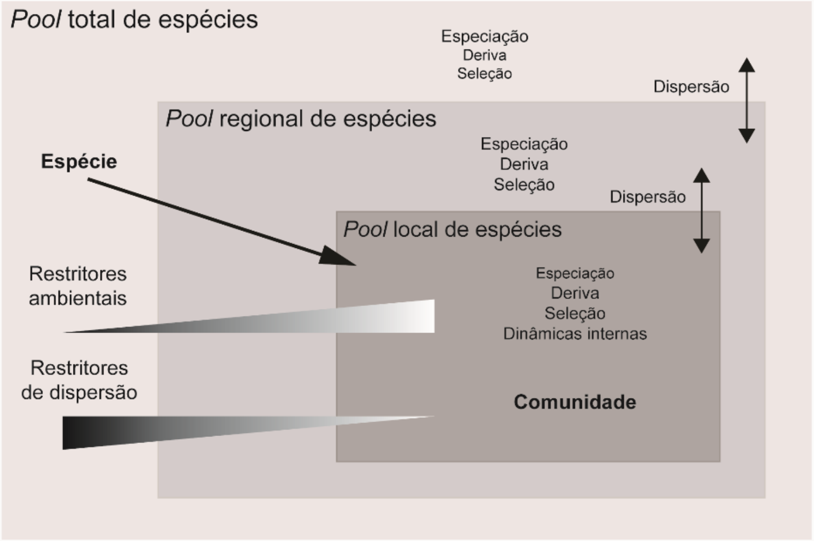
Deixando de lado a questão semântica ainda em aberto, o objetivo da ecologia de comunidades é entender a maneira pela qual os agrupamentos de espécies estão distribuídos espacial e temporalmente na natureza, e o modo como estes agrupamentos podem ser influenciados pelo ambiente abiótico e pelas interações entre as populações de espécies (BEGON et al., 2006; VELLEND, 2010). Em outras palavras, o cerne da ecologia de comunidades está em investigar as ‘regras de montagem’ (*assembly rules*) das comunidades (DIAMOND, 1975; CONNOR & SIMBERLOFF, 1979) ou os processos e mecanismos envolvidos na associação ou interação das espécies dentro de um espaço ecológico definido pelo grupo de organismos em estudo, pelo espaço físico e pelo tempo (MAGNUSSON, 2013).

Apesar dos vários mecanismos descritos, quatro processos básicos estão envolvidos na estruturação das comunidades biológicas: seleção (diferença determinística na aptidão entre indivíduos de diferentes espécies), deriva (mudanças aleatórias na abundância relativa das espécies), especiação (surgimento de novas espécies) e dispersão (movimentação dos organismos ao longo do espaço) (VELLEND, 2010). A importância destes processos pode variar dependendo da escala, onde a produção de espécies e a imigração são mais importantes em amplas escalas enquanto que as interações ecológicas são mais importantes para a diversidade local (Figura 1) (RICKLEFS, 2008a, 2008b). Uma espécie fará parte da comunidade local se ela superar os restritores de dispersão (for capaz de chegar ao local) e os filtros ambientais (for capaz de persistir no ambiente) (LAWTON, 1999; BEGON et al., 2006). A dinâmica dentro do conjunto de espécies que conseguiu chegar e persistir no ambiente determinará a composição e abundância das espécies da comunidade (coexistência). Neste contexto, processos históricos e eventos estocásticos que ocorrem em larga escala espacial e temporal são também importantes para o surgimento e extinção de espécies (RICKLEFS & SCHLUTER, 1993).

A percepção da importância das escalas (RICKLEFS, 1987; WIENS, 1989), especialmente a espacial, na estruturação das comunidades teve grande influencia no desenvolvimento da teoria de metacomunidades (LEIBOLD et al., 2004; HOLYOAK et al., 2005; LOGUE et al., 2011). A metacomunidade é formada por um conjunto de comunidades locais ligadas pela dispersão de várias espécies que potencialmente interagem entre si (LEIBOLD et al., 2004). Foram descritos quadro modelos teóricos para a caracterização de uma metacomunidade: *species sorting*, *mass effects*, *patch dynamics* e *neutral* (Figura 2) (LEIBOLD et al., 2004; LOGUE et al., 2011).

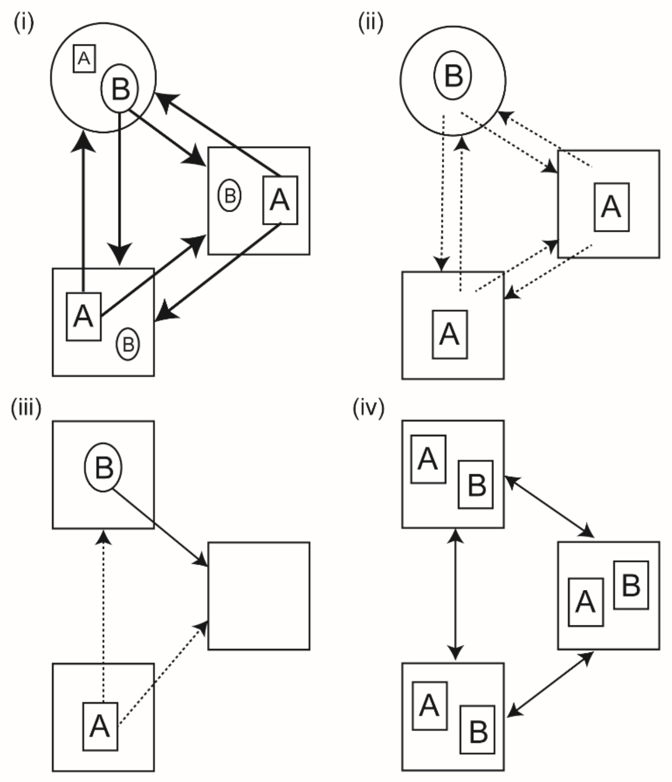
O paradigma *species sorting* enfatiza que a qualidade do ambiente e as interações entre as espécies são determinantes na estruturação da comunidade. A dispersão é suficiente para permitir que as espécies consigam acompanhar a variação nas condições ambientais (LEIBOLD et al., 2004; SOININEN, 2014). Neste paradigma, as condições ambientais permitem que espécies coexistam regionalmente por meio da diversificação de nicho (LEIBOLD, 1998).

Figura 1 – Modelo teórico da ecologia de comunidades mostrando a relação entre os diferentes *pools* de espécies e os processos ecológicos relacionados. Uma espécie do *pool* total de espécies fará parte da comunidade local se conseguir passar pelos restritores ambientais e de dispersão. Alguns processos ecológicos possuem maior importância em maiores escalas (e.g. especiação) enquanto outros possuem me menores escalas (e.g. dinâmicas internas). Adaptado de Begon et al. (2006) e Vellend (2010).



O resgate de espécies da exclusão competitiva, em comunidades onde ela é uma pior competidora, via imigração de indivíduos de áreas onde ela é uma boa competidora, é característico de uma metacomunidade guiada por *mass effects* (LEIBOLD et al., 2004). Neste modelo, há uma alta dispersão de indivíduos de sítios considerados de melhor qualidade para sítios de pior qualidade de recursos. Espera-se que o efeito de *mass effects* seja mais importante em extensões espaciais menores devido à maior proximidade dos sítios, independentemente da qualidade ambiental (HEINO et al., 2015a, 2015b).

Figura 2 – Representação esquemática dos quatro paradigmas da teoria de metacomunidades para duas populações de espécies competidoras A e B. Linhas sólidas indicam taxas maiores de dispersão do que linhas pontilhadas. Quadrados e círculos grandes indicam diferenças na qualidade ambiental para cada espécie. A espécie competidora dominante é representada pela igualdade de símbolos grandes (hábitats) e pequenos (espécies) em determinado sítio. Os paradigmas representados são: (i) *mass effects*, (ii) *species sorting*, (iii) *patch dynamics* e (iv) *neutral*. Adaptado de Leibold et al. (2004).



No paradigma *patch dynamics* há um *trade-off* entre a habilidade de dispersão e competição entre as espécies, onde espécies que são melhores competidoras podem excluir espécies que são piores competidoras. Em contrapartida, espécies que são piores competidoras podem ser boas colonizadoras e ocupar manchas vagas de hábitat que são ideais para ambas as espécies (LOGUE et al., 2011).

Em uma metacomunidade neutra as espécies são consideradas similares em sua habilidade competitiva, capacidade de dispersão e aptidão (HUBBELL, 2001), embora possam ser diferentes em seus traços ecológicos. A dinâmica da diversidade de espécies é fruto da probabilidade de perda (extinção e emigração) e ganho (imigração e especiação) de espécies (LEIBOLD et al., 2004). Winegardner et al. (2012) propuseram que *mass effects* e *patch dynamics* seriam variações de *species sorting*, conforme os diferentes níveis de capacidade de dispersão das espécies em cada modelo (alta, limitada ou eficiente, respectivamente). Dessa forma, os esforços dos estudos de metacomunidades devem ser direcionados para o papel relativo da heterogeneidade ambiental e da dispersão que são os processos estruturadores fundamentais das metacomunidades (LINDSTRÖM & LANGENHEDER, 2012). A definição dos termos relacionados à teoria de metacomunidades usados ao longo deste trabalho pode ser encontrada no Quadro 1.

A metacomunidade pode ser guiada por mais de um paradigma (LEIBOLD et al., 2004) e a importância relativa dos modelos teóricos pode variar conforme a escala de estudo (RICKLEFS, 2008a; DECLERCK et al., 2011) e também entre ambientes e grupos de espécies devido às diferenças inerentes aos tipos de ecossistemas e da capacidade de dispersão das espécies (LOGUE et al., 2011; SOININEN, 2014). Vários processos ecológicos são dependentes da escala (LEVIN, 1992), pois influenciam as comunidades de forma distinta entre as escalas local e continental (HUTTUNEN et al., 2014). As populações de espécies flutuam ao longo do tempo devido à variação demográfica, variação climática, mudanças ambientais e/ou interações com outras espécies, e o *turnover* temporal pode também ser útil na identificação dos principais processos estruturadores das comunidades locais (LEGENDRE et al., 2010). Além disso, o efeito temporal tem sido pouco investigado dentro da teoria de metacomunidades (ELLIS et al., 2006), embora possa ter um efeito importante sobre a dispersão (STOFFELS et al., 2015) e variação na heterogeneidade ambiental (BELLIER et al., 2014). As associações entre espécies também flutuam no tempo e espaço (MAGNUSSON, 2013), e podem às vezes ser independentes da alteração ambiental (WIENS et al., 2009).

O aumento da escala espacial em estudos recentes foi fundamental para o entendimento dos processos que geram os padrões de diversidade de espécies na perspectiva de metacomunidades (LOGUE et al., 2011) e vários estudos têm demonstrado a dependência da escala dos processos envolvidos na geração e manutenção da diversidade beta (e.g. FORBES & CHASE, 2002; HEIKKINEN et al., 2004; CADOTTE, 2006; FREESTONE & INOUYE, 2006; CORNELL et al., 2007; MACNEIL et al., 2009; TAMME et al., 2010; DECLERCK et al., 2011; GILADI et al., 2011; MEYNARD et al., 2013; MACEDO-SOARES et al., 2014). Porém, existe uma grande variação da importância dos efeitos ambientais e espaciais entre diferentes grupos de organismos e tipos de ecossistemas (SOININEN, 2014; HEINO et al., 2015a), e esta variação ainda foi pouco explorada quando consideradas diferentes escalas espaciais. A relação do efeito de processos ambientais e espaciais, e a interação entre ambos, com a diversidade beta pelas escalas espaciais em estudo ainda carece de suporte empírico, uma vez que esta relação muitas vezes depende do nível espacial da escala, do tamanho do gradiente ambiental e mecanismos ecológicos envolvidos (HEINO et al., 2015a). Assim, devem ser considerados simultaneamente os diferentes níveis da escala em estudo, as taxas de dispersão, a extensão espacial do estudo e o tamanho do gradiente ambiental, pois a importância relativa dos mecanismos estruturadores das comunidades é determinada por estes fatores (LEIBOLD et al., 2004; LOGUE et al., 2011; BINI et al., 2014; DATRY et al., 2014).

Um ponto chave para verificar a importância relativa dos processos relacionados à metacomunidade está na identificação e utilização de gradientes ambientais e/ou espaciais como possíveis cenários de estudo (LEGENDRE et al., 2005). Mundialmente, as florestas tropicais são os cenários de maior impacto da atividade humana, principalmente devido à alteração, degradação e supressão da vegetação nativa para a expansão agropecuária e urbanização (VIEIRA & GARDNER, 2012), o que as torna excelentes modelos para o estudo da importância de diferentes processos ecológicos na estruturação das comunidades biológicas frente às crescentes mudanças ambientais que nelas ocorrem.

Quadro 1 – Definições dos termos relacionados à teoria de metacomunidades usados ao longo deste trabalho. Adaptado de Leibold et al. (2004), Vellend (2010) e Heino et al. (2015a, 2015b).

Termo	**Definição**
Ecologia de comunidades	Estudo dos padrões na diversidade, abundância e composição de espécies nas comunidades, e dos processos inerentes a estes padrões (VELLEND, 2010)
Comunidade	Indivíduos de todas as espécies que potencialmente interagem entre si dentro de uma mancha ou área local de hábitat em determinando tempo (LEIBOLD et al., 2004; VELLEND, 2010)
Metacomunidade	Conjunto de comunidades locais que são ligadas pela dispersão de espécies que potencialmente interagem entre si (WILSON, 1992)
Assembleia	Grupo de espécies relacionadas filogeneticamente em uma mesma comunidade (FAUTH et al., 1996)
Guilda	Grupo de espécies não necessariamente relacionadas taxonomicamente ou filogeneticamente que explora recursos bióticos e abióticos de forma similar (ROOT, 1967; FAUTH et al., 1996)
Dinâmica da comunidade	Mudanças ao longo do tempo na abundância relativa das espécies em uma área específica, incluindo extinções e adição de espécies via dispersão e especiação (VELLEND, 2010)
Escala espacial	A escala espacial tem dois componentes: *grain* e *extent*. *Grain* refere-se ao tamanho da unidade amostral usado no estudo; e*xtent* refere-se ao tamanho da região que engloba todos os sítios em uma unidade de região (WIENS, 1989)
Nível de unidade de região	A unidade de região compreende um *pool* regional de espécies. Ex.: rio, bacia hidrográfica, ecorregião (HEINO et al., 2015a)
Sítio	Área discreta de hábitat que consegue abrigar populações ou comunidades, onde as interações bióticas e as respostas das espécies às condições ambientais ocorrem (LEIBOLD et al., 2004; HEINO et al., 2015a). Definição semelhante à de *patch* ou *locality* de Leibold et al. (2004)
Região	Ampla área de hábitat contendo vários sítios e capaz de suportar uma metacomunidade (LEIBOLD et al., 2004)
Condições ambientais	Características ambientais de um sítio que são agentes do modelo *species sorting* (LEIBOLD et al., 2004)

Heterogeneidade ambiental	Diferenças ambientais entre dois ou mais sítios ou variabilidade nas condições ambientais entre sítios dentro de uma unidade de região (ANDERSON et al., 2006)
Diversidade beta	Diferenças biológicas entre dois ou mais sítios ou variabilidade na composição de espécies entre sítios dentro de uma unidade de região (ANDERSON et al., 2006)
Species sorting	Paradigma da teoria de metacomunidades onde as espécies são ‘filtradas’ por fatores ambientais e interações bióticas para ocorrer em sítios adequados ambientalmente. Taxas de dispersão adequadas são necessárias para permitir às espécies acompanhar a variação nas condições ambientais entre sítios (LEIBOLD et al., 2004)
Mass effects	Paradigma da teoria de metacomunidades onde altas taxas de dispersão uniformizam a estrutura da comunidade em sítios adjacentes independentemente das condições ambientais e obscurecem o efeito de *species sorting* (LEIBOLD et al., 2004)
Patch dynamics	Paradigma da teoria de metacomunidades onde há um balanço (*trade-off*) entre colonização-competição, sendo que melhores colonizadores dominam comunidades isoladas ou recentes, enquanto melhores competidores os levam à extinção em comunidades menos isoladas ou maduras (HEINO et al., 2015b)
Neutral	Paradigma da teoria de metacomunidades onde todas as espécies são consideradas similares na habilidade competitiva, movimentação e aptidão. A aleatoriedade na especiação, extinção, emigração e imigração determinam a estrutura da comunidade (HUBBELL, 2001)
Neutralidade	Estado no qual todos os organismos individuais compartilham propriedades demográficas idênticas (VELLEND, 2010)
Dinâmica espacial	Qualquer mecanismo pelo qual a distribuição ou movimentação de indivíduos ao longo do espaço influencia a dinâmica populacional local ou regional (LEIBOLD et al., 2004)
Dispersão	Movimento de indivíduos de um sítio (emigração) para outro (imigração) (LEIBOLD et al., 2004)
Limitação de dispersão	Algumas espécies são impedidas de ocorrer em sítios adequados porque sítios ocupáveis mais próximos estão além da capacidade de movimentação dos indivíduos. A

	limitação de dispersão impede que o perfeito efeito de *species sorting* ocorra porque as espécies não conseguem ocupar todos os sítios ambientalmente adequados (LEIBOLD et al., 2004)
Taxa de dispersão	A taxa na qual os indivíduos se movimentam entre dois sítios. Se as taxas de dispersão são altas, elas podem dissociar comunidades do controle ambiental local (NG et al., 2009). Se as taxas de dispersão são baixas, elas resultam em uma ‘filtragem’ imperfeita de espécies porque nem todas elas conseguem ocupar todos os sítios ambientalmente adequados (HEINO & PECKARSKY, 2014)
Barreira à dispersão	Qualquer fator que impede as espécies de dispersar para todos os sítios dentro de uma unidade de região (HEINO et al., 2015a)
Estruturação espacial	A composição da comunidade mostra uma estruturação espacialmente se ela é significativamente relacionada com a localização espacial ou varia significativamente com o aumento da distância espacial entre os sítios (HEINO et al., 2015b)
Processo espacial	Processo externo que afeta a comunidade local, independentemente das condições ambientais locais. Processos espaciais são tipicamente relacionados à dispersão das espécies entre sítios, mas nenhuma distinção é feita se as taxas de dispersão são altas, médias ou baixas. A importância potencial dos processos espaciais em uma metacomunidade pode ser vista como uma variação na estrutura da comunidade explicada puramente por variáveis preditoras que descrevem a posição espacial de um sítio ou distâncias entre os sítios (mas não as que descrevem as condições ambientais) (HEINO et al., 2015b).
Diversidade funcional	Distribuição das espécies e suas abundâncias no espaço de traços funcionais em uma comunidade (MASON et al., 2005)
Traço funcional	Variável mensurável que tem o potencial de afetar o desempenho e a aptidão de uma espécie, podendo ser física, bioquímica, comportamental, fenológica ou temporal. As espécies consistem em conjuntos de indivíduos que compartilham traços similares (MCGILL et al., 2006; CADOTTE et al., 2011)
Desconstrução da comunidade	Método que particiona os dados de espécies-por-sítios em subgrupos homogêneos baseados nos traços das espécies (HEINO & PECKARSKY, 2014)

Partição da variação	Abordagem usada comumente nas análises de regressão e ordenação restrita (*constrained ordination*) para examinar quanto da variação na estrutura da comunidade local é explicada por fatores ambientais, variáveis espaciais e temporais, e por efeitos compartilhados (PERES-NETO et al., 2006)

SISTEMA DE ESTUDO

As florestas tropicais abrigam cerca de dois terços da biodiversidade terrestre do planeta e proporcionam benefícios locais, regionais e globais ao ser humano através do fornecimento de bens econômicos e serviços ecossistêmicos (GARDNER et al., 2009). A biodiversidade das florestas tropicais é influenciada por uma gama de processos antrópicos que operam em diferentes escalas temporais e espaciais, onde a fragmentação, a transformação e a perda de hábitat, aliadas à crescente intensificação do uso do solo (FAHRIG, 2003; GARDNER et al., 2009; FAHRIG et al., 2011) têm causado, direta ou indiretamente, a redução e a perda de diversidade biológica.

No Brasil, este cenário é alarmante devido à grande área de floresta tropical presente em seu território. O Brasil é o quinto país em extensão territorial do planeta, mas entre os maiores é, sem dúvida, o que mais se destaca pela sua megadiversidade (COSTA et al., 2000; MYERS et al., 2000; COSTA et al., 2005; GIULIETTI et al., 2005; LEWINSOHN et al., 2005; MITTERMEIER et al., 2005). Esta grande riqueza de espécies se deve principalmente à sua localização, pois a maior parte de seu território (incluindo as florestas) está dentro da faixa tropical. Os dois principais biomas florestais brasileiros, a Floresta Amazônica e a Mata Atlântica, há muito tempo têm enfrentado sérios problemas de desmatamento e transformação da vegetação devido à atividade humana (TABARELLI et al., 2004; FEARNSIDE, 2005; TABARELLI et al., 2005).

Entre os biomas mais fragmentados e ameaçados do Brasil está a Mata Atlântica. A Mata Atlântica, originalmente, era o segundo bioma em termos de extensão de floresta tropical presente na América do Sul, cobrindo mais de 1,5 milhões de km^2 pelo litoral brasileiro, desde o Rio Grande do Sul ao Rio Grande do Norte, nordeste da Argentina e sudeste do Paraguai (TABARELLI et al., 2005; RIBEIRO et al., 2009). Esta floresta está distribuída em diferentes condições topográficas e climáticas, desde áreas em contato com o mar até altitudes próximas de 2.700 metros (METZGER, 2009).

A Mata Atlântica é o bioma brasileiro mais ameaçado em termos de conservação de sua biodiversidade (MYERS et al., 2000; LAURANCE, 2009), restando cerca de 12% de seu tamanho original que está altamente fragmentado, com alto grau de isolamento e, na maior parte, em estado sucessional intermediário (METZGER et al., 2009; RIBEIRO et al., 2009; VIEIRA & GARDNER, 2012). De seu estado atual, menos de 2% está situado em áreas de proteção ambiental, embora esteja presente entre os 25 *hotspots* mundiais de biodiversidade (TABARELLI et al., 2005). Historicamente, o litoral do Brasil sempre teve a maior concentração populacional e industrial, e dessa forma, a Mata Atlântica tem sido afetada pelo crescimento e desenvolvimento do país (VIEIRA & GARDNER, 2012). Este cenário também é encontrado no estado de Santa Catarina.

Santa Catarina é o terceiro estado do país com maior área de Mata Atlântica, com 17% de sua cobertura original, além de possuir o terceiro maior remanescente florestal de Mata Atlântica (RIBEIRO et al., 2009). Na porção leste de Santa Catarina podem ser encontradas manchas de floresta ombrófila densa. Floresta ombrófila mista com araucária (*Araucaria angustifolia* (Bertol.) Kuntze) existe nas terras altas e mais frias do interior. Florestas decíduas ocupam algumas áreas na bacia do rio Uruguai (KLEIN, 1978, 1980, 1981; BEHLING, 1995; LAGO, 2000). Até 1950, a agricultura dominava a economia de Santa Catarina, mas foi em 1970 que o setor agrícola diminuiu enquanto o setor de serviços e as indústrias cresciam no estado, resultando em um aumento da cobertura florestal após 1975 (BAPTISTA & RUDEL, 2006). Contudo, muito do ganho em cobertura florestal durante a expansão industrial do estado deveu-se ao plantio de espécies exóticas como *Pinus elliottii* Engelm. e *Pinus taeda* L. em regiões de clima frio. O eucalipto (*Eucalyptus* spp.) também está entre as espécies exóticas plantadas no estado, embora em menor área (BAPTISTA & RUDEL, 2006). Entre os demais usos comuns do solo em Santa Catarina estão a produção de cerais e leguminosas, além da criação de bovinos, suínos e frangos (SANTA CATARINA, 2013).

O litoral de Santa Catarina se estende por aproximadamente 561 km (25º58” e 28º37” Sul; 48º25” e 48º49” Oeste) compreendendo 36 municípios costeiros (MORAES, 1995; SCHERER et al., 2006). A região central litorânea de Santa Catarina, onde se encontra a Ilha de Santa Catarina, que abriga a capital Florianópolis, é caracterizada pela presença de praias, costões rochosos e ramificações das Serras do Leste Catarinense (SCHERER et al., 2006). Esta região, em especial a Ilha de Santa Catarina, era coberta por densa floresta e a ocupação europeia, iniciada no século XVII (OLIMPIO, 1995), teve severos impactos na floresta e fauna devido ao desmatamento para agricultura (CARUSO, 1990; GRAIPEL et al., 2001). Devido à beleza natural presente na Ilha e municípios vizinhos, nas últimas décadas houve uma expansão da ocupação urbana e da pressão do setor imobiliário, especialmente em função do elevado turismo, o que tem causado impactos negativos aos ecossistemas costeiros ali presentes.

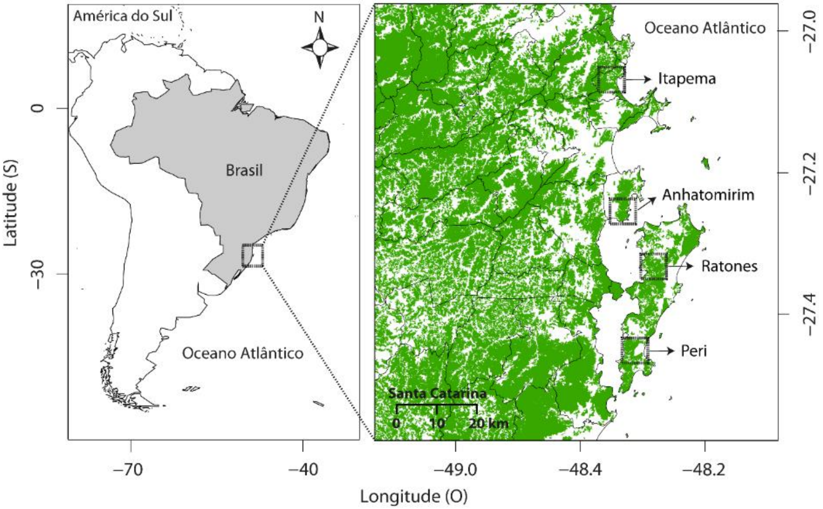
Santa Catarina apresenta um elevado grau de conservação de suas florestas em relação ao estado atual da Mata Atlântica no Brasil (RIBEIRO et al., 2009). Entretanto, estas florestas constituem-se de fragmentos de diferentes tamanhos em uma matriz heterogênea, composta basicamente por diferentes usos agropecuários e silviculturais do solo, além da intensa urbanização presente principalmente no litoral. Dessa forma, caracterizar a biota e entender os processos (e.g. ciclagem de matéria orgânica) nos quais ela esta envolvida são prioridades dentro do bioma Mata Atlântica (MYERS et al., 2000). Assim, a Mata Atlântica presente no litoral catarinense representa um importante cenário para a investigação de questões ecológicas relacionadas com o manejo e conservação da biodiversidade e funções ecossistêmicas.

Para o desenvolvimento do estudo, foram selecionadas quatro grandes áreas de Mata Atlântica localizadas no leste de Santa Catarina, sendo duas no continente e duas na Ilha de Santa Catarina. As duas áreas amostradas no continente estavam localizadas nos municípios de Itapema (áreas de proteção permanente) e Governando Celso Ramos (Área de Proteção Ambiental de Anhatomirim). As duas áreas na Ilha de Santa Catarina estavam localizadas no município de Florianópolis: localidade de Ratones ao norte da Ilha e Parque Municipal da Lagoa do Peri no sul da Ilha (Figura 3). Em cada uma das quatro áreas foram amostrados cinco sítios de Mata Atlântica.

OBJETO DE ESTUDO

Devido às várias limitações (de pessoal, tempo e investimento) que estudos de ampla extensão espacial ou temporal podem apresentar (GARDNER et al., 2008a), estas previsões têm sido muitas vezes baseadas em organismos indicadores (HALFFTER & FAVILA, 1993). Estes organismos devem ter uma íntima relação com o ecossistema e responder de forma rápida e mensurável às mudanças ambientais, além de ter sua taxonomia e biologia bem conhecidas (NOSS, 1990; ALLABY, 1992; HALFFTER & FAVILA, 1993; MCGEOCH, 1998; BÜCHS, 2003). Besouros escarabeíneos (Coleoptera: Scarabaeidae: Scarabaeinae) têm sido repetidamente propostos como um grupo útil para inventários e monitoramentos (SPECTOR, 2006), pois possuem todas as características de um táxon indicador ideal, e já têm sido utilizados em pesquisas ecológicas e levantamentos de biodiversidade por todo o mundo (HALFFTER & FAVILA, 1993; MCGEOCH, 1998; DAVIS et al., 2001; SPECTOR, 2006).

Figura 3 – Distribuição das áreas de Mata Atlântica amostradas no estudo. Áreas de proteção permanente em Itapema; Área de Proteção Ambiental Anhatomirim em Governador Celso Ramos; Áreas de Proteção Permanente em Ratones, Florianópolis; Parque Municipal da Lagoa do Peri, Florianópolis.



Besouros da subfamília Scarabaeinae destacam-se quanto à sua atuação na decomposição de material orgânico. Este grupo compreende cerca de 7.000 espécies de besouros extremamente importantes no funcionamento dos ecossistemas tropicais, uma vez que participam ativamente da ciclagem de nutrientes utilizando material orgânico em decomposição na alimentação tanto de larvas como de adultos (HALFFTER & MATTHEWS, 1966; HALFFTER & EDMONDS, 1982). A maioria das espécies se alimenta de fezes (coprófagos) ou de carcaças (necrófagos), estando intrinsecamente associados aos mamíferos que produzem seu recurso alimentar (HALFFTER & MATTHEWS, 1966; HALFFTER & EDMONDS, 1982; GILL, 1991; HANSKI & CAMBEFORT, 1991; ESTRADA et al., 1993; NICHOLS et al., 2007; FILGUEIRAS et al., 2009; CULOT et al., 2013; BOGONI & HERNÁNDEZ, 2014).

Algumas espécies de Scarabaeinae possuem alta especificidade de hábitat (HALFFTER, 1991) e não conseguem estender suas populações para áreas abertas ou de monoculturas (KLEIN, 1989; GARDNER et al., 2008b). Tais espécies são fortemente influenciadas pela fragmentação e perda de hábitat, podendo ter sua distribuição restrita ou mesmo desaparecer localmente (DAVIS & PHILIPS, 2005; HERNÁNDEZ & VAZ-DE-MELLO, 2009; BARLOW et al., 2010). Assim, os escarabeíneos podem ser utilizados em programas de monitoramento, uma vez que suas assembleias apresentam distintos padrões de organização associados ao uso do solo, sendo sensíveis a perturbações, o que lhes confere capacidade de bioindicação, ou seja, os padrões de estruturação são afetados por modificações antropogênicas ou não, muitas vezes diminuindo a riqueza, abundância ou biomassa das espécies ou alterações de suas guildas em áreas que sofreram alterações do hábitat (KLEIN, 1989; HALFFTER & FAVILA, 1993; DAVIS et al., 2001; GARDNER et al., 2008b; HERNÁNDEZ & VAZ-DE-MELLO, 2009; BARLOW et al., 2010; SILVA & DI MARE, 2012; CAMPOS & HERNÁNDEZ, 2013; SILVA et al., 2013; AUDINO et al., 2014; HERNÁNDEZ et al., 2014). Além disso, a riqueza de espécies de escarabeíneos é fortemente correlacionada com a de vários outros grupos taxonômicos, podendo ser utilizados como indicadores de diversidade (BARLOW et al., 2007). Outra vantagem dos escarabeíneos em estudos que avaliam as consequências ecológicas das mudanças ambientais é o alto desempenho da sua utilização, que combina baixos custos de coleta com protocolos padronizados e certa facilidade na identificação de espécies (GARDNER et al., 2008a).

Em geral, a estruturação das comunidades de escarabeíneos é fortemente influenciada pela elevada competição (SIMMONS & RIDSDILL-SMITH, 2011) por recursos alimentares escassos e efêmeros onde suas larvas se desenvolvem (HALFFTER & MATTHEWS, 1966; HANSKI & CAMBEFORT, 1991). A maior parte da biomassa da comunidade de escarabeíneos provém dos recursos obtidos das fezes de mamíferos (SPECTOR & FORSYTH, 1998). A partição de recursos entre as espécies coexistentes está baseada em diferentes modos de utilização do hábitat. Além do hábito alimentar (coprófagos, necrófagos ou saprófagos) e da forma de alocação do recurso (espécies escavadoras, roladoras e residentes), existem diferenças entre espécies na seleção de macrohábitat (florestas, campos, etc.) e microhábitats (de solo ou arborícolas) (DAVIS et al., 1997), na atividade diária (diurnos e noturnos) (HERNÁNDEZ, 2002) e no tamanho e forma do corpo (HERNÁNDEZ et al., 2011). Estas diferenças facilitam a coexistência entre espécies competidoras e incrementam a diversidade do grupo (HALFFTER & MATTHEWS, 1966; HANSKI, 1991; HALFFTER et al., 1992; CAMBEFORT, 1994).

Os escarabeíneos participam da ciclagem de nutrientes e promovem o revolvimento do solo e a incorporação da matéria orgânica, auxiliando na limpeza do ambiente e na regulação de propriedades físico-químicas do solo (HALFFTER & EDMONDS, 1982; HANSKI, 1991; BANG et al., 2005; SLADE et al., 2007; YAMADA et al., 2007; SLADE et al., 2011; BRAGA et al., 2013; GRAY et al., 2014). A construção de túneis para nidificação permite a aeração e hidratação do solo, assim como a incorporação dos nutrientes presentes nas fezes, carcaças de animais e frutos que são enterrados nessas galerias (HALFFTER & MATTHEWS, 1966; HALFFTER & EDMONDS, 1982; HANSKI, 1991, NICHOLS et al., 2008). Estes insetos enterram ovos de moscas, endoparasitas e outros organismos que também utilizam estes recursos como fonte alimentar e para reprodução (RIDSDILL-SMITH, 1981).

As funções ecológicas exercidas pelos escarabeíneos fazem deles excelentes alvos na investigação dos serviços ecossistêmicos relacionados à função de regulação, que compreende a capacidade dos ecossistemas de regularem processos e sistemas de suporte (DE GROOT et al., 2002; NICHOLS et al., 2008). Além disso, as assembleias de escarabeíneos respondem positivamente ao tempo de restauração de florestas (DAVIS et al., 2003), inclusive dentro do bioma Mata Atlântica (AUDINO et al., 2014; HERNÁNDEZ et al., 2014). Assim, ferramentas que auxiliem no manejo e na conservação do ambiente natural e seus recursos são extremamente necessárias, e o conhecimento da estrutura das comunidades contribui com informações que auxiliam as atividades de manejo de áreas naturais e políticas conservacionistas (DUFRÊNE & LEGENDRE, 1997). A biologia única dos escarabeíneos faz deles modelos empíricos excelentes para se explorar conceitos gerais de ecologia (ROSLIN & VILJANEN, 2011; SIMMONS & RIDSDILL-SMITH, 2011), incluindo as abordagens sugeridas pela teoria de metacomunidades, onde há a inclusão de aspectos ambientais, espaciais, de comunidades e populações.

Baseado no extenso arcabouço de evidências em estudos de metacomunidades de diferentes organismos e ecossistemas (e.g. LEIBOLD et al., 2004; HOLYOAK et al., 2005; HEINO et al., 2015a, 2015b) espera-se que a variação na heterogeneidade ambiental (*species sorting*) seja mais importante para a estruturação das assembleias de Scarabaeinae na menor escala espacial, enquanto que efeitos espaciais (e.g. limitação da dispersão) sejam mais importantes conforme o aumento da escala espacial. Esta relação com as condições ambientais resultará em assembleias espacialmente estruturadas conforme a variação nas condições ambientais entre os sítios estudados, mostrando associações significativas entre as espécies de Scarabaeinae e determinadas variáveis ambientais. Espera-se ainda que a resposta aos efeitos, ambientais, espaciais e temporais da metacomunidade seja semelhante para composição, abundância, biomassa e diversidade funcional dos escarabeíneos. Diferentes grupos de espécies baseados em conjuntos de traços funcionais irão apresentar respostas distintas aos efeitos ambientais, espaciais e temporais.

OBJETIVOS

OBJETIVO GERAL

O objetivo deste estudo é investigar a importância de diferentes escalas espaciais sobre os efeitos espaciais, temporais e da heterogeneidade ambiental em áreas de Mata Atlântica na estruturação das assembleias de Scarabaeinae em um cenário de continente-ilha no sul do Brasil.

OBJETIVO DOS ARTIGOS

- **Artigo I:** Analisar a estrutura e a composição das assembleias de Scarabaeinae relacionando-as com a heterogeneidade ambiental de remanescentes florestais de Mata Atlântica;

- **Artigo II:** Verificar em diferentes escalas espaciais os efeitos espaciais e da heterogeneidade ambiental na composição, abundância e biomassa de Scarabaeinae em remanescentes florestais de Mata Atlântica em um cenário de continente-ilha no sul do Brasil;

- **Artigo III:** Avaliar a movimentação das espécies de Scarabaeinae em área de Mata Atlântica no sul do Brasil e testar o protocolo de distância entre armadilhas de queda para estudos de biodiversidade dessa fauna;

- **Artigo IV:** Investigar em diferentes escalas espaciais os efeitos espaciais, temporais e da heterogeneidade ambiental utilizando as abordagens de diversidade funcional e desconstrução da comunidade.

ARTIGO I: SPATIAL VARIATION OF DUNG BEETLE ASSEMBLAGES ASSOCIATED WITH FOREST STRUCTURE IN PROTECTED REMNANTS OF BRAZILIAN ATLANTIC FOREST

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> “Intelligence is the ability to adapt to change.”
>
> (Stephen Hawking)

Spatial variation of dung beetle assemblages associated with forest structure in protected remnants of Brazilian Atlantic Forest

Abstract The Brazilian Atlantic Forest is one of the world's biodiversity hotspots, and is currently highly fragmented and disturbed due to human activities. Variation in environmental conditions in the Atlantic Forest can influence the distribution of species, which may show associations with some environmental features. Dung beetles (Coleoptera: Scarabaeinae) are insects that act in nutrient cycling via organic matter decomposition and have been used for monitoring environmental changes. The aim of this study is to identify associations between the spatial distribution of dung beetle species and Atlantic Forest structure. The spatial distribution of some dung beetle species was associated with structural forest features. The number of species among the sampling sites ranged widely, and few species were found in all remnant areas. Principal coordinates analysis indicated that species composition, abundance and biomass showed a spatially structured distribution according to the forest structure of the areas sampled, and these results were corroborated by permutational multivariate analysis of variance. The redundancy analysis showed an association of several dung beetle species with some explanatory environmental variables related to Atlantic Forest structure. This work demonstrated the existence of a spatially structured distribution of dung beetles, with significant associations between several species and forest structure in Atlantic Forest remnants from Southern Brazil.

Keywords Beta diversity; Species composition; Species diversity; Spatial distribution; Tropical forest.

Introduction

Tropical forests host most of the earth's biodiversity, and provide several benefits to human beings through the provision of economic goods and ecosystem services (Gardner et al. 2009). In contrast, the drastic reduction of biodiversity and maintenance of ecosystem processes associated with biodiversity depend on effective conservation initiatives, which are major challenges to conservationists and decision makers (Gardner et al. 2009; Rands et al. 2010; Tabarelli et al. 2010). There are many barriers to the creation of effective conservation policy decisions, including lack of established conservation practices tailored to different local conditions, a paucity of basic information on species abundance, distribution and conservation status, and perhaps most importantly, the potentially large number of unknown species (Pimm et al. 2014). Such shortcomings in our knowledge about species identity and local or regional distribution are referred to as Linnean and Wallacean shortfalls (Whittaker et al. 2005). Some of these gaps can be filled by connecting important issues such as the fulfillment of basic studies (e.g. associations between species and environmental conditions) in order to contribute to the knowledge on species distribution and also to the potential to discover new species. Furthermore, these studies can bring new information on spatial distribution of species associated with the variation in environmental conditions, which may be taken into consideration in planning conservation initiatives.

In Brazil, Atlantic Forest hosts a large part of the biodiversity of South American rainforests (Myers et al. 2000; Tabarelli et al. 2005) and was the second largest rainforest type in South America, covering about 150 million hectares of the Brazilian coast, northeastern Argentina and southeastern Paraguay (Tabarelli et al. 2005; Ribeiro et al. 2009; Vieira and Gardner 2012). Historically, the Brazilian coast has always had the highest human population and industrial concentration and, thus, the Atlantic Forest has been affected by the growth and development of the country over the last five centuries (Dean 1996), mainly in the last century. The Atlantic Forest is currently the most endangered Brazilian ecosystem in terms of biodiversity conservation (Myers et al. 2000). Recent studies indicate that only 12% of its original area remains, much of it fragmented with a high degree of isolation, and most in an intermediate state of regeneration (Ribeiro et al. 2009). Regardless, the fragments are usually of different sizes and exist in a heterogeneous matrix, consisting mainly of areas being used for various agriculture and forestry purposes. These features make the Atlantic Forest a very heterogeneous ecosystem, housing species with different environmental requirements.

The study of the diversity-environmental heterogeneity relationship of organisms that have key ecological functions and can be used as ecological indicators, such as dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae), is a first step to support biodiversity conservation initiatives and management of ecosystem processes in tropical forests. Dung beetles are detritus-feeding insects that aid in organic matter decomposition and nutrient cycling (Halffter and Matthews 1966; Hanski and Cambefort 1991; Simmons and Ridsdill-Smith 2011) by burying and consuming portions of feces, animal carcasses and rotting plant matter, thereby making the nutrients in these materials available to the ecosystem once again (Nichols et al. 2008). These insects construct tunnels in the soil, increasing aeration and water infiltration. They also bury eggs of cattle parasites (e.g., flies and nematodes) and secondarily disperse fruit seeds previously consumed by mammals on which they feed (Andresen and Feer 2005; Nichols et al. 2008).

Dung beetles have been used as a tool for monitoring environmental changes in tropical forests because they are sensitive to fragmentation, disturbance and habitat loss (Klein 1989; Halffter and Favila 1993; Davis et al. 2001; Nichols et al. 2007; Gardner et al. 2008b; Korasaki et al. 2013; Viegas et al. 2014) and because they respond positively to increased restoration time in tropical forests (Davis et al. 2003; Audino et al. 2014; Bett et al. 2014; Hernández et al. 2014). However, few studies have been identified important associations between dung beetle species and small changes in forest features (e.g. Hernández and Vaz-de-Mello 2009; Campos and Hernández 2013). Most studies investigate the Scarabaeinae community response when there is a clear environmental change, such as forest vs. open habitats (Lopes et al. 2011; Costa et al. 2013; Silva et al. 2014), forest vs. monocultures (Gardner et al. 2008b; Barlow et al. 2010), or distinct vegetation formations (Almeida and Louzada 2009).

Changes in environmental conditions in small spatial extents may be key drivers of compositional and structural differences in dung beetle communities in tropical forests (Feer 2013; Medina and Lopes 2014; Silva and Hernández 2014). Changes in dung beetle communities affect their ecological functions, and hence proper ecosystem functioning (Vulinec 2002; Andresen 2003; Horgan 2005; Slade et al. 2007; Gardner et al. 2008b; Kunz and Krell 2011; Slade et al. 2011; Braga et al. 2012; Braga et al. 2013). In addition, these beetles are correlated with other taxa, particularly mammalian fauna (Barlow et al. 2007; Culot et al. 2013). Thus, the evaluation of the spatial distribution of dung beetle fauna, which combines ease of identification and low-cost and standardized sampling methods (Gardner et al. 2008a), may contribute to research concerning effectiveness of conservation management, especially in a heterogeneous environment as the Atlantic Forest.

The aim of this study was to determine whether small differences in forest structure affect the distribution of Scarabaeinae dung beetles in remnants of Atlantic Forest in southern Brazil. We predict that dung beetle fauna will show spatial distribution in relation to structural features of the Atlantic Forest.

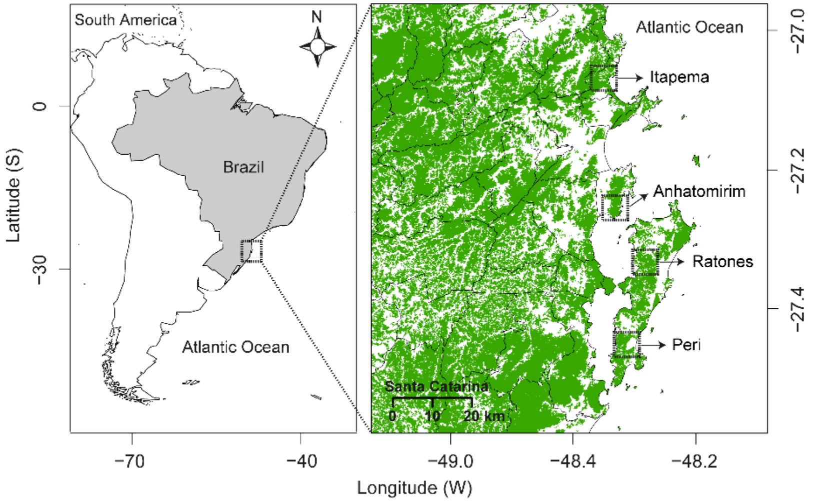
Methods

Study area

The study was performed in four large, non-contiguous areas of Atlantic Forest in Santa Catarina state, southern Brazil (Fig. 1). Two areas are located on the Island of Santa Catarina: Peri Lagoon Municipal Park (PER, 27°42’ and 27º46’S; 48°32’ and 48º30’W) and Permanent Protection Areas of Ratones (RAT, 27°30’ and 27º32’S; 48°30’ and 48º27’W), both located in Florianópolis city. Other two areas are located on the mainland near the Brazilian Atlantic coast: Anhatomirim Environmental Protection Area (ANH, 27º22’ and 27º26’S; 48º35’ and 48º33’W) located in Governador Celso Ramos city, and Permanent Protection Areas of Itapema (ITA, 27º02’ and 27º05’S; 48º38’ and 48º35’W) located in Itapema city. The Island of Santa Catarina is approximately 54 km (north-south length) with a maximum width of 18 km, with a total area of 424.4 km². The distance between the island and mainland varies, with a minimum distance of 500 m and maximum around 10 km. Despite the conversion of forest for agricultural, livestock and forestry activities, the state of Santa Catarina in southern Brazil still contains the third highest Atlantic Forest area among the states, with 17% of its original cover; it also contains the third largest Atlantic Forest remnant (Ribeiro et al. 2009). Regardless, the fragments are usually of different sizes and exist in a heterogeneous matrix, consisting mainly of areas being used for various agriculture and forestry purposes.

All sampled areas contain dense ombrophilous forest (Veloso et al. 1991) within the Atlantic Forest biome, with vegetation in different stages of succession. According to the Köppen classification the climate is Cfa, humid subtropical (mesothermal) with hot summers (average 25°C), no dry season and well distributed rainfall throughout the year averaging around 1,500 mm annually (Veloso et al. 1991). Over the decades there have been several conflicts of interest regarding these areas, primarily related to illegal occupation and lack of public administration oversight. The altitude of the sampled sites ranged between 28 and 265 m asl. The distance between the protected areas ranged between 13.5 and 71 km, and the distance among sampling sites within areas varied between 500 m to several kilometers (ca 6 km).

Fig. 1. Map of the Atlantic Forest remnants where dung beetles were sampled during January and February 2012. Anhatomirim Environmental Protection Area in Governandor Celso Ramos city; Permanent Protection Areas of Itapema city; Peri Lagoon Municipal Park in Florianópolis city; Permanent Protection Areas of Ratones in Florianópolis city.



Dung beetle sampling

Dung beetles were sampled at each of the four study areas at five different sampling sites per area located on hillsides near rivers. Baited pitfall traps were used for sampling dung beetles. Each sampling site consisted of 10 traps distributed in pairs, with each pair spaced 50 m apart. A minimum distance of 50 m decreases the risk of influence of other sets of traps on sampling of dung beetles (Larsen and Forsyth 2005). Paired traps were spaced 5-10 m apart. Each pair of traps was considered a sampling unit, and all traps remained in the field for 48 h.

The traps consisted of plastic containers (15 cm diam. x 20 cm depth) buried with their edge level with the ground. A rain guard was placed above the traps to prevent trap overflow and to support the bait. Traps contained a solution of water and detergent (300 ml) for catching fallen beetles. Traps contained two different bait types, including human feces and rotting flesh (30 g) (i.e., to attract coprophagous and necrophagous species, respectively). The baits were individually wrapped in thin cloth and tied in the central portion of the rain guard. All beetles collected were sorted, mounted on entomological pins and dried in an oven (60°C for 72 h) then weighed. They were identified by experts (Fernando Vaz-de-Mello and David Edmonds) and deposited in the Entomological Collection of the Centro de Ciências Biológicas at the Universidade Federal de Santa Catarina, Brazil. The samplings were performed during the summer of 2012 (January and February). This period is characterized by high regional temperatures, as well as being the period of greatest dung beetle abundance in southern Brazil (Hernández and Vaz-de-Mello 2009; Silva et al. 2013).

Forest structure

For each area, forest structure was described by 15 environmental variables, which were tested for influence on dung beetle distribution. Variation in tree features, such as density, height and canopy cover, can change microclimatic conditions that may affect dung beetles (Feer 2008, 2013). Furthermore, the physical structure of the forest floor, such as increased leaf litter, can affect the nesting activities of some guilds of dung beetles (Nichols et al. 2013). Measurement of variables was performed using the adapted point-centered quarter method (Cottam and Curtis 1956). Briefly, a plastic cross was placed in the center of each pair of traps (i.e., at each sampling point), dividing the sampling point into four quadrants (northwest, southwest, southeast and northeast). Tree, shrub and soil environmental variables were measured in each quadrant as follows: (1) circumference at breast height when diameter at breast height [DBH] > 5 cm), (2) height, (3) top diameter and (4) distance from the nearest tree to the center of cross, (5-8) repeated same measures for shrubs with circumference at ankle height when DBH < 5 cm and with a minimum height of 1 m, (9) land slope, (10) altitude, (11) canopy cover, (12) percentage of leaf litter cover, (13) green (vegetation up to 1 m height) cover, (14) exposed soil, and (15) height of leaf litter. Additional information on the methods used and environmental measures can be found in Appendices A and B.

Data analysis

The sampling effort was verified by smoothed species accumulation curves using data of the number of individuals for each sampling site and area. The data were extrapolated two times in relation to the number of samples per site (Colwell et al. 2012). Species richness was compared graphically between sampling sites and areas using the rarefaction method. The estimated species richness was obtained by using Chao 1 estimator (and its confidence interval) that it takes into account the abundance of species. We used the EstimateS 9.1 program for these analyzes (Colwell 2013).

We performed a Principal Coordinates Analysis (PCoA) to map the similarity between sites regarding to composition, abundance and biomass of dung beetle assemblages. These analyses were based on Bray-Curtis similarity, and abundance data were square root transformed prior to analysis. A Permutational Multivariate Analysis of Variance (PERMANOVA) was used to test for significant differences in dung beetle assemblages between sampling areas. PCoA and PERMANOVA were performed in R 3.0.1 program (R Core Team 2014) and Primer 6 with PERMANOVA+ package (Clarke and Warwick 2005; Anderson et al. 2008), respectively.

The Indicator Value Index – IndVal (Dufrêne and Legendre 1997) was used to assess possible associations of dung beetle species with sampling areas (De Cáceres and Legendre 2009). This method combines the degree of specificity of an ecological status, presenting the percentage of occurrence and significance for each species independently (McGeoch et al. 2002). This analysis was performed in R 3.1.1 program (R Core Team 2014) using the indicspecies package (De Cáceres 2013) with 999 permutations, using data for dung beetle abundance.

Redundancy Analysis (RDA) was used to verify the linear relationship between dung beetle abundance and forest structure. Abundance data was Hellinger-transformed prior to the analysis in order to eliminate the disparity between values (Legendre and Gallagher 2001). The Pearson correlation coefficient was used to correlate the RDA-axes and environmental variables.

Results

We collected a total of 3,004 Scarabaeinae beetles belonging to 21 species (Appendix C). Most extrapolated species accumulation curves reached the asymptote (Appendix D). Similar patterns were found for species accumulation curves for each area, which demonstrates the success in sampling dung beetle assemblages (Appendix D). The rarefied species richness showed differences in the number of species between sites and areas sampled (Appendix E). This difference was greater for ITA and PER. According to the species richness estimator Chao 1, based on the abundance, there were an estimated capture of species richness between 70 and 100% for the sampling sites (Appendix E), with averages above 88.2% in each of the four areas.

Dichotomius sericeus (Harold, 1867), *Canthon rutilans cyanescens* Harold, 1868, and *Canthidium* aff. *trinodosum* (Boheman, 1858) were the most abundant species, representing 71 percent of the total individuals captured (Appendix C). Only eight species (38.1%) were found in all four areas. The number of species per site ranged between five and 14. Only one species occurred in all sampling sites (*C. rutilans cyanescens*). Three species were sampled in at least 19 sites (*Deltochilum morbillosum* Burmeister, 1848, *Deltochilum multicolor* Balthasar, 1939, and *D. sericeus*). Five species were responsible for 92.8% of the total dung beetle biomass (*D. sericeus*, *Coprophanaeus saphirinus* (Sturm, 1826), *C. r. cyanescens*, *D. multicolor* and *D. morbillosum*) (Appendix C).

In general, PCoA analyses explained more than 58% of total variation in dung beetle assemblages. According to the PCoA species composition, species abundance and species biomass showed a spatial distribution according to the forest areas sampled (Fig. 2). PERMANOVA results confirmed the differences visually observed for composition (Pseudo-F = 3.199; p = 0.001), abundance (Pseudo-F = 4.053; p = 0.001) and biomass (Pseudo-F = 4.135; p = 0.001).

Several dung beetles species were significantly associated with some protected area, according to the results of the IndVal analysis (Table 1). Seven species were associated with RAT only (on the island). *Deltochilum furcatum* (Castelnau, 1840) was the only species associated with the ITA (on the mainland). *Eurysternus cyanescens* Balthasar, 1939 was the only species associated with the ANH (on the mainland).

Redundancy Analysis constrained 27% of the dung beetle variance in relation to the explanatory variables (Fig. 3). The first and second canonical axes were significant and accounted for 67.7% of the constrained variance. The first axis (RDA1, F = 13.982; p = 0.001) accounted for 36.9% of the variance, and was positively correlated with leaf litter height (r = 0.46), green cover (r = 0.38) and distance of shrubs (r = 0.26); it was negatively correlated with altitude (r = -0.82), shrub height (r = -0.20) and shrub basal area (r = -0.20). The second axis (RDA2, F = 7.167; p = 0.001) accounted for 22.9% of the variance, and was positively correlated with leaf litter height (r = 0.42), altitude (r = 0.41), land slope (r = 0.38), distance of shrubs (r = 0.37), canopy cover (r = 0.34) and distance of trees (r = 0.20); it was negatively correlated with tree height (r = -0.42), shrub height (r = -0.30) and tree basal area (r = -0.24).

Fig. 2. Principal coordinates analysis (PCoA) of dung beetle species based on Bray-Curtis similarity. The analysis was performed using composition (A), abundance (B) and biomass (C) data. ANH: Anhatomirim Environmental Protection Area; ITA: Permanent Protection Areas of Itapema; PER: Peri Lagoon Municipal Park; RAT: Permanent Protection Areas of Ratones.

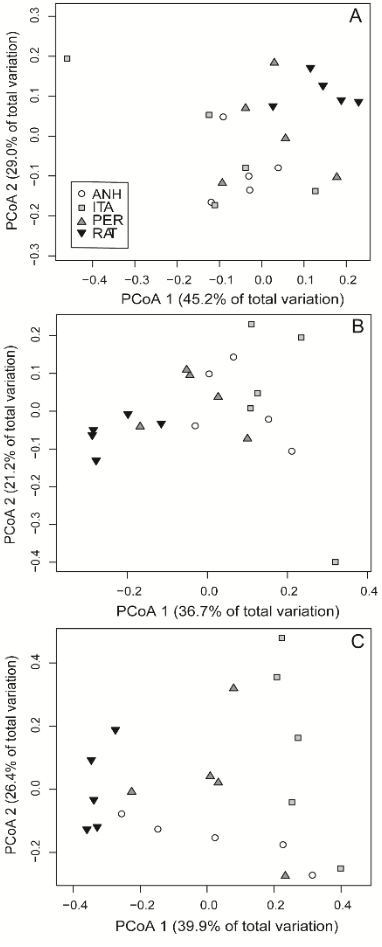


Table 1. IndVal analyses of dung beetle species with significant associations with areas and sites.

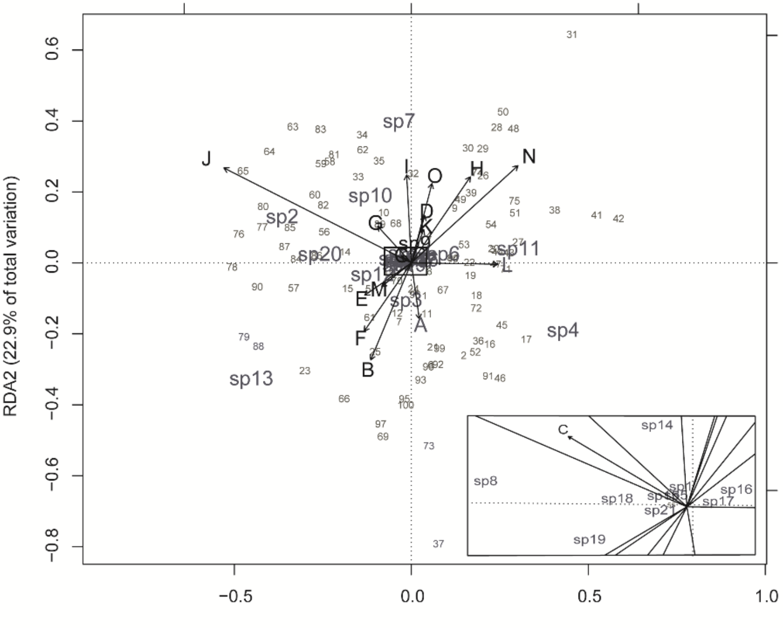
	IndVal	*P*-value	Group
Area			
Canthidium aff. *trinodosum*	0.626	0.002	Ratones
Canthon luctuosus	0.481	0.007	Ratones
Deltochilum brasiliense	0.432	0.009	Ratones
Deltochilum furcatum	0.490	0.002	Itapema
Deltochilum rubripenne	0.658	0.001	Ratones
Dichotomius sericeus	0.790	0.001	Ratones
Eurysternus cyanescens	0.447	0.003	Anhatomirim
Phanaeus splendidulus	0.487	0.003	Ratones
Uroxys sp. 1	0.777	0.001	Ratones

Analyses of species distribution plots (Fig. 3) indicated that *C.* aff. *trinodosum* and *Uroxys* sp. 1 were associated to sites with higher altitude values and lower green (vegetation) cover values. *Canthon r. cyanescens* was associated to sites with lower altitude values, small-sized trees, higher leaf litter height and green (vegetation) cover values. *Coprophanaeus saphirinus* was associated to sites with higher sized trees, canopy cover and land slope values. *Deltochilum multicolor* was associated to sites with higher values of green (vegetation) cover and leaf litter height, while *D. morbillosum* was associated to sites with higher altitude and wide-crowned shrubs. *Dichotomius sericeus* was associated to sites with higher sized trees and lower values of leaf litter height.

Discussion

The results indicate significant differences in species richness, abundance and biomass, as well as in the composition of dung beetle assemblages between remnant areas in the Atlantic Forest, and that these differences are associated with the distribution of environmental characteristics of remnants along the spatial gradient studied. Different historical processes of anthropogenic occupation and land use may have produced these associations. However, several other mechanisms and processes may be associated with patterns of species distribution due to isolation and fragmentation of areas and the mainland-island landscape (Silva and Hernández 2014), as well as differences in current human activity among areas.

Fig. 3. Redundancy Analysis ordination for dung beetle abundance constrained by environmental variables. Triplot with explanatory variables, species and samples: sp1: *Bdelyrus braziliensis*; sp2: *Canthidium* aff. *trinodosum*; sp3: *Canthon luctuosus*; sp4: *Canthon rutilans cyanescens*; sp5: *Canthonella* aff. *instriata*; sp6: *Coprophanaeus dardanus*; sp7: *Coprophanaeus saphirinus*; sp8: *Deltochilum brasiliense*; sp9: *Deltochilum furcatum*; sp10: *Deltochilum morbillosum*; sp11: *Deltochilum multicolor*; sp12: *Deltochilum rubripenne*; sp13: *Dichotomius sericeus*; sp14: *Dichotomius quadrinodosus*; sp15: *Dichotomius* sp.; sp16= *Eurysternus cyanescens*; sp17: *Eurysternus parallelus*; sp18: *Paracanthon* aff. *rosinae*; sp19: *Phanaeus splendidulus*; sp20: *Uroxys* sp. 1; sp21: *Uroxys* sp. 2; A: Basal area of first tree; B: Height of first tree; C: Top diameter of first tree; D: Distance to first tree; E: Basal area of first shrub; F: Height of first shrub; G: Top diameter of first shrub; H: Distance to first shrub; I: Land slope; J: Altitude; K: Leaf litter cover; L: Green cover; M: Exposed soil; N: Height of leaf litter; O: Canopy cover; 1-25: ANH sampling points; 26-50: ITA sampling points; 51-75: PER sampling points; 76-100: RAT sampling points.



Dung beetles are very dependent on mammals as a main food resource (Culot et al. 2013), and mammal populations can also be negatively affected by fragmentation (Canale et al. 2012; Santos-Filho et al. 2012), as well as by human-driven defaunation that occurred on the Island of Santa Catarina (Graipel et al. 2001). Historically, sea level of the Atlantic Ocean was lower and the island and mainland were united during the last ice age (~10,000-100,000 y ago), which probably enabled migration of species between the areas of the mainland to the island (Klein et al. 2006). With the increase in sea level (~10,000 y ago) and urbanization (in the last century), several areas of forests became fragmented and isolated, a common scenario in current Atlantic Forest areas (Tabarelli et al. 2005; Klein et al. 2006; Ribeiro et al. 2009). These large fragments now act as “islands”, with isolated communities and low dispersal and colonization rates (May et al. 2013), especially of organisms that are severely affected by forest fragmentation and habitat loss. These characteristics can adversely affect the long-term conservation of biodiversity and related ecological processes.

In addition to the historical processes, the IndVal and RDA analyses of dung beetle species distribution indicated that several species showed some degree of association with environmental characteristics of forest structure among areas. *Canthidium* aff. *trinodosum*, *D. morbillosum* and *Uroxys* sp. 1 were associated to sites with higher altitude values, while *C. r. cyanescens* showed an opposite response. Altitude ranged between 28 and 265 m asl among sites, a common feature of the Brazilian Atlantic Forest (Ribeiro et al. 2009). Altitude is an important feature for dung beetle distribution as highlighted by Escobar et al. (2005) in the Colombian Andes. However, we expected that altitude in our study might be a proxy that represents an environmental variable we did not measure, such as soil type, soil penetrability, soil texture, or other variable describing soil condition, which influences dung beetle distribution in our sampled areas. These soil conditions may be related to a greater or lesser distance from the sampling site to the sea.

Our results also showed that *C. saphirinus* was associated to sites with higher values of height of trees, canopy cover and land slope. *Deltochilum multicolor* was associated to sites with higher values of green (vegetation) cover and leaf litter height. *Deltochilum morbillosum* was also associated to sites with wide-crowned shrubs. *Dichotomius sericeus* was associated to sites with higher sized trees and lower values of leaf litter height. Hernández and Vaz-de-Mello (2009) and Campos and Hernández (2013) also showed that some of these features were also important determinants of dung beetle distribution in Atlantic Forest areas in São Paulo and Santa Catarina, respectively. Increased leaf litter is expected to affect negatively the nesting activities of some roller species (Nichols et al. 2013), but our resuts did not show such association. Dung beetle species associated to sites with higher or smaller sized trees or shrubs may be affected by related microclimatic variation (Feer 2008), which may influence reproductive aspects of species (Martínez and Vásquez 1995). Differences in environmental characteristics across study areas may represent the degree of change, or the status of succession of the forest structure in Atlantic Forest areas. In general, the distribution of dung beetles along different environmental characteristics may show discrete associations with particular biotypes within the landscape (Davis et al. 2001; Viegas et al. 2014), and evidence suggests that species richness, abundance and biomass are negatively impacted in disturbed habitats (Gardner et al. 2008b). These environmental characteristics are also expected to affect the distribution of some mammalian species and, therefore, the intake of food resources for dung beetles.

The Ratones (on the island) and Itapema (on the mainland) sites showed the highest and lowest abundance and biomass, respectively. Differences in dung beetle abundance between forest remnants can be attributed to the increased attractiveness of the baits used in sites of natural dung scarcity (Nichols 2012) due to the loss of several mammalian species. Some studies on the distribution of mammalian species along the coast of Santa Catarina have shown that mammal composition may be not very similar (Graipel et al. 2001; Cherem et al. 2004), including the remnants sampled in this study. The Island of Santa Catarina has suffered with forest loss and hunting of large mammals for at least two centuries (Caruso 1990; Graipel et al. 2001), and differently of mainland areas the mammals have a restricted spatial movement and dispersal on the island, being more susceptible to hunting. Furthermore, the intake of food resources by remaining mammal species may be greater due to greater mammal density on the island.

This work demonstrated the existence of significant associations between several species of dung beetles and the environmental structure of Brazilian Atlantic Forest remnants. Species richness, abundance and biomass, and the composition and structure of dung beetle assemblages were also associated with structural features of the studied habitats. This result reveals the importance of spatial distribution of these areas for the maintenance and conservation of dung beetle species, as well as for the response of these species to environmental changes. We expect that providing basic information on species distribution and community structure may be useful in the evaluation and monitoring of the protected Brazilian Atlantic Forest remnants.

The spatial distribution and the occurrence of spatially structured environmental characteristics of Atlantic Forest remnants can host a high gamma diversity of dung beetles. Because these insects show responses similar to several other taxa (Barlow et al. 2007; Culot et al. 2013), we expect that the remnants in this study contribute to the maintenance of wildlife from several taxonomic groups of organisms. We know that both the mammal community and environmental heterogeneity influence the distribution of dung beetle assemblages. Knowing the relative importance of these two factors is a demand for future studies on factors influencing the spatial distribution of dung beetles.

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Supporting Information

Appendix A Methods to obtain environmental variables

Forest structure was described by 15 environmental variables, which were tested for influence on dung beetle distribution. Measurement of variables was performed using the adapted point-centered quarter method. Briefly, a plastic cross was placed in the center of each pair of traps (i.e., at each sampling point), dividing the sampling point into four quadrants (northwest, southwest, southeast and northeast). Tree, shrub and soil environmental variables were measured in each quadrant as follows: (1) circumference at breast height when diameter at breast height [DBH] > 5 cm), (2) height, (3) top diameter and (4) distance from the nearest tree to the center of cross, (5-8) repeated same measures for shrubs with circumference at ankle height when DBH < 5 cm and with a minimum height of 1 m, (9) land slope, (10) altitude, (11) canopy cover, (12) percentage of leaf litter cover, (13) green (vegetation up to 1 m height) cover, (14) exposed soil, and (15) height of leaf litter.

Tree and shrub height was visually estimated using a 4 m ruler. Circumference and distance were measured with a millimeter tape. The percentage of litter, green cover (vegetation up to 1 m height), and exposed soil coverage in each quadrant was estimated in different percentage classes (0-5, 6-25, 26-50, 51-75, 76-95, 96-100%) using a 1 m square placed about 20 cm away from the cross. Land slope was obtained at the center of the square using a clinometer. Altitude was obtained using a hand-held GPS at ground level. Litter height was measured using a ruler at five points inside the square (near each corner and in the center). Using the same classes described above, the percentage of canopy cover was visually estimated using a hollow square of 10 cm side length, placed at a distance of 60 cm from the eye of the observer at a 20° angle in relation to the zenith. The basal area of trees and shrubs was calculated from the trunk circumference (based on the area of the circle). For each variable, a measure of central tendency was calculated based on the Shapiro-Wilk normality test. Thus, each environmental variable represented a central value (mean or median, as appropriate) of the four measures of each point.

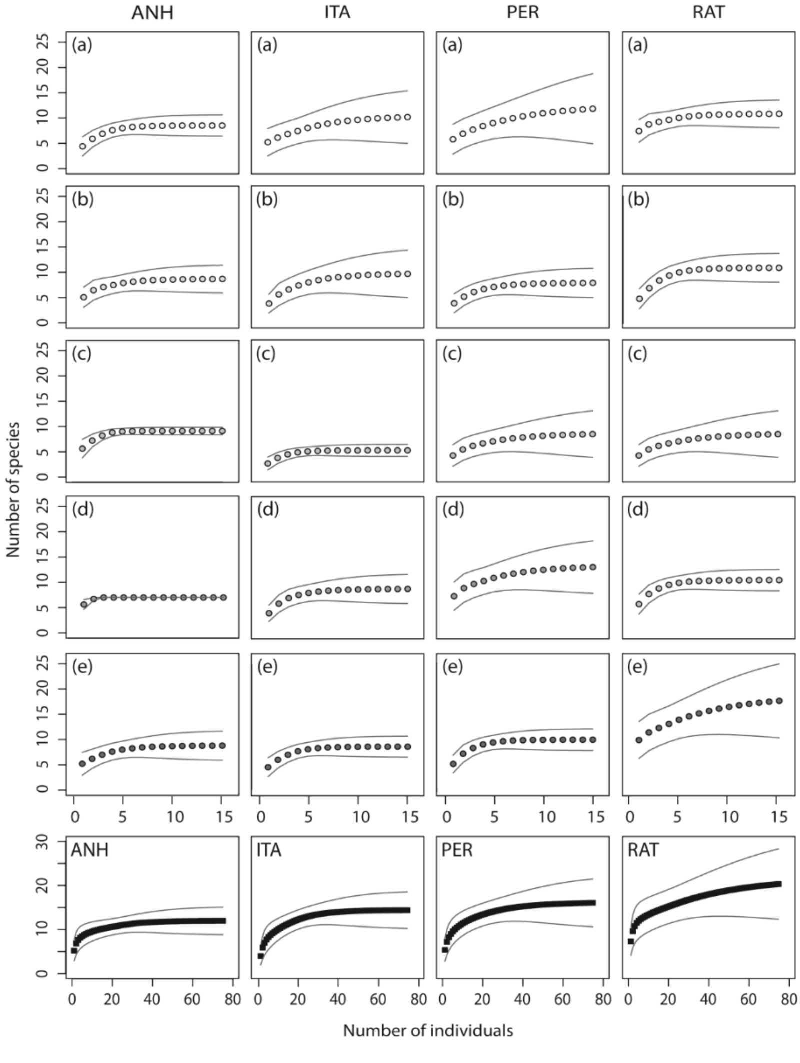
Appendix B Average environmental variables. BAFT: Basal area of first tree; (cm^2) HFT: Height of first tree (m); TDFT: Top diameter of first tree (m); DFT: Distance to first tree (m); BAFS: Basal area of first shrub (cm^2); HFS: Height of first shurb (m); TDFS: Top diameter of fisrt shrub (m); DFS: Distance to first shrub (m); LS: Land slope (º degrees); ALT: Altitude (m); LLC: Leaf litter cover (%); GC: Green (vegetation) cover (%); ES: Exposed soil (%); HLL: Height of leaf litter (cm); CC: Canopy cover (%).ANH: Anhatomirim Environmental Protection Area; ITA: Permanent Protection Areas of Itapema; PER: Peri Lagoon Municipal Park; RAT: Permanent Protection Areas of Ratones. A-E represent the sites sampled within each area

	BAFT	HFT	TDFT	DFT	BAFS	HFS	TDFS	DFS	LS	ALT	LLC	GC	ES	HLL	CC
ANH A	101.35	8.46	4.35	1.99	5.18	2.77	0.88	1.03	25.25	110.80	85.00	15.00	15.00	3.40	91.25
ANH B	51.83	9.80	4.98	1.53	5.29	2.74	1.05	1.06	21.35	95.40	91.25	26.25	8.75	2.57	85.00
ANH C	76.50	7.88	4.66	1.72	2.79	1.99	0.85	0.89	17.70	104.20	91.25	26.25	8.75	3.77	97.50
ANH D	141.08	8.34	4.85	2.22	4.00	2.83	1.11	0.95	19.30	72.60	85.00	37.50	2.50	3.50	91.25
ANH E	130.81	9.40	5.48	2.21	8.75	2.98	1.14	1.15	18.80	132.40	97.50	15.00	2.50	3.10	85.00
ITA A	86.15	6.32	4.33	2.54	2.88	1.79	0.98	1.25	17.90	126.00	97.50	50.00	2.50	4.72	97.50
ITA B	130.27	8.44	4.87	2.46	4.02	2.23	1.35	1.36	21.15	87.80	91.25	26.25	2.50	4.49	97.50
ITA C	71.28	10.04	5.64	2.57	4.07	2.16	1.12	1.09	16.80	35.40	97.50	26.25	2.50	5.18	91.25
ITA D	93.46	7.70	5.05	2.52	4.61	2.45	1.31	1.18	25.10	169.00	85.00	37.50	15.00	4.55	97.50
ITA E	166.94	13.28	5.08	2.96	3.36	2.09	1.00	1.13	19.95	61.80	85.00	15.00	8.75	3.29	97.50
PER A	73.26	7.43	4.68	2.22	6.34	2.20	1.27	0.92	19.90	83.00	85.00	37.50	15.00	2.51	91.25
PER B	103.30	9.22	4.84	2.36	2.80	2.53	1.06	1.01	15.90	130.00	73.75	37.50	15.00	2.66	91.25
PER C	56.48	9.09	5.00	2.37	4.60	2.77	1.11	0.90	29.70	185.20	85.00	26.25	15.00	2.67	91.25
PER D	147.43	10.84	5.05	2.27	3.93	2.35	1.27	1.12	20.88	241.60	91.25	37.50	8.75	3.93	91.25
PER E	174.86	8.50	5.08	2.08	6.75	3.12	1.32	1.24	22.55	92.80	85.00	50.00	15.00	2.87	97.50
RAT A	118.04	9.26	4.79	2.69	4.48	2.38	1.34	1.29	21.75	216.00	85.00	15.00	15.00	2.83	91.25
RAT B	114.15	11.88	5.15	2.28	4.44	2.85	1.11	0.68	18.45	78.60	91.25	37.50	8.75	2.75	85.00
RAT C	97.60	10.35	3.98	2.06	8.00	3.16	1.11	1.14	20.70	90.40	91.25	62.50	8.75	2.57	73.75
RAT D	151.35	10.83	6.83	2.16	13.47	3.03	1.42	1.12	13.15	193.60	91.25	15.00	8.75	1.98	91.25
RAT E	151.51	11.18	5.18	2.58	7.98	2.54	1.08	0.75	15.65	243.60	97.50	26.25	2.50	2.58	91.25

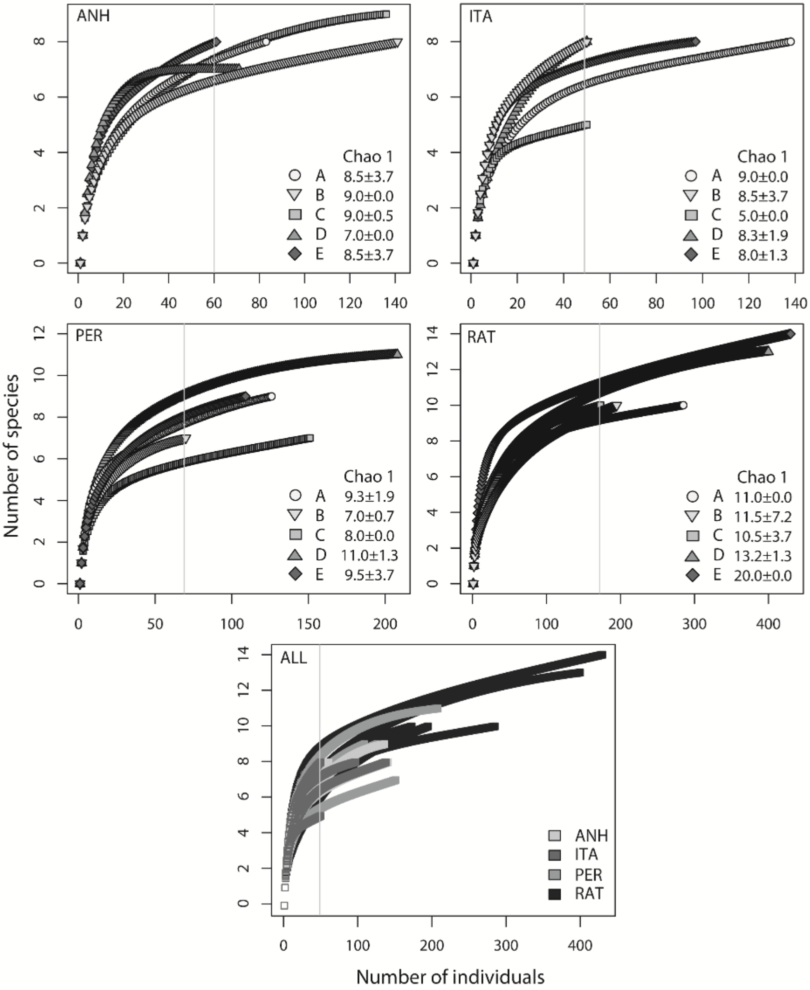
Appendix C Species richness, abundance and biomass of dung beetles in five sites within four protected Atlantic Forest remnants. A-E letters depict the sites sampled in each area. Anhatomirim: sites A and C were sampled at Jan 14, 2012, and sites B, D and E at Jan 27, 2012. Itapema: sites A and D were sampled at Jan 6, 2012, and sites B, C and E at Jan 7, 2012. Peri: sites A and C were sampled at Jan 18, 2012; sites B and D at Jan 19, 2012, and site E at Jan 20, 2012. Ratones: sites A and D were sampled at Feb 24, 2012; sites B and C at Feb 29, 2012, and site E at Feb 3, 2012. T = total

Species	Anhatomirim						Itapema						Peri						Ratones						T
	A	B	C	D	E	T	A	B	C	D	E	T	A	B	C	D	E	T	A	B	C	D	E	T	
1. *Bdelyrus braziliensis*	1					1																			1
2. *Canthidium* aff. *trinodosum*	3	13	1	6	12	35	7		12	2	4	25		7	1	91	3	102	72		3	91	54	220	382
3. *Canthon luctuosus*								1			2	3		1		3	1	5	1	2	5	2	1	11	19
4. *Canthon rutilans cyanescens*	13	18	75	16	17	139	73	11	20	9	21	134	25	32	18	11	42	128	24	47	29	23	36	159	560
5. *Canthonella* aff. *instriata*		1				1	1		1			2				2		2		1	1		1	3	8
6. *Coprophanaeus dardanus*									5			5													5
7. *Coprophanaeus saphirinus*	6	6	6	4	2	24	33	9		28	20	90	14		10	23	11	58	8	5	5	18	33	69	241
8. *Deltochilum brasiliense*							1					1				1		1	1			2	4	7	9
9. *Deltochilum furcatum*								2		3	1	6													6
10. *Deltochilum morbillosum*	8	14	11	6	1	40	9	12		2	20	43	25	4	23	26	4	82	20	1	2	13	40	76	241
11. *Deltochilum multicolor*	1	3	4	14	13	35	4	3	11	1	17	36	12	2	4	3	8	29		3	4	2	14	23	123
12. *Deltochilum rubripenne*		1	2			3							2			15	2	19	4	4	14	4	20	46	68
13. *Dichotomius sericeus*	48	84	32	19	11	194	9	10		3	11	33	43	21	93	28	36	221	140	124	108	218	154	744	1192
14. *Dichotomius quadrinodosus*										1		1													1
15. *Dichotomius* sp.																							1	1	1
16. *Eurysternus cyanescens*	2		2		1	5																			5
17. *Eurysternus parallelus*													1				1	2				1		1	3
18. *Paracanthon* aff. *rosinae*													2		1			3					1	1	4
19. *Phanaeus splendidulus*			2	5	3	10		1				1	1					1	4	1	1	5	3	14	26
20. *Uroxys* sp. 1														2		4		6	10	6		19	67	102	108
21. *Uroxys* sp. 2																						1		1	1
Number of species	8	8	9	7	8	11	8	8	5	8	8	13	9	7	7	11	9	14	10	10	10	13	14	16	21
Number of individuals	82	140	135	70	60	487	137	49	49	49	96	380	125	69	150	207	108	659	284	194	172	399	429	1478	3004
Total dry biomass (g)	12.2	18.5	12.4	9.5	6.9	59.7	16.4	6.0	5.7	10.4	12.0	50.6	17.9	4.9	20.3	19.3	14.9	77.6	25.1	24.2	22.3	38.1	50.4	160.2	348.2

Appendix D Extrapolated (two times) species accumulation curves for dung beetle assemblages in five sites within four protected Atlantic Forest remnants. ANH = Anhatomirim Environmental Protection Area, ITA = Permanent Protection Areas of Itapema, PER = Peri Lagoon Municipal Park, RAT = Permanent Protection Areas of Ratones. A-E represent the sites sampled within each area



Appendix E Rarefaction curves for dung beetle communities in five sites within four protected Atlantic Forest remnants. Chao 1 estimator was used to estimate species richness (±SD). ANH = Anhatomirim Environmental Protection Area, ITA = Permanent Protection Areas of Itapema, PER = Peri Lagoon Municipal Park, RAT = Permanent Protection Areas of Ratones



ARTIGO II: LOCAL AND REGIONAL EFFECTS ON COMMUNITY STRUCTURE OF DUNG BEETLES IN A MAINLAND-ISLAND SCENARIO

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> "[…] we are pattern seeking mammals. It's part of our evolution. We look for patterns. We're designed to look for them."
> (Christopher Hitchens)

Local and regional effects on community structure of dung beetles in a mainland-island scenario

Abstract

Understanding the ecological mechanisms driving beta diversity is a major goal of community ecology. Metacommunity theory brings new ways of thinking about the structure of local communities, including processes occurring at different spatial scales. In addition to new theories, new methods have been developed which allow the partitioning of individual and shared contributions of environmental and spatial effects, as well as identification of species and sites that have importance in the generation of beta diversity along ecological gradients. We analyzed the spatial distribution of dung beetle communities in areas of Atlantic Forest in a mainland-island scenario in southern Brazil, with the objective of identifying the mechanisms driving composition, abundance and biomass at three spatial scales (mainland-island, areas and sites). We sampled 20 sites across four large areas, two on the mainland and two on the island. The distribution of our sampling sites was hierarchical and areas are isolated. We used standardized protocols to assess environmental heterogeneity and sample dung beetles. We used spatial eigenfunctions analysis to generate the spatial patterns of sampling points. Environmental heterogeneity showed strong variation among sites and a mild increase with increasing spatial scale. The analysis of diversity partitioning showed an increase in beta diversity with increasing spatial scale. Variation partitioning based on environmental and spatial variables suggests that environmental heterogeneity is the most important driver of beta diversity at the local scale. The spatial effects were significant only at larger spatial scales. Our study presents a case where environmental heterogeneity seems to be the main factor structuring communities at smaller scales, while spatial effects are more important at larger scales. The increase in beta diversity that occurs at larger scales seems to be the result of limitation in species dispersal ability due to habitat fragmentation and the presence of geographical barriers.

Introduction

Community ecology aims to understand and explain the processes that influence the patterns of distribution, abundance and composition of species [1,2] over space and time [3], both locally and regionally [4,5]. Community structure may be influenced by several ecological processes that involve biotic and abiotic factors operating at different spatial and temporal scales [6-8]. When we consider large scales, historical, evolutionary and stochastic processes become critical to the understanding of these patterns [5,9-11]. Further, studying only local processes may not be sufficient for understanding how communities are structured locally and regionally [5], because local and regional processes may act in different ways in relation to the increase or decrease in species diversity [11].

Despite the large number of mechanisms (theories and models) proposed as drivers of patterns of species distribution, only four processes are fundamentally involved: selection, drift, speciation and dispersal [2]. Three main hypotheses are proposed to explain the origin of beta diversity (i.e., variation in the identities and relative abundance of species among sites) with respect to these processes [12]. The first hypothesis suggests that the species composition may be stable over large areas, and that biological interactions (e.g., competition inter- and/or intraspecific) play an important role in maintaining beta diversity [12]. The second hypothesis states that species composition varies in a random and autocorrelated way, emphasizing spatially limited dispersal [12]. The last hypothesis suggests that species distribution is driven by environmental conditions, and that landscapes are mosaics in which local environmental drivers control species composition [12]. These hypotheses seem to be somewhat related regardless of the organismal group or ecosystem, and testing them is crucial for elucidating issues on ecosystem functioning and biodiversity conservation initiatives [12].

In community ecology there exists a variety of concepts and methodologies commonly employed by ecologists to measure beta diversity and to identify the processes related to its generation [12-17]. Recent approaches have been based on the dependence of environmental, spatial and random processes, with the goal of explaining which processes have more influence on beta diversity, e.g., by using variation partitioning methods [18] on composition or abundance community data among groups of explanatory variables (e.g., environmental and spatial) [12]. These methods are used to attempt to explain how beta diversity is influenced by environmental and/or spatial factors, or by random factors [19]. Despite being criticized [20,21], variation partitioning has long been used in the context of metacommunity theory [1] and it highlights the importance of increasing the spatial scale in understanding the ecological processes structuring biological communities locally and regionally [22].

A metacommunity is defined as a set of communities connected by the dispersal of multiple interacting species [1,22]. There are four theoretical paradigms (models) to explain metacommunity dynamics (species sorting, mass effects, patch dynamics and neutral) and they take into account three (drift, selection and dispersal) of the four basic processes aforementioned [2]; differences in species dispersal ability and environmental characteristics are important factors for determining which model best describes the metacommunity [1,22]. Mass effects (high dispersal) and patch dynamics (low dispersal) would be variations of species sorting (efficient dispersal), as there are different levels of dispersal ability of species in each metacommunity model [23]. The adoption of metacommunity theory has led to substantial changes in the way that ecologists interpret ecological phenomena at both local and metacommunity (regional) scales [1].

A key point in assessing the relative importance of proposed metacommunity processes is the identification and use of environmental and/or spatial gradients as study scenarios [12]. Direct gradient ordination techniques (e.g., redundancy analysis) followed by variation partitioning [18] allows determination of the fraction of beta diversity explained solely by environmental or spatial predictors, and by shared effects of both sets of predictors [12]. The prevalence of environmental effects indicates species sorting, the predominance of spatial effects indicates neutral processes, historical events and/or dispersal limitation, and shared effects of both environmental and spatial predictors indicate species sorting, dispersal limitation or a combination of both (mass effects and patch dynamics sensu [1]) [23,24]. The relative importance of metacommunity paradigms is still dependent on spatial scale, spatial extent or spatial distances between sites [25,26], and varies between environments and groups of species due to inherent differences of ecosystem type and species dispersal ability [27]. Recent techniques have also allowed the identification of species and sites that may contribute to beta diversity along an ecological gradient by using community dataset total variance as an estimate of beta diversity [15].

The Brazilian Atlantic Forest is one the most threatened biomes in terms of biodiversity conservation [28]. About 12% of its original size, it is highly fragmented with a high degree of isolation, existing primarily in intermediate successional state [29]. Less than 2% of Atlantic Forest areas are located in protected zones [29], despite being considered global biodiversity hotspots [30]. Historically, the coast of Brazil has always showed the highest population and industrial concentration, and thus, the Atlantic Forest has been affected by the growth and development of the country [29]. An understanding of how species respond to anthropogenic modifications to the structure or complexity of habitats is fundamental for the development of future conservation initiatives, especially for organisms that play key roles in the maintenance and/or restoration of ecosystems, such as dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae).

Dung beetles feed on decaying organic matter (e.g., mammalian feces, animal carcasses, rotting vegetation) [31] and they play several ecosystem services [32]. In tropical ecosystems they are used as indicators of diversity, as well as for monitoring environmental changes, because they respond quickly in terms of species composition, richness, abundance and biomass to the effects caused by habitat destruction, fragmentation and/or isolation [33-37]. These beetles are easily sampled using standardized, efficient and low-cost sampling methods [34]. They have wide distribution and are correlated with other taxa (e.g., mammals) [33,34,38]. Therefore, community changes have potential to affect ecological functions performed by dung beetles and hence, ecosystem function [35,39-42]. As such, dung beetles are an excellent model system [31] with which to investigate the main processes that influence community structure in Atlantic Forest regions.

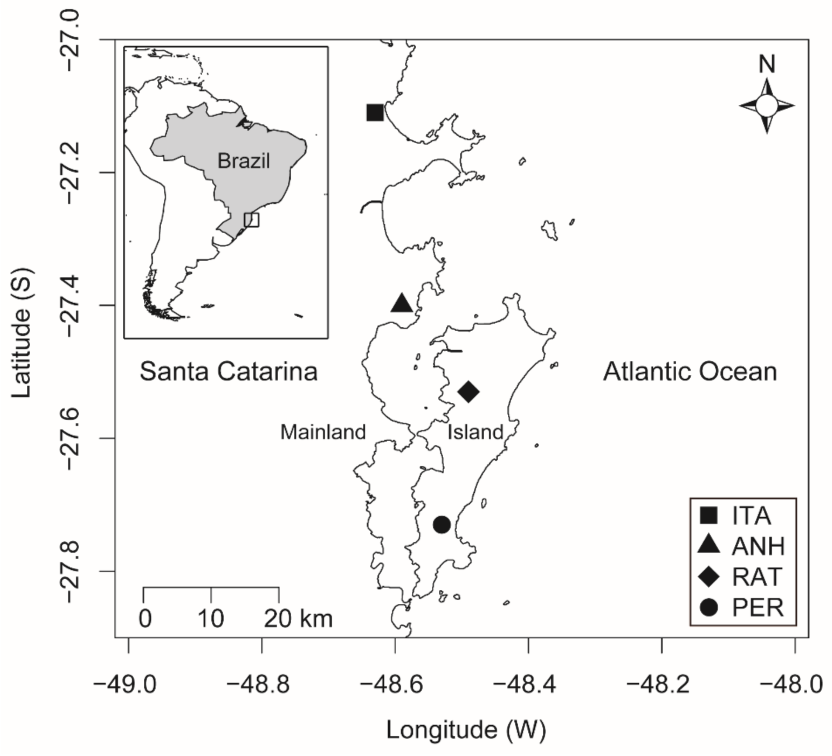
Therefore, the aim of our study was to investigate the effect of spatial scales on the patterns of species diversity of dung beetles in Brazilian Atlantic Forest and to identify the mechanisms that drive these patterns applying aspects of metacommunity theory. We tested the hypothesis that the distribution of dung beetles in the Atlantic Forest is associated with differences in forest structure and that high levels of beta diversity will be found with increasing spatial scale due to dispersal limitation. Our predictions are as follows: (i) because dung beetles are sensitive to environmental changes, environmental gradients should result in high beta diversity among sites via species sorting, (ii) due to differences in habitat structure of each site, environmental characteristics and dung beetle species distribution are spatially structured, (iii) because of dispersal limitation among areas (mainland-island and fragmented landscape), the spatial effect has high importance in structuring communities at increased spatial scales.

Material and methods

Study area

The study was conducted at four large Atlantic Forest areas in the state of Santa Catarina, Brazil, two on the island of Santa Catarina (Florianópolis city) and two on the mainland, both on the east coast (Figure 1). The island of Santa Catarina is approximately 54 km north-south and maximally 18 km wide, with a total land area of 424.4 km². The distance between the mainland and the island varies greatly, with minimum of 500 m and maximum around 10 km.

Figure 1. Map of the study region. Location of the four areas sampled in eastern Santa Catarina state, Brazil. ANH: Environmental Protection Area of Anhatomirim; ITA: Permanent Protection Area of Itapema; PER: Lagoa do Peri Municipal Park; RAT: Permanent Protection Area of Ratones.



On the island, the study areas were within the Lagoa do Peri Municipal Park (PER, 27°43’30”S, 48°32’18”W) and the Permanent Protection Area of Ratones (RAT, 27°31’52”S, 48°30’45”W). On the mainland, the areas sampled were within the Environmental Protection Area of Anhatomirim in Governador Celso Ramos city (ANH, 27º25’1”S, 48º34’25”W), and in Permanent Protection Area in Itapema city (ITA, 27º05’13”S, 48º35’54”W). According to the Brazilian Forest Code (Law nº. 12.651/2012), permanent protection areas are sites with characteristics that have the environmental function of preserving water, biodiversity resources, and landscape and geological stability, and for facilitation floral and faunal gene flow. The distance among areas is approximately 21 km between PER and RAT, 34 km between PER and ANH, 71 km between PER and ITA, 13.5 km between ANH and RAT, 50 km between ITA and RAT, and 37 km between ANH and ITA. The altitude of the sampling sites ranged between 28 and 265 m. All sites sampled are near the Brazilian Atlantic coastline and have dense rain forest vegetation within the Atlantic Forest biome, with various levels of vegetation succession [43]. According Köppen classification, the climate in the eastern region of Santa Catarina is Cfa, humid subtropical (mesothermal) without dry season, with hot summers (average of 25°C) and well distributed rainfall throughout the year, with annual average of 1500 mm approximately [43]. Santa Catarina shows four seasons of the year well defined.

Scarabaeinae sampling

We sampled dung beetles using baited pitfall traps, as they are a highly efficient method to capture this group [44]. The traps were made with plastic containers (15 cm diameter x 20 cm depth) buried with the top edge at ground level, allowing insects to fall in. To prevent overflow, the traps were protected against rain using a small sheet supported by wooden sticks, placed approximately 10 cm above the trap. A mixture (300 ml) of water and detergent (neutral) was added to each container to catch and kill insects. We used human feces and rotting flesh (aged in plastic container at room temperature three days prior to sampling) as bait to attract dung beetles, as both satisfy the two main eating habits of dung beetles – coprophagy and necrophagy, respectively [31]. Approximately 30 g of both baits were wrapped in thin cloth and tied in the central part of the rain protection above the traps.

The insects collected were sorted, mounted on entomological pins and dried in an oven (60°C for 72 h), then weighed on a precision balance (0.0001 g). Species identities were confirmed by experts. The beetles were deposited in the Entomological Collection of the Centro de Ciências Biológicas at the Universidade Federal de Santa Catarina, Brazil. We thank the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/MMA) and Fundação do Meio Ambiente (FATMA-SC) for permission to collect (permit #32333-3 to MIMH). The field study did not involve endangered or protected species. Dataset S1 provides the database of values for abundance and biomass of dung beetle species across the study sites.

Sampling design

Samples were taken at five different forested (hillside) sites within each sampling area. Each site contained five pairs of traps spaced 5-10 m apart, each pair containing the two kinds of bait. The pairs were spaced 50 m apart, as a minimum distance of 50 m decreases the influence between sets of traps in sampling Scarabaeinae [45]. Each pair of traps was regarded as a sampling point, and remained in the field for 48 h prior to collection.

The samplings were carried out during the summer of 2012 (January and February), because of high temperatures, and it being the period of greatest dung beetle abundance in subtropical regions in Brazil [46,47]. Due to the spatial configuration of our sampling design, the large distance among the four areas, and the effect of spatial discontinuity between mainland-island, the sampling sites showed a hierarchical distribution. Thus, it was possible to investigate the variation in dung beetle communities at three spatial scales, i.e. mainland-island, areas, and sites. Sites represent the local spatial scale, i.e., the smallest spatial extent in our study that encompasses five sampling points. Areas represent the intermediate spatial scale with five sites per area. Mainland-island represents the regional spatial scale, i.e., the largest spatial extent in our study that encompasses two areas each one. Variation in dung beetle species composition, number of individuals, and dry biomass was used to assess the influence of environmental and spatial factors at each spatial scale.

Environmental variables

We measured 20 environmental variables related to habitat structure to test their influence on dung beetle distribution. Differences in environmental conditions (environmental variables measured) among sampling sites is defined as environmental heterogeneity. Measurement was performed using the adapted point-centered quarter method [48,49]. This method was chosen for its simplicity and common use in phytosociological surveys [50]. Briefly, a plastic pipes crossing in an x-shape were placed in the center of each pair of traps (i.e., at each sampling point), dividing the sampling point into four quadrants (northwest, southwest, southeast and northeast). Tree, shrub and soil environmental variables were measured in each quadrant as follows: (1) circumference at breast height when diameter at breast height > 5 cm), (2) height, (3) top diameter and (4) distance away from the nearest tree to the center of cross, (5-8) same measures for the greater tree distant up to 10 m, (9-12) similar measures for shrubs (circumference at ankle height when < 5 cm and with a minimum height of 1 m), (13) land slope, (14) canopy cover, (15) percentage of leaf litter cover, (16) green cover and (17) exposed soil, (18) height and (19) dry biomass of leaf litter, and (20) altitude.

The height of trees and shrubs was visually estimated with a ruler of 4 m length. Circumference and distance were measured with a millimeter tape measure. The percentage of litter, green cover, and exposed soil coverage in each quadrant was estimated in different classes (0-5, 6-25, 26-50, 51-75, 76-95, 96-100%) using a square of 1 m plastic pipes, placed about 20 cm away from the cross. Land slope was obtained at the center of the square using an inclinometer. Litter height was measured using a mm ruler at five points inside the square (near each corner and in the center). A five-inch square was constructed in the center of the 1 m square, and a portion of litter was removed. Litter was later dried in an oven (60°C for 72 hours) and weighed to obtain dry biomass. Using the same classes described above, the percentage of canopy cover was visually estimated using a hollow square of 10 cm side length, placed at a distance of 60 cm from the eye of the observer at a 20° angle in relation to the zenith [50]. Altitude was obtained using a hand-held GPS at ground level. The basal area of trees and shrubs was calculated from the trunk circumference (based on the area of the circle). For each variable, a measure of central tendency was calculated based on the Shapiro-Wilk normality test. Thus, each environmental variable represented a central value (mean or median, as appropriate) of the four measures of each point; this was done to minimize the effects of visual estimation. A subset of the variables analyzed (three basal area, three heights, DBH) is used by the Conselho Nacional do Meio Ambiente, the

Brazilian Council of Environmental issues, to characterize successional stages of Atlantic Forest in the state of Santa Catarina [51]. Dataset S1 provides the database of values for each environmental variable across the study sites.

Spatial variables

Spatial predictors were created using a method called Principal Coordinates of Neighbour Matrices [19], which is part of a set of spatial eigenfunction analyses called Moran's Eigenvector Maps [52]. The creation of spatial predictors was performed using *create.MEM.model* function [25] for the program R [53], because the sampling sites in our study showed a spatial hierarchical structure [54] with large distances between sites in different areas. This function produces a staggered matrix arranged in blocks from the geographical coordinates, generating information on the number of blocks (or groups) and sampling sites in each block [54]. Each block represents the hierarchical spatial distribution of sampling points, and in the staggered matrix the blocks from another hierarchy receive value of zero (0) for each spatial variable created. These variables represent the spatial variation at different spatial scales and may be used as predictors in gradient analysis to model the spatial relationship of the community data [25]. To create the spatial variables, we used data from geographic coordinates (Universal Transverse Mercator) obtained at each sampling point using a hand-held GPS. Dataset S1 provides the database of geographic coordinates for each study site.

Data analysis

Beta diversity across spatial scales

A recent approach called "true diversity" [55] has been used to partition diversity into its different components in an additive or multiplicative way [14]. The additive partitioning approach ($\gamma = \alpha + \beta1 + \beta2 + \beta3$) was used to estimate the beta diversity at the different spatial scales. Alpha (α) is the average species richness in local communities, while gamma (γ) refers to the total richness observed in the entire set of samples. Each component of beta diversity refers to different spatial scales studied: $\beta1$ = between sampling sites, $\beta2$ = between areas, $\beta3$ = between mainland-island. We used data on species richness and individual abundance (i.e., true Shannon diversity) for the hierarchical analysis of diversity partitioning. Partitioned components of diversity based on abundance were natural log-transformed to make them additive (i.e., Shannon entropy [55]). These analyses were performed in Partition 3.0 program [56].

Species and local contributions to beta diversity

The total beta diversity (BD_{Total}) was analyzed by calculating the total variance of the species matrix using *beta.div* function [15] for R program [53]. This method calculates the total sum of squares of the species matrix and from it, one may obtain an index of the total data variance that represents the total beta diversity, and it may be compared among sampling units. The BD_{Total} may then be partitioned in Species Contribution to Beta Diversity (SCBD, or degree of variation of the species along the studied area) and Local Contribution to Beta Diversity (LCBD, or comparative indicators of ecological uniqueness of the sampling sites) [15]. The values of LCBD were tested using random and independent permutations (in columns) of the species matrix, testing whether species are randomly and independently distributed between sampling sites [15]. This approach was used to identify the species and sites that contributed most to the beta diversity index throughout the spatial gradient. Before running the analysis, species data (composition, abundance and biomass) were Hellinger-transformed, after which Euclidean distance was used in the execution of the analysis. We used Spearman correlation to assess the association between the values of LCBD and species richness, abundance and biomass, in order to determine whether sampling site contribution is related to the number of species, number of individuals, and total biomass. Analyses were performed in R 3.0.1 program [53].

Variation partitioning explained by explanatory variables

Double stopping criterion [57] was used as forward selection procedure of explanatory variables in order to avoid type I error, and to avoid overestimating the amount of explained variance in the species matrix before variation partitioning [54,57]. Variation partitioning allows partitioning the variation in the species data explained by pure environmental effects [a], spatially structured environmental variables [b], pure spatial effects [c], and unexplained variation (i.e., residuals or fraction [d]) [18,58]. This method estimates and tests the percentage of variation (R^2_{adj}) attributed to each unique set of explanatory variables [18]. Three steps were necessary to perform the variation partitioning: (1) implementation of a redundancy analysis (RDA) with sets of environmental and spatial variables, (2) a second RDA with environmental data, controlling for spatial effects (E | S), (3) a third RDA with spatial data, controlling for environmental effects (S | E) [18]. Variation partitioning was performed for the composition, abundance and biomass of dung beetles at each spatial scale studied. Before running RDAs, species datasets were Hellinger-transformed in order to eliminate the disparity between values [59]. The proportion of variance explained by each set of explanatory variables is described by R^2_{adj} according to the Ezekiel correction [18], and significance levels are calculated by permutation tests (N = 999) [54]. We tested for a linear spatial trend and found a significant longitudinal trend for dung beetle composition data ($F = 3.34$; df = 2; $p < 0.01$), abundance ($F = 6.77$; df = 2; $p < 0.01$), and biomass ($F = 7.35$; df = 2; $p < 0.01$). Thus, all datasets were detrended prior to the analyses [54]. R^2_{adj} values were indicated in percentage format in the text and tables. The analyses were conducted in R 3.0.1 program [53] using Packfor [60] and Vegan [61] packages.

Results

Species richness, abundance and biomass across spatial scales

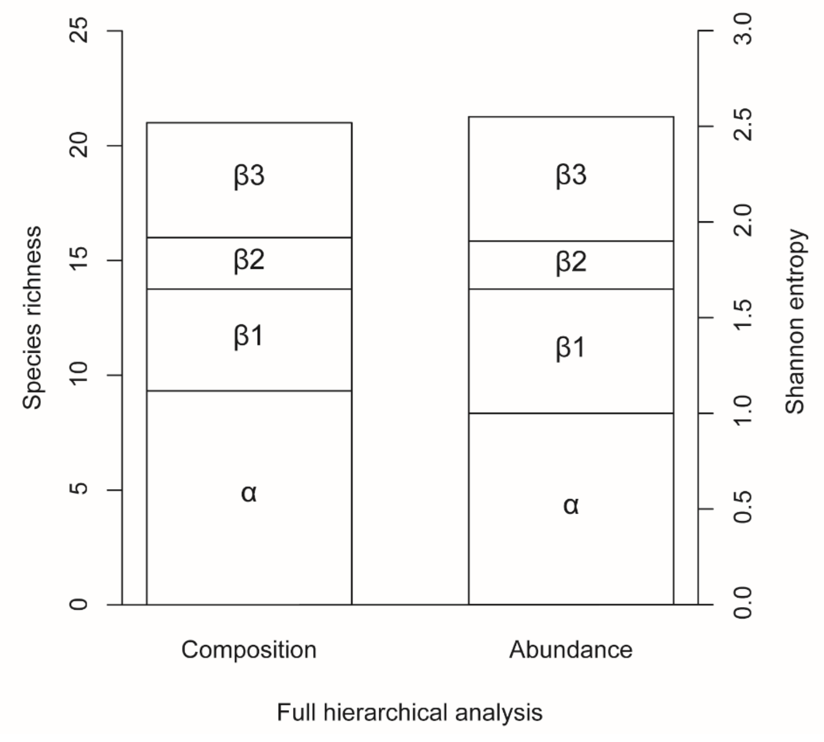
Regionally, we collected a total of 3,004 individuals of Scarabaeinae, belonging to 21 species (Table S1). The mainland and the island had the same total number of species (16), sharing 11. On the island, the number of individuals was 2.5 higher, and total biomass was 2 times higher compared to the mainland. Among areas, RAT had the greatest number of species and individuals, and greatest biomass, followed by PER (both island areas). Only eight species (38.1%) were shared by all four areas.

The number of species per site ranged between five and 14 (Table S1). Only one species occurred in all sampling sites (*Canthon rutilans cyanescens*). Three species were sampled at least 19 sites (*Deltochilum morbillosum*, *Deltochilum multicolor*, and *Dichotomius sericeus*). Five species were responsible for 92.8% of the total dung beetle biomass (*D. sericeus*, *Coprophanaeus saphirinus*, *C. rutilans cyanescens*, *D. multicolor* and *D. morbillosum*) (see Figure S1 for a spatial comparison of species richness, abundance and biomass).

Beta diversity across spatial scales

The hierarchical partitioning analysis of diversity based on species richness data showed a large contribution of regional ($\beta3 = 5$ species) and local ($\beta1 = 4.4$ species) spatial scales to gamma diversity (Figure 2). Beta diversity among areas ($\beta2 = 2.2$ species) was relatively small when compared to other spatial scales. A similar pattern was observed for Shannon entropy based on species abundance. The hierarchical partitioning of diversity analysis also indicated a small contribution of β2, and a large relative contribution of β3 and β1, respectively.

Figure 2. Full hierarchical analysis of diversity partitioning. The partitioning was performed for species richness and Shannon entropy of dung beetles. α = local diversity, β1 = diversity among sites, β2 = diversity among areas, β3 = diversity among mainland-island.



Our results show that there were five species found only on the mainland (*Bdelyrus braziliensis*, *Coprophanaeus dardanus*, *Deltochilum furcatum*, *Dichotomius quadrinodosus*, and *Eurysternus cyanescens*), and five only found on the island (*Dichotomius* sp., *Eurysternus parallelus*, *Paracanthon* aff. *rosinae*, *Uroxys* sp. 1, and *Uroxys* sp. 2).

Bdelyrus braziliensis and *Eurysternus cyanescens* were found only in ANH, on the mainland. *Coprophanaeus dardanus, Deltochilum furcatum* and *Dichotomius quadrinodosus* occurred only in ITA, on the mainland. *Dichotomius* sp. and *Uroxys* sp. 2 occurred only in RAT, on the island. *Paracanthon* aff. *rosinae* and *Uroxys* sp. 1 were only shared between RAT and PER.

Species and local contributions to beta diversity index

The partitioning of the total variance in components of the contribution of species and sites to beta diversity showed different results when data on composition, abundance and biomass of dung beetles were analyzed. For composition, the total sum of squares (SS_{Total}) was 38.183 and the index of variance of beta diversity (BD_{Total}) was 0.395 for dung beetle data across all sampling sites. SCBD values ranged between 0.002 and 0.145, and 10 species contributed above the mean (0.047) to beta diversity (Table 1 left). The values of LCBD ranged between 0.003 and 0.032, indicating the uniqueness of the dung beetle community at each sampling site. Six sampling points were statistically significant to beta diversity (Figure 3A), all within two ITA sites and one PER site. LCBD values were negatively correlated with species richness ($r = -0.45$, $p < 0.001$) indicating that, in general, sites with unique species composition have a low number of species.

For abundance data, the SS_{Total} was 35.691 and the BDTotal was 0.360. SCBD values ranged between 0.0003 and 0.179, and five species contributed above the mean (0.047) to beta diversity (Table 1 center). LCBD values ranged between 0.002 and 0.040, and seven sampling points were statistically significant (Figure 3B), all occurring in the same two ITA sites sampled for composition data. LCBD values were negatively correlated with abundance at each sampling point ($r = -0.32$, $p < 0.001$), demonstrating that sites with unique species composition, in general, have low abundance.

For biomass data, the SS_{Total} was 35.275 and the BDTotal was 0.356. SCBD ranged between $6.915e^{-06}$ and 0.235, and six species contributed above the mean (0.047) to beta diversity (Table 1 right). LCBD values ranged between 0.002 and 0.042, and eight sampling points were statistically significant (Figure 3C). LCBD values were negatively correlated with biomass of each sampling point ($r = -0.49$, $p < 0.001$), and as well as to species richness and abundance, suggesting that sites with unique species composition, in general, have low dung beetle biomass.

Only four species (*C. rutilans cyanescens*, *C. saphirinus*, *D. multicolor* and *D. morbillosum*) contributed to the beta diversity index taking into account the composition, abundance and biomass of dung beetles. Although these species are very common among the sampled sites, this result suggests that they had strong local spatial variation in terms of occurrence, number of individuals and total biomass between sites.

Table 1. Partitioning of the total variance in species contribution to beta diversity (SCBD) based on the beta diversity index (BD_{Total}) and the total sum of squares (SS_{Total}).

Species	Composition SS_{Total} = 38.183 BD_{Total} = 0.395	Abundance SS_{Total} = 35.691 BD_{Total} = 0.360	Biomass SS_{Total} = 35.275 BD_{Total} = 0.356
Canthidium aff. *trinodosum*	0.121	0.141	
Canthon luctuosus	0.061		
Canthon rutilans cyanescens	0.055	0.153	0.113
Coprophanaeus saphirinus	0.100	0.123	0.235
Deltochilum multicolor	0.145	0.116	0.155
Deltochilum morbillosum	0.109	0.101	0.067
Deltochilum rubripenne	0.068		
Dichotomius sericeus	0.059		0.230
Phanaeus splendidulus	0.063		0.490
Uroxys sp. 1	0.053		

Environmental and spatial effects on community variation at different spatial scales

The variation partitioning based on community composition, abundance and biomass showed different responses at each spatial scale when we analyzed each species dataset. The variation in species composition at mainland-island scale showed a greater and significant environmental effect (Table 2A left). Altitude was the only environmental variable selected to compose the environmental model and it explained 4.5% of variation at this scale. When the spatial configuration was removed from the environmental model the explanation decreased to 4.4%. The spatial effect was not significant for variation in species composition, and after the environmental effect was removed the spatial model was still not significant. The variation explained by spatially structured environmental variables [b] explained only 0.02%.

Figure 3. Map of the sampling points showing significant values (red) of the local contribution to beta diversity (LCBD). LCBD analysis used composition, abundance and dry biomass data. ANH: Environmental Protection Area of Anhatomirim; ITA: Permanent Protection Area of Itapema; PER: Lagoa do Peri Municipal Park; RAT: Permanent Protection Area of Ratones. The circles are proportional to the total value of LCBD for each analysis.

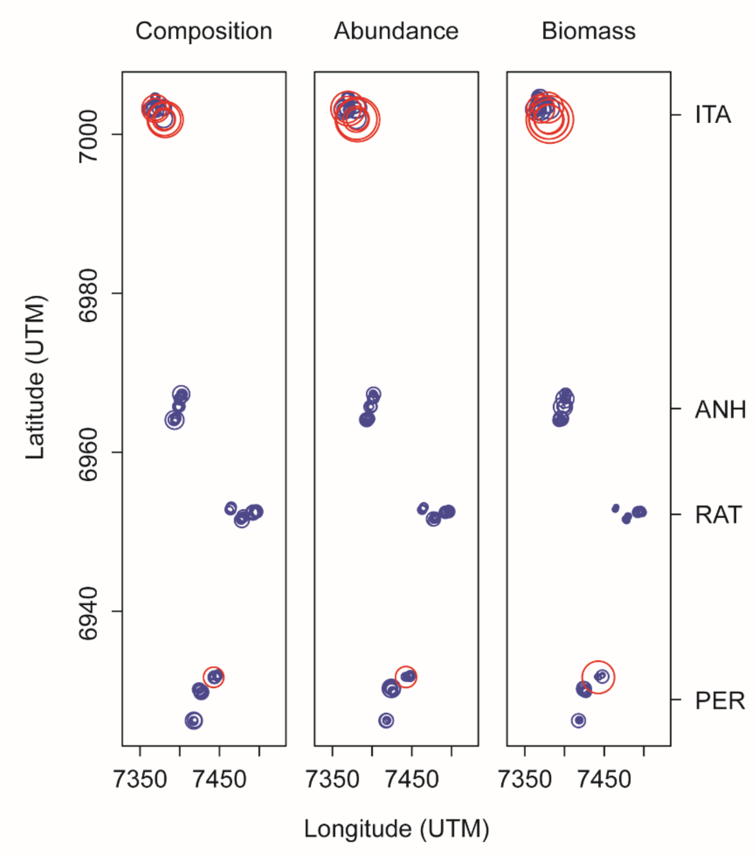


Table 2. Partitioning of variation in dung beetle communities at three spatial scales using redundancy analysis on composition, abundance and biomass.

		Composition				Abundance				Biomass			
		R^2_{adj}	DF	F	P	R^2_{adj}	DF	F	P	R^2_{adj}	DF	F	P
A) Mainland-island													
E	[a + b]	**4.5**[a]	1	5.62	0.001	**9.9**[e]	3	4.62	0.001	**9.9**[e]	3	4.61	0.001
S	[b + c]	0.4[b]	2	1.19	0.268	**1.4**[f]	1	2.40	0.016	**2.8**[b]	1	3.88	0.003
E | S	[a]	**4.4**	1	5.53	0.001	**10.0**	3	4.70	0.001	**9.9**	3	4.69	0.001
S | E	[c]	0.4	2	1.19	0.242	**1.6**	1	2.68	0.006	**2.8**	1	4.11	0.001
B) Areas													
E	[a + b]	**4.5**[a]	1	5.62	0.001	**9.9**[e]	3	4.62	0.001	**9.9**[e]	3	4.61	0.001
S	[b + c]	**13.2**[c]	5	4.02	0.001	**17.4**[g]	7	3.98	0.001	**16.6**[h]	6	4.28	0.001
E | S	[a]	**1.2**	1	2.27	0.012	**7.3**	3	3.97	0.001	**8.4**	3	4.45	0.001
S | E	[c]	**9.9**	5	3.27	0.001	**14.8**	7	3.69	0.001	**15.1**	6	4.21	0.001
C) Sites													
E	[a + b]	**4.5**[a]	1	5.62	0.001	**9.9**[e]	3	4.62	0.001	**9.9**[e]	3	4.61	0.001
S	[b + c]	-11.2[d]	40	0.75	0.999	-20.2[d]	40	0.58	1.000	-22.9[d]	40	0.53	1.000
E | S	[a]	**9.0**	1	6.19	0.001	**15.8**	3	3.98	0.001	**17.2**	3	4.20	0.001
S | E	[c]	-6.7	40	0.83	0.976	-14.2	40	0.67	0.999	-15.5	40	0.64	0.999

E: environmental model, S: spatial model, constructed from MEM variables, E | S: environmental model without spatial patterns within each spatial scale, S | E: spatial model without environmental patterns within each spatial scale, R^2_{adj}: data variation explained by the model (values are in percentage), DF: degrees of freedom of model. Significant models are in bold.

[a]Environmental model constructed from the altitude variable; [b]Spatial model constructed from the MEM1 and MEM2 variables; [c]Spatial model constructed from the MEM4, MEM9, MEM5, MEM3, and MEM1 variables; [d]Spatial model constructed from all MEM variables; [e]Environmental model constructed from the altitude, green cover and land slope variables; [f]Spatial model constructed from the MEM1 variable; [g]Spatial model constructed from the MEM4, MEM9, MEM3, MEM7, MEM1, MEM2, and MEM5 variables; [h]Spatial model constructed from the MEM4, MEM3, MEM2, MEM5, MEM7, and MEM1 variables.

At the scale of areas, spatial effects were stronger than environmental effects, and it explained 13.2% of the variation in species composition (Table 2B left). After environmental effects were removed, the spatial model explained 9.9% of the variation in the data. The environmental model, which was composed of altitude only, explained only 1.2% after spatial effects were removed. Spatially structured environmental variables [b] explained 3.3% of the variation in the data. At the smallest scale, i.e. sites, only the environmental model was significant and explained 9.0% of the data variation after spatial effects were removed (Table 2C left). At this scale, the spatial model showed no significant patterns. The variation explained by spatially structured environmental variables [b] showed negative values.

Almost 10% of the variation in composition (using species abundance) at the scale of mainland-island was attributed to the environmental model, which included altitude, green cover and land slope (Table 2A center). After spatial effects were removed, the environmental model explained 10.0% of the variation in the data. The spatial model was also significant, but explained only 1.4%. Both models were significant when only the pure effects were analyzed. Spatially structured environmental variables [b] showed negative values.

At the area scale, the spatial effect was significant (explaining 17.4% of the variation) and greater than the environmental effect. Both models were significant when only the pure effects were analyzed, in which the spatial model explained 14.8% and the environmental model explained 7.3% of the variation (Table 2B center). The variation explained by spatially structured environmental variables [b] explained 2.5% of the variation in the data. At the site scale, the environmental model had greatest relative importance for dung beetle abundance (Table 2C center). After spatial effects were removed, the variables that composed the environmental model explained 15.8% of the variation in abundance data. The spatial model showed no significant spatial patterns at this scale. Spatially structured environmental variables [b] showed negative values.

At the mainland-island scale, analysis of the variation in species composition based on biomass showed that both environmental and spatial effects were significant (Table 2A right). The environmental model composed of altitude, green cover and land slope explained 9.9% of the variation, and spatial effects explained 2.8% of the variation in the data (after corrections). The variation explained by spatially structured environmental variables [b] explained 0.002% of the variation in the data.

At the area scale, the spatial model was significant and explained the greatest amount of the variation in the biomass data (16.6%) followed by the environmental model (9.9%) (Table 2B right). After correction, the spatial and environmental models explained 15.1% and 8.4%, respectively, of the variation in the biomass data. Spatially structured environmental variables [b] explained 1.5%. At the local scale, the environmental model explained 9.9% of variation, and when spatial effects were removed the proportion increased to 17.2%. The spatial model showed no significance at this scale. Values for the variation explained by spatially structured environmental variables [b] were negative.

Discussion

In recent decades, there has been increased interest in understanding scale-dependence of the structuring processes of biological communities, including studies of protozoa [62], zooplankton [25,63], ichthyoplankton [64], dragonflies [65], coral reefs [66], reef-fishes [67], freshwater fishes [65], plants [68,69], frogs [65], birds [70], and mammals [71], covering a wide variety of ecosystems. The unique biology of dung beetles makes them excellent models with which to explore general concepts in ecology [31], including new approaches suggested by metacommunity theory. Our results represent a first step towards a better understanding of the relative importance of ecological processes on dung beetle community structure in a coastal mainland-island landscape across three different spatial scales.

In this study, the environmental heterogeneity had greater importance at smaller scales, and may be the cause of high beta diversity in terms of species richness and abundance (i.e., Shannon entropy) found among sampling sites. Local environmental factors seem to be crucial in the structuring of local communities; such factors may be responsible for high beta diversity at the local scale, as has been demonstrated for several groups of organisms in a variety of ecosystems [25,72-77]. Thus, the ecological gradient evaluated here appears to have a distribution defined by spatially structured environmental heterogeneity, which may have strong effects on dung beetle community structure locally.

Beta diversity at the area scale was lower than at the site scale, despite the increase in geographic distance among the sampling points.

At area scale, we found a significantly greater importance of spatial effects compared to environmental effects, even after the analysis of individual effects of the models. Beta diversity among areas appears to be mainly related to the spatial patterns of the sampling sites. The occurrence of shared environmental and spatial effects as drivers of beta diversity are very common with increasing spatial scale [24,75], and these shared effects may suggest significant limitations in species dispersal ability between site and area scales. Besides environmental effects, spatial limitation may be related to geographic distance, lack of connectivity caused by fragmentation, or the landscape structure between the mainland and the island.

Between the mainland and the island, beta diversity showed the highest values and at this scale only the environmental model was significant for species composition, while for abundance the environmental and spatial models were significant. The high beta diversity found between the mainland and the island has its origin at site and area scales, where environmental and spatial patterns have high relative importance. Thus, we observed that the distribution of dung beetles along an ecological gradient occurs in a spatially structured environment, where such patterns may be generated due to dispersal limitation at intermediate scales, and due to environmental heterogeneity at local scales.

The distribution pattern of dung beetle species composition was associated with the altitude gradient. This variable was significant at all scales studied after spatial effects were removed, demonstrating its strong influence on the species composition of dung beetle communities. Altitude ranged between 28 and 265 m among sampling sites. A study performed in the Colombian Andes demonstrated that dung beetle composition varied along an altitude gradient between 1,000 and 2,250 m at intervals of roughly 250 m [78]; the differences found in this study were associated with different environmental adaptations of the species. Environmental and climatic differences are also important for dung beetle distribution at low altitudes. The proximity to the sea and the effect of wind on humidity [46], and soils with higher salt concentration, although not measured in our study, could also affect the relative success of some species. Thus, the environmental and spatial configuration of sampling sites evaluated in the mainland-island landscape may influence the distribution of dung beetle species.

Except for at the mainland-island scale, in general species composition and abundance showed similar responses to the ecological gradient studied. However, the relative importance of the models was greater for abundance data. Although abundance may not sufficiently explain patterns of species distribution (i.e., due to confounding effects caused by highly abundant species), it may help to explain the responses of species across the environmental gradients, because it reflects changes in the relative success of each species against these gradients [25]. In our study, abundance and biomass data were explained by the same set of environmental variables, and showed very similar responses to the ecological gradients. In general, dung beetle biomass was more influenced by individual spatial effects than abundance data. Thus, biomass may be an important descriptor of changes in the relative success of dung beetles along ecological gradients, because it is mainly derived from nutrients obtained from mammal feces [79], and availability of this resource may also be affected by environmental heterogeneity.

In addition to altitude, the percentage of green cover and land slope were part of the environmental model describing the distribution of dung beetle abundance and biomass. Green cover has also been found to explain the distribution of dung beetles species in different-sized Atlantic forest fragments [80]. Variation in the percentage of green cover illustrates the differences among sites with greater or fewer small plants and shrubs covering the soil. Sites with greater spacing between trees and less tree cover allow more sunlight, which may influence the microclimate and soil moisture, as shown to occur in forest edges [81]. Land slope ranged between five and 36º degrees, and having some degree of slope is a common characteristic among our sampling sites, due to the fact that Atlantic Forest is typically located on hillsides with a large altitudinal range [29]. In another study of Atlantic Forest in Serra do Japi, located in the western region of São Paulo state’s Atlantic plateau, Brazil, dung beetle composition was shown to vary between the tops, hillsides and valleys, which are associated with differences in environmental structure [46]. Sites with high degrees of land slope may be most affected by rainfall, and may present unfavorable soil features for some dung beetle species. These environmental characteristics may influence the distribution of dung beetles, and may have greater power to affect relative species success.

Changes in the structural complexity of forested areas may modify the entire community associated with these habitats, diminishing the species richness of some taxonomic groups and increasing the others [33]. For example, the structure of the environment was more important in determining dung beetle community composition than resource availability in areas occupied by cattle in Mexico [82]. The distribution of dung beetles along different environmental characteristics may show discrete associations typical to particular biotypes within the landscape [83]. Species richness, abundance and biomass of dung beetles were negatively affected in disturbed habitats (e.g., secondary forests and *Eucalyptus* plantations in the Brazilian Amazon) when compared to primary forest habitats [35]. Microclimatic variations in tropical forests related to canopy height and opening affected dung beetle communities in French Guiana [84]. Thus, many species of dung beetles have relationships with certain habitat characteristics, likely to facilitate finding mates and/or food, or could be directly related to the presence of organisms that produce their food resource.

High inter- and intraspecific competition, random distribution, and ephemeral nature of food resources together suggest, a priori, that dung beetles are probably good dispersers [85]. However, relatively few quantitative descriptions of dispersal in these beetles exist [85]. The dispersal ability of *Canthon acutus* was investigated in Venezuela using capture-mark-recapture technique [45]. The authors installed pitfall traps baited with feces at different distances in a semi-deciduous tropical forest, and they found that 95% of individuals were collected up to 25 m. In contrast, using similar techniques, other authors [86] evaluated the dispersal ability of *Canthon cyanellus cyanellus* across a Mexican landscape that contained different components such as forest fragments, hedgerows and pastures. They found a maximum movement distance among the different landscape components of 1,560 m for males (average 390 m) and 860 m for females (average 290 m), suggesting that landscape type change is not a barrier to dispersal for some species. In fact, some species from continuous Amazonian forest fragments do not extend their activities to adjacent open areas, and this effect is reduced when there is presence of secondary forest in these areas [40]. We may expect a similar pattern in the Brazilian Atlantic Forest.

Besides differences in dispersal ability, several species of dung beetles are associated with certain habitat types [35,46,47,87-91] due to microclimatic factors [84] or resource availability [31]. Data on differences in dispersal ability in the species sampled in this study are still lacking. Based on our results, it is possible that the high beta diversity found among sites reflects low dispersal ability due to environmental and spatial effects. Many species of dung beetles that inhabit forests tend to not extend their range to open areas [40,92], which influences their ability to disperse and colonize new habitats when the matrix is not favorable. However, species that live in forest edges or in the matrix [83,86] may have a stronger ability to disperse and colonize new habitats compared to those living inside the forests.

The high beta diversity of dung beetle communities found among our sampling sites throughout the ecological gradient could still be related to historical events [5,11] or neutral processes [10]. In a biogeographical context, the island of Santa Catarina shows similar physiographic and structural features to those of the mainland, since the island and the mainland were connected during past periods when the Atlantic Ocean level was low [93]. During that time, the small minimum distance between mainland and island (minimum of 500 m) and low maximum depth between them (about 30 m) may have allowed a favorable environment for dispersal of the species from the mainland to the island. Site “C” of ITA is unique in that is separated from the continuous forest that occurs in each area due to fragmentation caused by a highway; it had the lowest values for species richness (five) and for number of individuals (49), and was the exclusive site of occurrence of *Coprophanaeus dardanus*. This site also showed the lowest average altitude, and like others, this site has significant contribution to the negative relationship between LCBD values and community descriptors (species richness, abundance and biomass).

Due to the current fragmented structure of the landscape and the negative impacts on many coastal environments that urbanization has caused [93,94], the Atlantic Forest landscape is highly fragmented and in different stages of succession, with each functioning as “islands”. The communities are isolated and dispersal and colonization rates are low [95] due to insertion in a matrix of inhospitable environments [96] for forest-inhabiting dung beetle species. Our results show that there were five species found only on the mainland, and five only found on the island. On the mainland, three species occurred only in ITA, and two only in ANH. On the island, two species occurred only in RAT, and two others were shared between RAT and PER. These results, as well as the analysis of the local contribution to beta diversity (significant sampling points occurred only near the ends of the spatial gradient, Figure 3) reflect the high importance of large-scale spatial effects in structuring dung beetle communities. The distinct occurrence of species between mainland-island may be result of isolation processes [95,97], or local extinction due to lack of certain food sources (e.g., presence of certain mammals [38]) or simple inability to colonize [98]. Alternatively, species may persist at a given location due to biotic and/or abiotic conditions in spatially structured environmental conditions [99]. We propose that the processes listed above act as joint drivers of the current distribution of dung beetle species in the landscape studied, and our result suggest that the relative importance of each process depends on the spatial scale.

Environmental control (i.e., the species sorting paradigm) seems to be the dominant structuring process in the metacommunity at the local scale. However, environment was also important at larger scales, and environmental factors were spatially structured along the ecological gradient studied. Spatial effects were more important at larger scales, where there was an increase in beta diversity that appears to be due to limitation in dispersal ability of the species due to geographic barriers and fragmented landscape. Contrary to what was found in other studies [25], our results suggest that the increase in the spatial scale was related to increased environmental heterogeneity, although only mildly, agreeing with the general findings for stream insect communities [26]. We believe that our results, extrapolated with caution, represent general patterns that serve as the basis for other organisms with similar characteristics and requirements.

Appropriate management of spatially heterogeneous ecosystems requires an understanding of both local and regional processes by which beta diversity is created and maintained, in order to preserve the spatial organization or species-environment relationships on which beta diversity is dependent [12,100]. Due to current scenario of fragmentation and isolation of remaining fragments of the Brazilian Atlantic Forest [29], knowing these answers is of great interest to managers and decision makers to plan appropriate conservation strategies in an increasingly human-modified world.

Supporting Information

Figure S1 Map of the sampling sites showing the distribution of species richness, abundance and total biomass of dung beetles. ANH: Environmental Protection Area of Anhatomirim; ITA: Permanent Protection Area of Itapema; PER: Lagoa do Peri Municipal Park; RAT: Permanent Protection Area of Ratones. The circles represent the proportion to the total for each analysis.
(TIF)

Dataset S1 Dataset of abundance and dry biomass of dung beetle species, environmental variables, and geographical coordinates. Samplings were performed in Brazilian Atlantic Forest, Santa Catarina, Brazil using baited pitfall traps from January to February 2012.
(XLXS)

Table S1 Dung beetle species sampled in Atlantic Forest in eastern Santa Catarina, Brazil. ANH: Environmental Protection Area of Anhatomirim in Governador Celso Ramos; ITA: Permanent Protection Area of Itapema; PER: Lagoa do Peri Municipal Park, Florianópolis; RAT: Permanent Protection Area of Ratones, Florianópolis. Letters A to E depict the sampled sites in each area. T: total.
(XLXS)

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Supporting Information

Dataset S1 Dataset of abundance and dry biomass of dung beetle species, environmental variables, and geographical coordinates. Samplings were performed in Brazilian Atlantic Forest, Santa Catarina, Brazil using baited pitfall traps from January to February 2012.

Disponível online em:
http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0111883#s5

Figure S1 Map of the sampling sites showing the distribution of species richness, abundance and total biomass of dung beetles. ANH: Environmental Protection Area of Anhatomirim; ITA: Permanent Protection Area of Itapema; PER: Lagoa do Peri Municipal Park; RAT: Permanent Protection Area of Ratones. The circles represent the proportion to the total for each analysis.

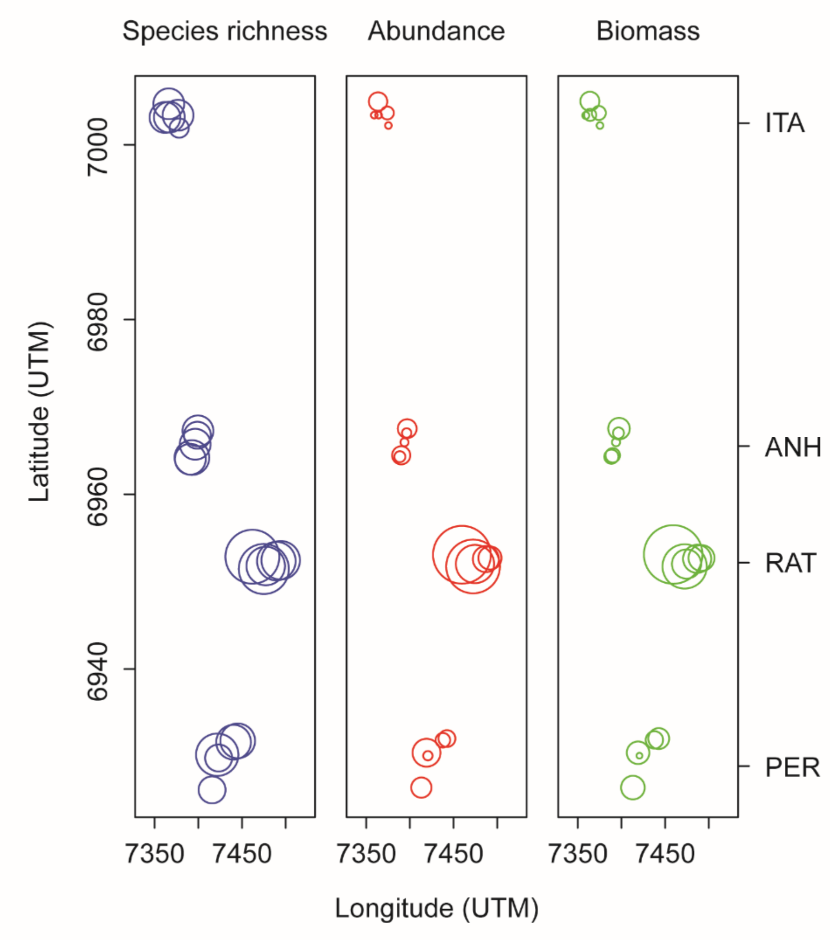

Table S1 Dung beetle species sampled in Atlantic Forest in eastern Santa Catarina, Brazil. ANH: Environmental Protection Area of Anhatomirim in Governador Celso Ramos; ITA: Permanent Protection Area of Itapema; PER: Lagoa do Peri Municipal Park, Florianópolis; RAT: Permanent Protection Area of Ratones, Florianópolis. Letters A to E depict the sampled sites in each area. T: total.

Species	ANH						ITA						PER						RAT					
	A	B	C	D	E	T	A	B	C	D	E	T	A	B	C	D	E	T	A	B	C	D	E	T
Bdelyrus braziliensis	1					1																		
Canthidium aff. *trinodosum*	3	13	1	6	12	35	7		12	2	4	25		7	1	91	3	102	72		3	91	54	220
Canthon luctuosus								1			2	3		1		3	1	5	1	2	5	2	1	11
Canthon rutilans cyanescens	13	18	75	16	17	139	73	11	20	9	21	134	25	32	18	11	42	128	24	47	29	23	36	159
Canthonella aff. *instriata*		1				1	1		1			2				2		2		1	1		1	3
Coprophanaeus dardanus									5			5												
Coprophanaeus saphirinus	6	6	6	4	2	24	33	9		28	20	90	14		10	23	11	58	8	5	5	18	33	69
Deltochilum brasiliense							1					1				1		1	1			2	4	7
Deltochilum furcatum								2		3	1	6												
Deltochilum morbillosum	8	14	11	6	1	40	9	12		2	20	43	25	4	23	26	4	82	20	1	2	13	40	76
Deltochilum multicolor	1	3	4	14	13	35	4	3	11	1	17	36	12	2	4	3	8	29		3	4	2	14	23
Deltochilum rubripenne		1	2			3							2			15	2	19	4	4	14	4	20	46
Dichotomius sericeus	48	84	32	19	11	194	9	10		3	11	33	43	21	93	28	36	221	140	124	108	218	154	744
Dichotomius quadrinodosus										1		1												
Dichotomius sp.																							1	1
Eurysternus cyanescens	2		2		1	5																		
Eurysternus parallelus													1				1	2				1		1
Paracanthon aff. *rosinae*													2		1			3					1	1
Phanaeus splendidulus			2	5	3	10		1				1	1					1	4	1	1	5	3	14
Uroxys sp. 1														2		4		6	10	6		19	67	102
Uroxys sp. 2																						1		1
Number of individuals	82	140	135	70	60	487	137	49	49	49	96	380	125	69	150	207	108	659	284	194	172	399	429	1478
Number of species	8	8	9	7	8	11	8	8	5	8	8	13	9	7	7	11	9	14	10	10	10	13	14	16
Total biomass (g)	12.2	18.5	12.4	9.5	6.9		16.4	6	5.7	10.4	12		17.9	4.9	20.3	19.3	14.9		25.1	24.2	22.3	38.1	50.4	

ARTIGO III: SPATIAL PATTERNS OF MOVEMENT OF DUNG BEETLE SPECIES IN A TROPICAL FOREST SUGGEST A NEW TRAP SPACING FOR DUNG BEETLE BIODIVERSITY STUDIES

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Artigo submetido para o periódico *PLoS ONE*.

> “Absence of evidence is not evidence of absence.”
>
> (Carl Sagan)

Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies

Abstract

A primary goal of community ecologists is to understand the processes underlying the spatiotemporal patterns of species distribution. Understanding the dispersal process is of great interest in ecology because it is related to several mechanisms driving community structure. Using mark-release-recapture technique we investigated the movement ability of dung beetles and tested the protocol of interaction distance between baited pitfall traps in the Brazilian Atlantic Forest. We found differences in mean movement rate between Scarabaeinae species and between species with different sets of ecological traits. Large-diurnal-tunneler species showed larger movements than both large-nocturnal tunneler and roller species. The minimum distance of 50 m between pairs of baited pitfall traps proposed about 10 y ago is inadequate as suggest our results based on the analyses of the whole community or the species with the highest number of recaptured individuals. Dung beetle species with different sets of ecological traits may differ in their dispersal ability, so we suggest a new minimum distance of 100 m between pairs of traps to minimize the interference between baited pitfall traps for sampling copro-necrophagous Scarabaeinae dung beetles.

Introduction

Understanding the patterns of the spatiotemporal distribution of species is still a challenge to community ecologists. Dispersal is the capacity that organisms have to move over space, being one of the four basic ecological processes driving such patterns [1]. This process is of great interest in ecology and evolution, because it is related to population and community dynamics, gene flow, speciation and extinction processes [2]. Dispersal is affected by several factors such as the ability to move through the landscape, perceptual resolution (shortest distance to detect resources), quality and distribution of the resource, and internal and external stimuli [3]. Species with dissimilar morphological and functional traits may have other resource requirements and thus have different rates of dispersal. Thus, species with individuals who have higher dispersal ability may alter strongly the structure of local communities via patch dynamics or mass effects [4].

Dispersal was the key point for the development of the metacommunity theory. The metacommunity is a set of local communities linked by the dispersal of multiple species [4, 5]. This theory is concerned with the role of dispersal between local communities in generating patterns of composition, abundance and species richness at multiple spatial scales. Understanding the dispersal process of species is critical in current scenarios of habitat loss, fragmentation and global climate change [6]. The study of the movement ability of organisms that play key roles in the maintenance and restoration of ecosystems, such as dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae), is an important starting point for planning conservation strategies.

Dung beetles are a very diverse group of detritus-feeding insects that play several ecological functions [7]. The diversity of the group is reflected in differences in body size [8, 9], body shape [10], resource relocation behavior for feeding and nesting [11, 12], and diel activity period [13, 14] for example. Dung beetle species may respond in different ways to change, disturbance, fragmentation, and loss of habitat [15], and they may be used as environmental indicators [16-18]. Several species from Neotropical forests exhibit varying degrees of habitat specificity, with many environmental specialists and generalists [19, 20]. So, environmental changes and fragmentation may be barriers to dispersal of some dung beetle species [19, 21].

The community structure of dung beetles is strongly influenced by reproductive competition [22] in patchy and ephemeral food resources [23]. The high inter- and intraspecific competition coupled with the random distribution and ephemerality of food suggest that dung beetles are probably good dispersers [24]. Studies on dispersal of Scarabaeinae dung beetles are few [25-30]. However, some authors suggest that there may be differences between the dispersal ability among species or individuals of a species due to different interspecific and intraspecific species traits [26, 29, 31]. For example, males of *Canthon cyanellus cyanellus* LeConte, 1859 have a faster movement rate than females, and young-mature individuals move more often than immature and old individuals in a Mexican dung beetle assemblage [29]. A diurnal large-bodied species, *Oxysternon conspicillatum* (Weber, 1801), was recaptured 1 km away two days after release in an Ecuadorian rain forest [26], a longer distance when compared to the distance moved by species of *Onthophagus* Latreille, 1807 and *Canthon* Hoffmannsegg, 1817, both small-bodied species. Therefore, knowing the ability to move within and between ecosystems may help in understanding how Scarabaeinae communities are structured locally and regionally.

An important issue on the study of dung beetles is the lack of a standardized sampling protocol [32]. The sample design and the distance between traps used for sampling dung beetles vary widely, making it difficult to compare diversity patterns or community responses between studies. For instance, the movement of *Canthon acutus* Harold, 1868 was investigated [28] in a mark-recapture experiment and the authors observed that 95% of recaptured individuals were attracted within 26.2 m from traps. These authors suggested that the minimum distance of 50 m between traps could reduce or eliminate the interference between pairs of baited traps in sampling Scarabaeinae. However, this distance may vary between species due to foraging behavior or body size, for example. So, testing the proposed distance among baited traps, based on the response of a single species, may provide new information about the suitability of the suggested distance for other species and different ecosystems [33]. Establishing a standardized sampling protocol where the interference between pairs of baited traps is minimal or none is an important issue for dung beetle biodiversity studies [28, 32], because independence among samples is a basic premise in statistics analyses. Avoiding effects of pseudoreplication is a central issue in ecological studies [34], and the spatial distance between samples has several consequences on results obtained [35] due to the intrinsic spatial variation that occurs in natural communities [36].

The aim of this study was to investigate the movement ability of dung beetles and to evaluate whether the current protocol of 50 m of distance between baited pitfall traps is adequate to eliminate interference (or dependence) between traps in Scarabaeinae community studies. Based on literature, our hypothesis suggests that there are differences in the movement ability between Scarabaeinae species and between individuals of each species within the same community due to some interspecific and intraspecific ecological traits (e.g. gender, age categories, body size, food relocation behavior, and diel activity period).

Materials and Methods

Study area

The study was developed in the Desterro Environmental Conservation Unit (UCAD) which is an environmental protected area of

Atlantic Forest, located in Florianópolis, Santa Catarina Island, Brazil. The UCAD is located in the northwest (27º30’48”, 27º32’34” S; 48º29’38”, 48º30’42” W) of Santa Catarina Island and it has 491 ha of dense ombrophilous forest [37] with secondary vegetation. The climate is Cfa according to the Köppen-Geiger classification. The average annual temperature is 21.1°C (23.4ºC in summer; 16.7ºC in winter) and average annual rainfall is ca 1500 mm [37]. The terrain is mostly mountainous, with elevation ranging between 0-300 m asl. The altitude of sampling points ranged between 83-244 m asl.

Sampling design

Dung beetles were sampled using baited pitfall traps during the spring and summer of 2013-2014 (November to March), which is the period of greatest abundance of this group in southern Brazil [38, 39]. For capturing the beetles we used plastic containers (15 cm diameter; 8 cm deep) with the cover cut into ¼ of its area to allow the entry but avoid the escape of trapped insects (type A [40]). Additionally, a protection against rain was placed above the traps. Each trap was baited alternately between each 48 h sampling period with ca 20 g of human feces or rotten meat, as both satisfy the two main eating habits of dung beetles: coprophagy and necrophagy, respectively [22, 40]. The baits were wrapped in a thin cloth and tied inside the trap for easy discard and to prevent manipulation by insects. Adjacent traps had the same bait in each sampling. The human samples used for the bait were from one of the authors (PGS).

Dung beetles were sampled using 23 traps (a map showing the sampling design is in Fig. 1; see Results). Eighteen traps were arranged along six linear and parallel transects spaced 50 m apart. Each transect had three traps. Traps were spaced 10 m apart in the first and in the last transect. In second and fifth transect, traps were spaced 25 m apart, and in third and fourth transect, traps were spaced 50 m apart. In addition, a trap was set 100 m before the first transect in an area with predominantly grassland and undergrowth vegetation and with little presence of trees. Another four traps were placed transversely to the latter transect distant 100, 200, 350 and 500 m. The distance between the first and the last trap was ca 1 km and the spatial distribution of the traps was adjusted for land condition and trail access of the study area. We used different distances between traps in each transect (i.e. 10, 25 and 50 m) because we expected that dung beetles would be more recaptured in closely spaced traps [28]. We calculated the area of study as the spatial distribution of traps using area formulas of geometric figures. We added 100 m to the sides of traps located in the extremes. The total study area was 0.23 km^2.

All traps were baited at the first day of each sampling period and insects were collected after 48 h. After beetles have been removed, the baits were removed and properly discarded, and traps were dismounted. Captured dung beetles were checked for marks and marked when they did not show any previous mark (see Mark-release-recapture section). The interval between each 48 h sampling period was 7.8 d on average (range 2-18 d due to the climatic conditions) to allow the movement of individuals within the forest without bait interference. Nineteen samplings with duration of 48 h were performed during the study period (November 2013 to March 2014). Marked beetles were resampled at each new 48 h sampling period and unmarked beetles were marked and released next day.

Mark-release-recapture

After each 48 h sampling period sampled dung beetles were cleaned, identified, sexed, marked, and classified into three age classes. The identification was performed by comparison with previously identified species by expert (Dr. Fernando Vaz-de-Mello, Universidade Federal de Mato Grosso, Brazil) from the Entomological Collection of the Universidade Federal de Santa Catarina. We sexed the beetles identifying characters of sexual dimorphism following the descriptions of species.

Individuals of each species were marked with a unique combination of points on the elytra and pronotum that allowed us to identify each specimen (S1 Fig.). Marking was performed by using an entomological needle with rough tip by scraping a thin layer of elytra and pronotum according to the distribution of the points. This technique is noninvasive and does not have the risk of being lost by the insect as some paints (previous laboratory observations). Marked individuals were kept in ventilated and moistened containers with leaf-litter to be released the next day in the same place (near the trap) of capture (the day after 48 h sampling period).

Age categories used were: (1) recently emerged or immature, (2) young-mature, and (3) old individuals. The assignment of age categories followed the following criteria: aspect and hardness of the cuticle of the body, wearing stage of the teeth and spur of anterior legs and clypeal teeth [29]. The relationship between the aspects of these characters with sexual maturity was previously established [29].

Dung beetle species were classified according to their behavioral guilds in dwellers (feed on and nest in the resource), rollers (build and roll food-balls over the soil until bury them), and tunnelers (bury portions of food under or next the resource) [41, 42]. The beetles were grouped into size categories: small (≤ 1.5 cm length) or large (> 1.5 cm length). Although sampled, individuals of the genera Canthonella Chapin, 1930 and Uroxys Westwood, 1842 were not incorporated into this study by the inability to mark them using the above technique due to the small size of individuals (< 0.5 cm length). The species were grouped into categories of diel activity periods in diurnal, nocturnal, and diurnal-nocturnal [13, 14].

The Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/MMA) issued the permits to collect specimens (permit #32333-3 to MIMH). The field study did not involve endangered or protected species.

Data analysis

Spatial patterns of movement

We used only data on recaptures to verify the movement patterns of dung beetles. The dataset used in this study is available as online supporting information (S1 Dataset). We calculated the mean, median and maximum movement distance for each species. The movement of all individuals recaptured by species was shown schematically according to the spatial distribution of pitfall traps in the study area. Linear models, followed by residual analysis, were used to test for differences in movement rate between species and between individuals of each species in relation to gender, age, body size, relocation behavior, and diel activity. We calculated the movement rate (m/day) for each individual based on the observed data (distance moved during 24 h between samplings), multiplying the distance values by one (24 h) and dividing by the number of days between capture and recapture. Species that had no or few values for each category were excluded from the analyses. After the analysis, we conducted a posteriori test to identify differences. The relation between movement distance (m) and time (d) was investigated using linear models for the entire community and individually for each species, with and without the use of data on recaptures at the same trap. Analyses were conducted using R 3.1.1 software [43] and associated packages.

Suitability of trap spacing

Nonlinear regression analyses were performed to verify the movement distance during 48 and 96 h using SigmaPlot 10.0 program. We estimated the linear distance traveled by dung beetles (in a straight line between two traps) in 48 and 96 h with the aim of establishing a minimum distance between baited pitfall traps that maximizes the sampling efficiency, reducing the sampling area and the possible interaction between traps [32]. Such periods are commonly used in studies of this fauna. We estimated the distance traveled by each individual during 48 and 96 h based on the observed data (distance moved during the period between each 48 h sampling period), multiplying the distance values by two (48 h) or four (96 h) and dividing by the number of days between capture and recapture of each individual. After that, we calculated the number of individuals recaptured by each distance category (0-10, 11-25, 26-50, 51-75, 76-100, 101-150, 151-300, 301-500, 501-750, and 751-900 m) and then divided the number of recaptures by the number of individuals recaptured at the smallest distance class. This proportion was used to reduce the effect of differences in the beetle's behavior [28] because although there was a long period between 48 h sampling periods, there was a large number of recaptures in the same trap, indicating that many individuals remained foraging or were buried near the traps for long periods. Our results showed that the 0-10 m category was represented by recaptures only at the same trap. In the analysis of nonlinear regression we used data on the proportion of individuals recaptured in each distance category and the minimum value of each category to avoid overestimation of the distance traveled by beetles. We calculated the definite integral of nonlinear regression analysis and determined the distance corresponding to 95 and 99% of the area under the curve [28]. This distance is the estimated radius of movement distance over a certain period of time in which 95 and 99% of individuals would be captured. These analyses were conducted for the entire community and also to the species with the highest number of recaptures in our study to test the effect of distance on the proportion of recaptured individuals. We also analyzed rotten meat and feces separately because these baits may attract dung beetle species differently. The radius of bait attraction and the distance moved by beetles without baits should be taken into account in establishing a distance between traps that minimizes interference between pairs of baited pitfall traps.

The geographical coordinates of each trap were recorded using a hand-held GPS at ground level. The distance between each pair of traps was corrected for differences in elevation using the triangle-rectangle formula (Pythagorean Theorem) to estimate more accurately the straight-line distance traveled by dung beetles.

Results

A total of 1806 individuals belonging to 17 species were marked and released (S1 Table). *Canthon rutilans cyanescens* Harold, 1868, *Dichotomius sericeus* (Harold, 1867), and *Deltochilum morbillosum* Burmeister, 1848 were the species with the highest number of marked and released individuals. A total of 112 (6.2%) individuals (58 males and 54 females) belonging to eight species were recaptured (Table 1) with an overall recapture rate of 6.3% (range 1.5-22%). Twelve individuals (seven males and five females) were recaptured twice and two other individuals (one male and one female) three times. Three species were classified as small and four as large. We recaptured six rollers and two tunnelers. Young-mature individuals accounted for almost 60% of recaptured individuals. Only three individuals of *Deltochilum rubripenne* (Gory, 1831) were classified as old individuals. We recaptured three diurnal, three diurnal-nocturnal, and two nocturnal species. Only *Canthon luctuosus* Harold, 1868 showed no movement between traps (Fig. 1). For individuals recaptured at the same trap, the average time to recapture was 14.2 d (range 5-67 d).

Spatial patterns of movement

The spatial patterns of movement of dung beetles may be seen in Fig. 1. *Canthon r. cyanescens* moved across the entire study area (Fig. 1). Similar numbers of males and females, mostly immature individuals, represented the recaptured individuals of *C. r. cyanescens*. *Coprophanaeus saphirinus* (Sturm, 1826) showed the longer movements of an individual among dung beetle species (ca 850 m in straight line) (Fig. 1), and we found similar numbers of recaptured males and females, and immature and young-mature individuals. Females of *Deltochilum brasiliense* (Castelnau, 1840), a large-bodied roller species, showed shorter movements (Fig. 1). Similar numbers of immature and young-mature males represented individuals of *D. morbillosum* (Fig. 1).

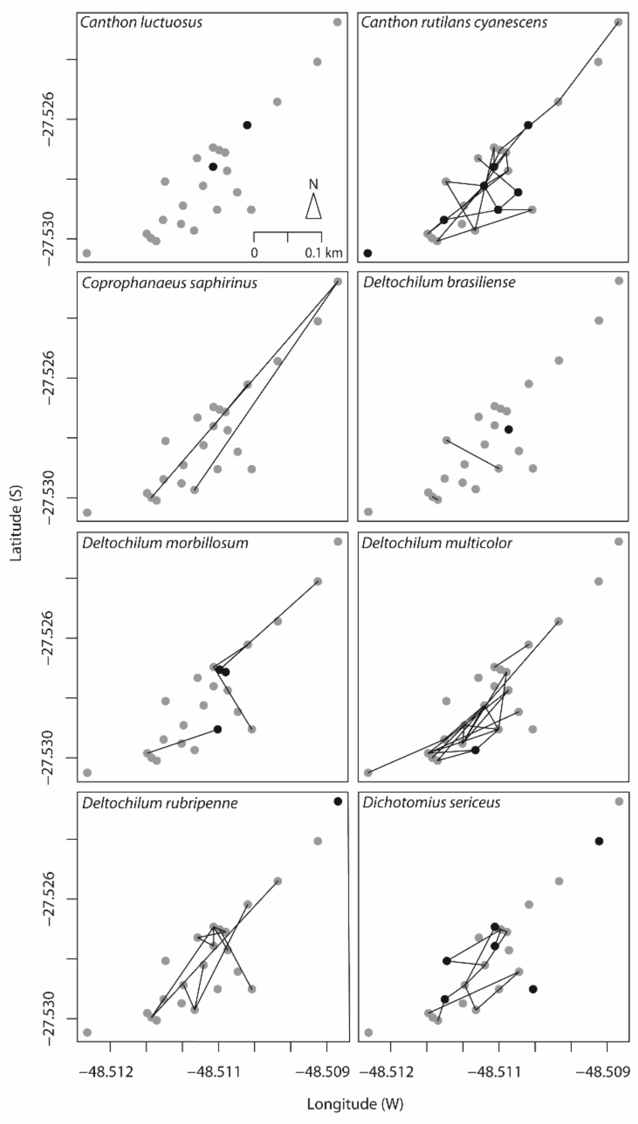
Table 1. Number of marked and recaptured individuals by gender and age categories, movement values and time between recaptures for Scarabaeinae species.

Species[a]	Individuals			Gender		Age			Movement					Time (range) in days
	Mk	Rc	%	M	F	IM	MA	OL	MMR	Same	Me	Md	Max	
A. *Canthon luctuosus* Harold, 1868 ^{S,R,DN}	133	2	1.5	0	2	1	1	0	0	2	-	-	-	7(7-7)
B. *Canthon rutilans cyanescens* Harold, 1868 ^{S,R,D}	677	35	5.2	17	18	23	12	0	9.82	11	143.51	85.95	504.72	24.7(7-82)
C. *Coprophanaeus saphirinus* (Sturm, 1826) ^{L,T,D}	61	3	4.9	2	1	1	2	0	36.03	0	607.79	807.98	852.74	16.6(14-22)
D. *Deltochilum brasiliense* (Castelnau, 1840) ^{L,R,N}	18	3	16.7	0	3	1	2	0	2.44	1	70.59	70.59	127.84	19(7-43)
E. *Deltochilum morbillosum* Burmeister, 1848 ^{S,R,DN}	168	9	5.4	7	2	4	5	0	3.96	3	194.74	186.93	358.43	40.7(6-87)
F. *Deltochilum multicolor* Balthasar, 1939 ^{L,R,DN}	100	22	22.0	10	12	6	16	0	12.61	1	205.98	206.68	551.76	24.8(7-74)
G. *Deltochilum rubripenne* (Gory, 1831) ^{L,R,D}	131	16	12.2	10	6	1	12	3	5.17	1	260.22	226.39	614.79	57.6(14-94)
H. *Dichotomius sericeus* (Harold, 1867) ^{L,T,N}	451	22	4.9	8	14	5	17	0	7.21	10	109.93	88.40	222.88	18.3(5-81)
Total	1606	112	6.2	54	58	42	67	3						

Marked (Mk) and recaptured (Rc) Dung beetle individuals. %: recapture rate. Gender: male (M) and female (M). Age categories: immature (IM), young-mature (MA), and old (OL) individuals. Movement (m): mean movement rate (MMR [m/d]), number of individuals recaptured at the same trap (Same), mean (Me), median (Md) and maximum (Max) movement distance for individuals that did move between traps.

[a] Size categories: small (S, ≤ 1.5 cm) and large (L, > 1.5 cm). Behaviour categories: roller (R) and tunneler (T) species. Diel activity: diurnal (D), nocturnal (N), and diurnal-nocturnal (DN) species.

Fig. 1. Movement patterns of dung beetle species. Circles depict the trap design. Black circles depict recaptures of individuals in the same trap. Each line segment depicts a beetle movement between two traps. Time between recaptures ranged 5-87 d.

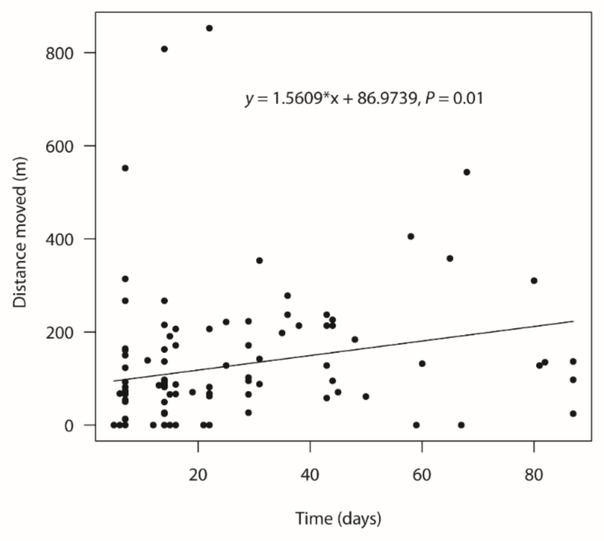


Deltochilum multicolor Balthasar, 1939 showed a concentration of movements at the southeast portion of the sampling area (Fig. 1). It was the most recaptured species (22% of recapture rate), and was represented by similar number of males and females, mostly young-mature individuals. *Deltochilum multicolor* was the only species that moved through the area with predominantly grassland and undergrowth vegetation and with little presence of trees (between the first trap and the first transect, ca 100 m away). *Deltochilum rubripenne* showed a concentration of movements at the middle portion of the sampling area (Fig. 1), and was represented mainly by young-mature males. *Deltochilum rubripenne* showed the second longest maximum movement of an individual (ca 614 m in straight line). *Dichotomius sericeus* showed a concentration of movements between the six transects located at the middle of the sampling area (Fig. 1). *Dichotomius sericeus* was mostly represented by young-mature females.

The mean movement rate varied among dung beetle species (F = 3.85, P = 0.002). *Coprophanaeus saphirinus* showed higher movement rate than other species (S2 Fig.). There was no difference in movement rate between species with different periods of diel activity (F = 0.55, P = 0.57), body size categories (F = 0.30, P = 0.58), and relocation behaviors (F = 1.31, P = 0.25). Relocation behavior and diel activity period showed a significant interaction (F = 4.57, P = 0.002). Diurnal-tunneler species showed the highest mean values of movement rate and differed from nocturnal-tunneler, diurnal-roller and nocturnal-roller species (S3 Fig.). The interaction between body size, diel activity and relocation behavior period was also significant (F = 3.85, P = 0.002) and showed that large-diurnal tunneler species had larger movement rate than other species (S4 Fig.). There were no differences in mean movement rate for remaining factors and interactions (S2 Table).

We observed a positive and significant relation between time and distance moved by dung beetles, including recaptures at the same trap (F = 5.70, P = 0.01; Fig. 2). This pattern was not observed when we did not use data from recaptures at the same trap (S5 Fig.). Using the equation of the linear model (Fig. 2), we find that the estimated movement distance traveled in 48 h by dung beetles is 90 m. For 96 h, the distance was 93 m. Only the distance of movement of *C. r. cyanescens* (F = 5.82, P = 0.02) was positively related to time (including recaptures at the same trap). The estimated distance traveled in 48 h was 79 m for this species.

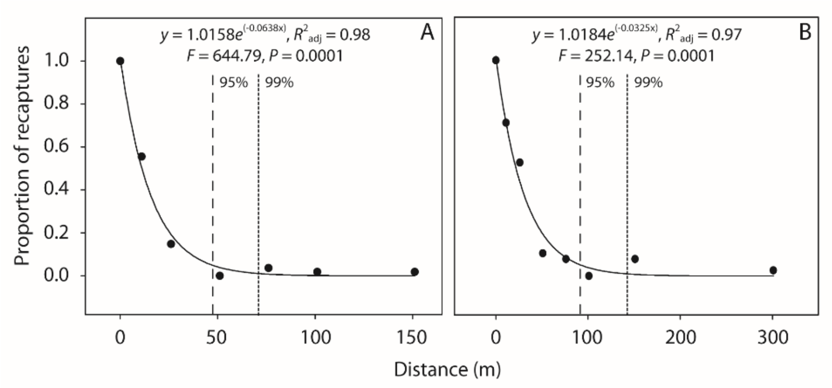
Fig. 2. Linear model between movement distance (m) and time (d) for recaptured individuals of Scarabaeinae, including recaptures at same trap.



Suitability of trap spacing

The nonlinear regression analysis showed that the proportion of recaptured beetles decreased rapidly with increasing distance in both 48 h ($y = 1.0158e^{(-0.0638x)}$, $R^2_{adj} = 0.98$, $F = 644.79$, $P = 0.0001$; Fig. 3A) and 96 h ($y = 1.0184e^{(-0.0325x)}$, $R^2_{adj} = 0.97$, $F = 252.14$, $P = 0.0001$; Fig. 3B). Calculating the area under the curve we estimated a radius of 47 m of movement distance where 95% of the beetles would be captured within 48 h (Fig. 3A). The radius was 72 m where 99% of individuals would be recaptured. The estimation of movement radius which 95% of the beetles would be recaptured for the period of 96 h was 92 m (Fig. 3B). Ninety-nine percent of individuals would be recaptured up to 143 m for this period. Using only the movement data of *C. r. cyanescens*, the distances where 95 and 99% of individuals would be recaptured at 48 h were 40.5 and 59 m ($y = 0.9982e^{(-0.0720x)}$, $R^2_{adj} = 0.99$, $F = 576.29$, $P = 0.0002$; Fig. 4A), respectively. At 96 h, the distances where 95 and 99% of individuals would be recaptured were 85.3 and 122 m ($y = 1.1287e^{(-0.0337x)}$, $R^2_{adj} = 0.84$, $F = 33.72$, $P = 0.0021$; Fig. 4B), respectively.

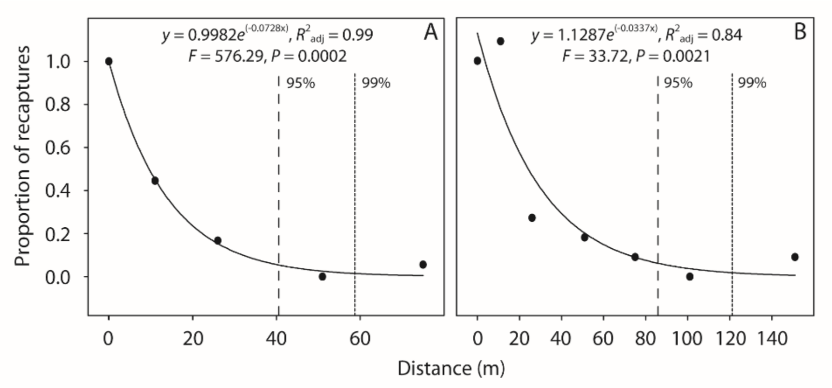
Fig. 3. Proportion of recaptured individuals of Scarabaeinae with increasing distance for estimated time periods of 48 (A) and 96 h (B). Each proportion was normalized by the number of beetles recaptured in the smallest distance category (0-10 m). Dashed and dotted lines represent the radius for 95 and 99% of recaptured individuals, respectively. The distance is an estimate based on the distance traveled by beetles during longer periods.



Similar results were found when we analyzed the two types of baits separately. For rotten meat, nonlinear regression analysis showed that the proportion of recaptured dung beetles decreased with increasing distance in both 48 h ($y = 1.0203e^{(-0.0672x)}$, $R^2_{adj} = 0.97$, $F = 291.27$, $P = 0.0001$; Fig. S6A) and 96 h ($y = 0.9878e^{(-0.0312x)}$, $R^2_{adj} = 0.92$, $F = 93.66$, $P = 0.0001$; Fig. S6B). Calculating the area under the curve we estimated a radius of 45.5 m and 68 m of movement distance where 95% and 99% of the beetles would be captured within 48 h, respectively (Figure S6A). For 96 h sampling period, we estimated a radius of 96 m and 146 m of movement distance where 95% and 99% of the beetles would be captured, respectively (Fig. S6B).

For human feces, nonlinear regression analysis showed no significance for 48 h sampling period ($F = 60.66$, $P = 0.081$). For 96 h sampling period, the proportion of recaptured dung beetles also decreased with increasing distance ($y = 1.0356e^{(-0.0435x)}$, $R^2_{adj} = 0.84$, $F = 23.05$, $P = 0.017$), and we estimated a radius of 57 m and 70.5 m of movement distance where 95% and 99% of the beetles would be captured, respectively.

Fig. 4. Proportion of recaptured individuals of *Canthon rutilans cyanescens* with increasing distance for estimated time periods of 48 (A) and 96 h (B). Each proportion was normalized by the number of beetles recaptured in the smallest distance category (0-10 m). Dashed and dotted lines represent the radius for 95 and 99% of recaptured individuals, respectively. The distance is an estimate based on the distance traveled by beetles during longer periods.



Discussion

Spatial patterns of movement

This study assessed the movement ability of a whole assemblage of dung beetles and our results indicated differences in the movement rate of species with different sets of ecological traits, such as relocation behavior of food resources, body size and diel activity period. This finding may have implications for how Scarabaeinae assemblages are structured locally and regionally. Due to low recapture rate of some species our results should be taken with caution, but we hope they are valuable to generate new hypotheses and contribute with new data in an area with large knowledge gap, as the dispersal of dung beetles and their implications for structuring communities.

The low recapture rate among Scarabaeinae [29] and related groups (e.g. Aphodiinae [44]) dispersal studies is very common (see S3 Table and references therein). Our results, however, showed that recapture rates vary between dung beetle species (1.5-22%), and not always the most abundant species has the highest recapture rate (e.g. [44]). These results imply that some species with high recapture rates may have a more limited spatial distribution than others, which may be related to variation of environmental characteristics at small spatial extents, availability of certain food resource or limited dispersal. In the other hand, one may expect that low recapture rates may be related to high dispersal rates, where species fly longer distances due to random distribution and ephemerality of food resources. Some dung beetle species also remain buried for long time periods while they are taking care their offspring [45], which may be associated with the high values in average time between recaptures (23.6 d, range 5-87 d). Therefore, the trade-off between longer flies and longer periods buried among dung beetle species may contribute to the low recapture rates commonly found in dispersal studies of this fauna. Perhaps the release of a large quantity of individuals of different species at the same time may provide better results in Scarabaeinae recapture rates.

Some dung beetle traits, such as body size (or biomass) and relocation behavior, have been identified as important for investigating the response of Scarabaeinae to tropical forest conversion [46, 47], forest fragmentation [19, 48, 49], and for ecological function performance [50-52]. We expected the same for differences in dispersal ability among dung beetle species, where some traits would be more important to differentiate species with high or low movement rates. Identifying these traits is crucial to our understanding of the role of dispersal in structuring communities locally and regionally.

Body size and wing loading are correlated [48], and large-bodied dung beetles with high wing loading usually use cruise flight foraging strategy [26, 31, 48], which allow them to have broader movements [48]. In contrast, small-bodied dung beetles with low wing loading usually use a perching strategy [26, 31, 53], which may restrict the ability to move for large distances. The tribe Phanaeini (represented by the genus *Coprophanaeus* Olsoufieff, 1924 in our study) has the largest dung beetles of the Neotropical region and generally its species are cruising beetles [54]. *Coprophanaeus saphirinus* showed the highest values of movement rate and maximum distance traveled in our study (ca 850 m in straight line). The interaction of body size, diel activity and relocation behavior was important and large-diurnal-tunnelers showed larger mean movement rate than other species. Thus, different sets of ecological traits may be important to understand differences in the dispersal ability of dung beetles. These findings have several implications in the context of metacommunity theory, mainly for those metacommunity models where dispersal has a key role, such as mass effects (high dispersal), species sorting (intermediate dispersal) and dispersal limitation (low dispersal) [4, 55]. Ecologists often mix “oranges with apples” [56], i.e. we usually expect that all species respond the same way to environmental and spatial processes, which may be not true. So, some species traits, such as body size, activity period and relocation behavior, may play an important role to distinguish dung beetle species that are more influenced by environmental or spatial processes (see [57]). In other words, some traits may facilitate dispersal of dung beetle species, so that they respond differently to different ecological processes.

Different flight periods in dung beetles may have evolved in correlation with defecation patterns of mammals, and the body size of dung beetles has great importance in the daily activity period of the species [58]. There are diurnal, nocturnal, diurnal-nocturnal, and crepuscular species and some have restricted fly time periods while others fly for long time periods [54]. Large tunnelers are generally nocturnal and small rollers are generally diurnal [42], but there are exceptions, such as *C. saphirinus* that are a diurnal large-bodied species.

In general, the temperature range between 25-42°C is optimal for dung beetles to fly [59]. The average maximum and minimum temperatures vary between 10-16 and 35-38°C, respectively, between November and March in the study region [60]. Thus, nocturnal species may have a higher limitation to do flights due to temperature conditions being more unfavorable at night. Energy expenditure may be higher for nocturnal species than for diurnal species, resulting in shorter flights. This hypothesis is among the demands for better understanding the relation between body temperature and activity period of dung beetles [59], since several species may increase body temperature during cold periods in order to fly [61]. However, we have no thermoregulation data on species sampled in our study.

The sun, the moon, the celestial polarization, and the milky-way are guidance mechanisms for dung beetles [62]. Diurnal and nocturnal species have eyes adapted for vision in dim light [63]. Photoreceptor mechanisms of nocturnal beetles show different responses depending on the speed of flight [63]. Cruising beetles can be divided into fast (typical for diurnal species) and slow fliers (typical for nocturnal species) [54]. The tribe Phanaeini has fast flier species that cover as much terrain as possible during flight, which may last many hours or short periods per day, such as in some *Coprophanaeus* species [54]. Flights with lower speeds provide greater visual resolution of obstacles, while leaving the nocturnal dung beetles at higher risk of predation. Flights at higher speeds cause a decline in the control of flight performance [64] leaving the nocturnal beetles as sloppy fliers [63]. Most nocturnal species fly close to the dung pats but not onto them; individuals land to a distance from the resource and walk to it, suggesting that “quick and dirty” is the best strategy for nocturnal dung beetles foraging flights [65]. In Neotropical forests nocturnal dung beetles have flight speeds much lower than diurnal species to reduce energy costs and maximize the time looking for food [54]. Due to the fact that canopy does not easily allow the viewing of celestial cues and light rays, do flights inside the forest may be a major difficulty for nocturnal species to move both on the ground and during flight. This fact may contribute to nocturnal species to have smaller movement distances than diurnal species within the forest, which could be more easily guided by the light rays during the day.

Another important issue associated with the high movement rates found for large-diurnal tunneler species is the predation pressure that one may expect to be more important at certain times of day, depending on the diel activity of predatory species. For nocturnal species, short periods of flight may be expected to reduce the pressure of visual predators. The opposite is expected for diurnal colorful species, such as *C. saphirinus*, that would travel greater distances avoiding visual predators due to their body coloration that blends with the forest environment or advertises their toxicity to predators. Among the predators we can generally cite some birds (e.g. owls), some mammals (e.g. bats), spiders and some species of beetles of the families Carabidae and Staphylinidae [54, 66, 67]. However, predation on dung beetles still needs to be further investigated, because its effect on species behavior or community structure may be minimal or insignificant as suggested by the meager available information [68].

Ecologically, a species is a set of individuals sharing similar traits that determine where and when they can live and how they interact with other species [69, 70]. Individually, a trait may not be enough to differentiate the species response to environmental and spatial processes because two species that respond differently to these processes can share this unique trait. For example, not all large-sized Scarabaeinae species are expected to perform large movements, because they can show differences in thermoregulation, flight speed or activity time. Therefore, investigating the interaction of some key species traits may be useful for understanding how and why species have a spatially structured distribution.

Suitability of trap spacing

The proportion of individuals recaptured with increasing estimated distance showed that the 50 m between baited traps for sampling dung beetles previously proposed [28] is inadequate for species from an assemblage in the Brazilian Atlantic Forest. Our results showed that the longer the time between recaptures the higher the distance traveled by dung beetles, as found by other authors [29]. When we analyzed the recaptures of individuals of all species, the radius of the effective sampling area (ESA) was estimated at 47 m and 92 m for 48 h and 96 h, in which 95% of individuals would be captured. When we analyzed only the recaptures of C. r. cyanescens, the radius of the ESA where 95% of individuals would be captured in 48 h and 96 h was 40.5 m and 85.3 m, respectively. Our results are also supported when we analyzed the two baits separately.

Based on recaptures of *C. acutus*, some authors [28] recommended a sample design of linear transect of 10 baited pitfall traps spaced by at least 50 m for sampling dung beetles, which was adopted by several authors. We agree with these authors [28] about the sample design, but according to our results, we suggest a new minimum of 100 m between pairs of baited traps for sampling Scarabaeinae during 48 h, taking into account the bait attraction and the estimated distance traveled by beetles during this period. When possible, we recommend the use of greater distances between baited pitfall traps, as already occurs in some studies performed in the Brazilian Amazonia (e.g. 200 m between pitfall traps [21, 71]). With this new spacing between baited traps we are not trying to use the traps as “true replicates” (see [34, 72]). Pseudoreplication is a problem among biodiversity studies in tropical forests and to obtain a real spatial variation within replicates is a need for ecological studies [34], which will be well represented if we have an adequate sampling design.

According to the vast literature, human feces remains the most efficient bait for the attraction of dung beetles in the Neotropical region [73], even compared with feces of native mammals [74, 75] or other baits like rotten meat or decaying fruit [76]. Human-pig mixes may be a promising alternative for sampling Scarabaeinae. However, obtaining human feces is much easier than pig feces, and human and human-pig feces show similar attractiveness [77]. The use of human feces and decaying meat as bait is useful for attracting dung beetle species with different food preferences (copro-necrophagous species) in the Neotropical region. The removal of insects and renewal of baits may be performed daily if necessary (e.g. [20, 21]), and series of sampling of 48 h may increase the sampling sufficiency.

Increasing sampling time must be followed by an increase in spacing between traps. We understand that the sample design may be restricted by physical characteristics of the study site [28] or may be spatially distributed according to the purpose of the study. Our new proposed trap spacing is suitable for sites with at least 1000 m in length, including border areas. If a site has this size, the new spacing can also be adopted for open areas. The use of linear design may be suitable for smaller sites placing two transects of five traps each or reducing the number of traps and conducting sampling series so there is at least a sampling effort of 10 traps, which seems an appropriate number of traps for the construction of sample sufficiency curves (see [78, 79]). For studies investigating the effect of fragmentation (e.g. fragment size), the use of smaller distances between baited pitfall traps should be adopted (e.g. [18]), according to the design of sample area or purpose of the study. Our new trap spacing may be very suitable for investigating the response of dung beetles to ecological processes that require a considerable spatial extent to reveal their effects (e.g. [80]), such as environmental filtering and spatial processes (i.e. high dispersal or dispersal limitation).

Dung beetles perform several ecological functions important for the maintenance of ecosystems [7]. These insects may be used for understanding and monitoring the relation between human-driven disturbance, patterns of biodiversity and ecosystem functioning [15, 21, 52] when they are properly sampled [28]. Knowing the movement process of dung beetles is critical to understand how communities are structured locally and in the metacommunity [80]. Species with different sets of ecological traits may have different movement patterns and thus they may influence local communities differently.

The use of standardized sampling protocols is essential to generate information necessary to investigate the processes that sustain biodiversity and ecosystem functioning [28], and make the results comparable between studies conducted in different regions of the world [32]. Based on our estimates, we suggest a new minimum distance of 100 m between traps to minimize the dependence between pairs of baited pitfall traps for sampling copro-necrophagous Scarabaeinae dung beetles in Neotropical forests. The use of this new minimum distance is also encouraged for other types of environments. The results of our and other studies (S3 Table) suggest that several species of dung beetles have high dispersal ability, which is related to some species traits and may be little known due to the difficulty of conducting such studies due to spatial limitations of the sampling design (or area) and the low recapture rate of this fauna.

Supporting Information

S1 Dataset. Dataset used to test for differences in movement rate by Scarabaeine dung beetle species. Samplings were performed in Brazilian Atlantic Forest, Santa Catarina, Brazil using baited pitfall traps from November 2013 to March 2014.
(XLXS)
S1 Fig. Marking points used in mark-release-recapture experiment. Distribution of marking points on elytra and pronotum used to mark scarabaeine dung beetles (A) and example of number #108 on an individual of *Dichotomius sericeus* (B).
(EPS)
S2 Fig. Boxplots of movement rate of dung beetle species. Letters in x-axis indicate species names in Table 1. Gray asterisks represent the mean movement rate.
(EPS)
S3 Fig. Boxplots of movement rate of dung beetle species with different reproductive behaviour and diel activity periods. Gray asterisks represent the mean movement rate.
(EPS)
S4 Fig. Boxplots of movement rate of dung beetle species with different body size, diel activity period and relocation behavior. Gray asterisks represent the mean movement rate. D: diurnal; DN: diurnal-nocturnal; N: nocturnal.
(EPS)
S5 Fig. Linear model between movement distance and time for recaptured individuals of Scarabaeinae, excluding recaptures at same trap. Distance in meters and time in days.
(EPS)
S6 Fig. Proportion of recaptured individuals of Scarabaeinae with increasing distance for estimated time periods of 48 (A) and 96 h (B) using rotten meat bait. Each proportion was normalized by the number

of beetles recaptured in the smallest distance category (0-10 m). Dashed and dotted lines represent the radius for 95 and 99% of recaptured individuals, respectively.
(EPS)

S1 Table. Summary of mark-release-recapture experiment. Number of marked and recaptured individuals, number of males and females, number of immature, young-mature and old individuals of dung beetles sampled in the Atlantic Forest in southern Brazil.
(XLXS)

S2 Table. Results of generalized linear models comparing movement rate between dung beetle species or individuals of each species. DF: degrees of freedom. Significant *P* values are in bold.
(XLXS)

S3 Table. Studies of dung beetle dispersal using mark-release-recapture conducted in the Neotropical region. Na: not applicable or not informed. Mean: mean movement distance. Max: maximum movement distance. Time: days.
(XLXS)

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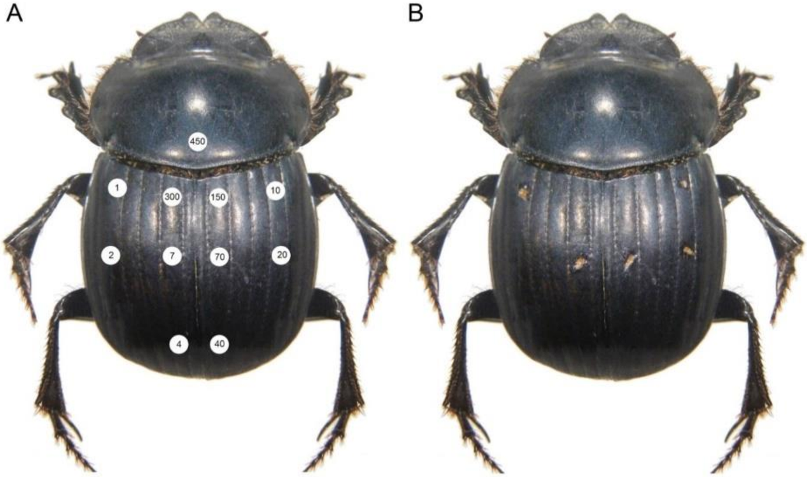
Supporting Information

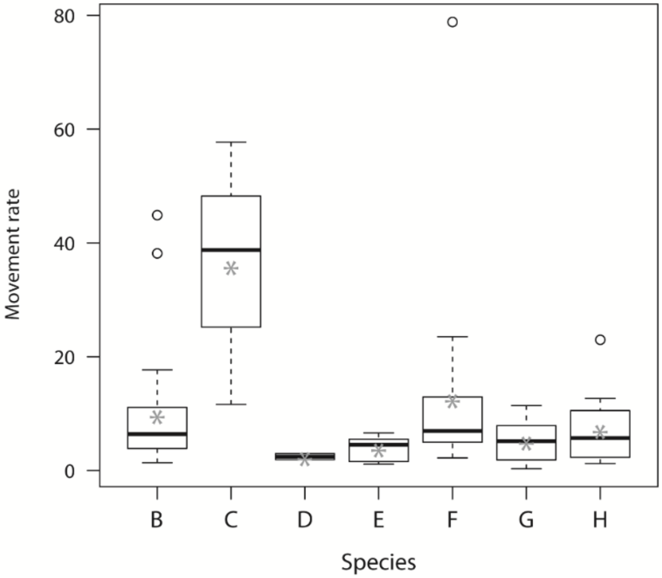
S1 Dataset. Dataset used to test for differences in movement rate by Scarabaeinae dung beetle species. Samplings were performed in Brazilian Atlantic Forest, Santa Catarina, Brazil using baited pitfall traps from November 2013 to March 2014.

Disponível online somente após a publicação.

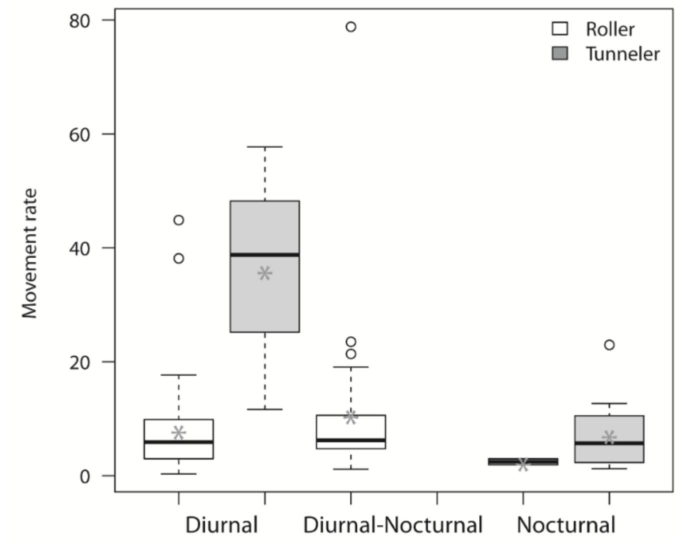
S1 Fig. Marking points used in mark-release-recapture experiment. Distribution of marking points on elytra and pronotum used to mark Scarabaeinae dung beetles (A) and example of number #108 on an individual of *Dichotomius sericeus* (B).



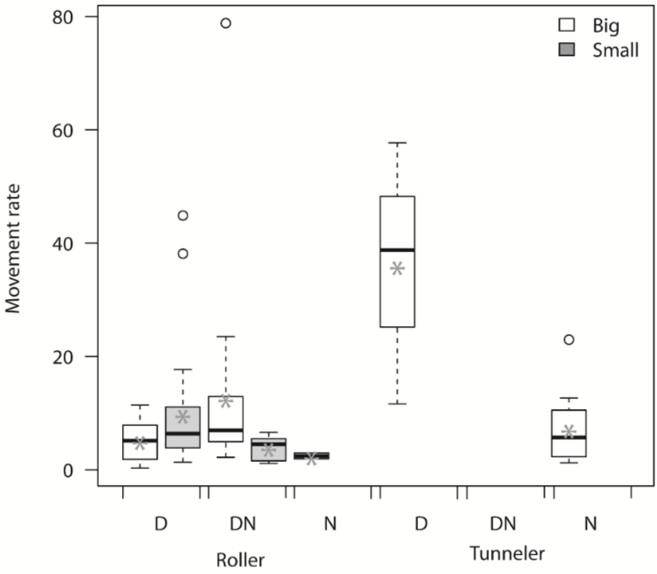
S2 Fig. Boxplots of movement rate of dung beetle species. Letters in x-axis indicate species names in Table 1. Gray asterisks represent the mean movement rate.



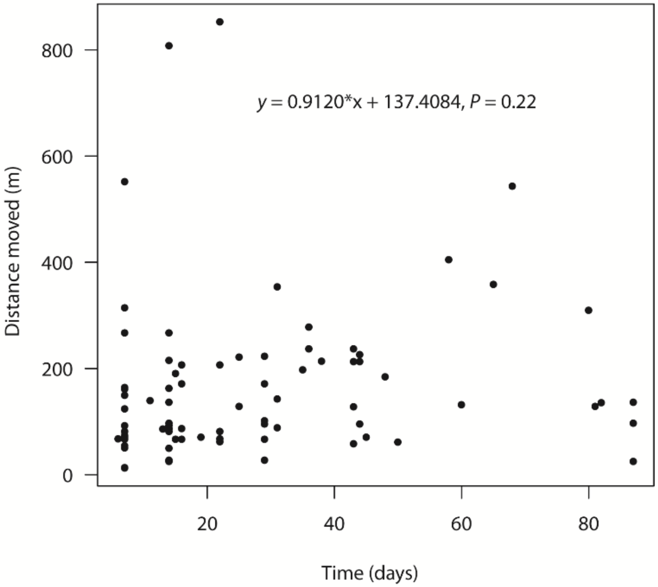
S3 Fig. Boxplots of movement rate of dung beetle species with different reproductive behavior and diel activity periods. Gray asterisks represent the mean movement rate.



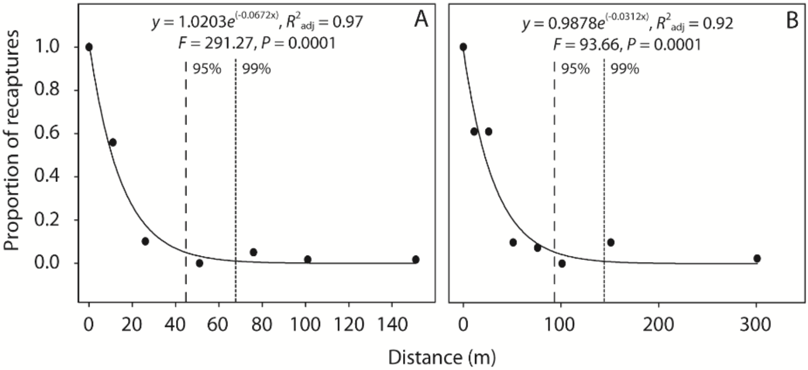
S4 Fig. Boxplots of movement rate of dung beetle species with different body size, diel activity period and relocation behavior. Gray asterisks represent the mean movement rate. D: diurnal; DN: diurnal-nocturnal; N: nocturnal.



S5 Fig. Linear model between movement distance and time for recaptured individuals of Scarabaeinae, excluding recaptures at same trap. Distance in meters and time in days.



S6 Fig. Proportion of recaptured individuals of Scarabaeinae with increasing distance for estimated time periods of 48 (A) and 96 h (B) using rotten meat bait. Each proportion was normalized by the number of beetles recaptured in the smallest distance category (0-10 m). Dashed and dotted lines represent the radius for 95 and 99% of recaptured individuals, respectively.



S1 Table. Summary of mark-release-recapture experiment. Number of marked and recaptured individuals, number of males and females, number of immature, young-mature and old individuals of dung beetles sampled in the Atlantic Forest in southern Brazil.

Species	Marked	Recaptured	Gender		Age		
			Male	Female	Immature	Mature	Old
Canthidium dispar	4	0	2	2	1	3	0
Canthidium aff. *trinodosum*	15	0	2	13	7	8	0
Canthon chalybaeus	1	0	1	0	0	1	0
Canthon luctuosus	133	2	78	55	83	50	0
Canthon rutilans cyanescens	677	35	365	312	356	318	3
Coprophanaeus saphirinus	61	3	39	22	3	58	0
Deltochilum brasiliense	18	3	1	17	10	8	0
Deltochilum morbillosum	168	9	107	61	41	126	1
Deltochilum multicolor	100	22	48	52	43	57	0
Deltochilum rubripenne	131	16	70	61	39	86	6
Deltochilum sp.	1	0	0	1	1	0	0
Dichotomius fissus	1	0	0	1	1	0	0
Dichotomius aff. *pigidialis*	14	0	9	5	4	10	0
Dichotomius sericeus	451	22	137	314	81	369	1
Eurysternus parallelus	27	0	9	18	8	18	1
Ontherus azteca	1	0	1	0	1	0	0
Phanaeus splendidulus	3	0	0	3	1	2	0
Total	1806	112	869	937	680	1114	12

S2 Table. Results of generalized linear models comparing movement rate between dung beetle species or individuals of each species. DF: degrees of freedom. Significant *P* values are in bold.

	F value	*P* value	DF
Species	3.858	**0.002**	6
Body size	0.306	0.581	1
Diel activity	0.554	0.577	2
Relocation behavior	1.315	0.255	1
Body size : Diel activity	0.845	0.501	4
Body size : Relocation behavior	0.663	0.518	2
Diel activity : Relocation behavior	4.573	**0.002**	4
Body size : Diel activity : Relocation behavior	3.858	**0.002**	6
Species : Age	0.402	0.845	5
Species : Gender	1.547	0.186	5
Species : Age : Gender	0.66	0.520	2

S3 Table. Studies of dung beetle dispersal using mark-release-recapture conducted in the Neotropical region. Na: not applicable or not informed. Mean: mean movement distance. Max: maximum movement distance. Time: days.

Species	Mean	Max	Time	Country	Habitat	Reference[G]
Canthidium centrale Boucomont, 1928	580	1320	15.1 d	Mexico	Landscape[D]	Díaz-Rojas (2003)
Canthon acutus Harold, 1868	Na	100	4 d	Venezuela	Semi-deciduous tropical forest	Larsen and Forsyth (2005)[F]
Canthon angustatus Harold, 1867	160	300	1 d	Ecuador	Primary rain forest	Peck and Forsyth (1982)
Canthon cyanellus cyanellus LeConte, 1859	340	1560	0.012[C]	Mexico	Landscape[E]	Arellano et al. (2008)
Deltochilum pseudoparile Paulian, 1938	465	740	194.8 d	Mexico	Landscape[D]	Díaz-Rojas (2003)
Dichotomius satanas (Harold, 1967)	755	1310	7.3 d	Mexico	Landscape[D]	Díaz-Rojas (2003)
Megathoposoma candezei (Harold, 1873)	Na	75	Na	Costa Rica	Tropical moist forest	Wille et al. (1974)
Onthophagus spp.[A]	90	100	1 d	Ecuador	Primary rain forest	Peck and Forsyth (1982)
Onthophagus spp.[A]	440	700	2 d	Ecuador	Primary rain forest	Peck and Forsyth (1982)
Oxysternon conspicillatum (Weber, 1801)	Na	50	< 2 min	Ecuador	Primary rain forest	Peck and Forsyth (1982)
Oxysternon conspicillatum (Weber, 1801)	Na	1000	2 d	Ecuador	Primary rain forest	Peck and Forsyth (1982)
Sulcophaneus leander (Waterhouse, 1891	Na	500[B]	1-5 d	Colombia	Wet lowland tropical forest	Noriega and Acosta (2011)

[A] They may be different species. [B] The value represents distance among areas sampled. [C] Time dependence of movement length, measured as the regression coefficient of log (distance) versus log (time between recaptures). [D] High evergreen forest, forest edge, corridors, grasslands and hedgerows. [E] Forest fragments, hedgerows and pastures. [F] Ninety-five percent of the recaptured beetles were attracted from within 26.2 m of the traps. [G] References are in the text.

ARTIGO IV: SCALE-DEPENDENCE OF PROCESSES STRUCTURING DUNG BEETLE METACOMMUNITIES USING FUNCTIONAL DIVERSITY AND COMMUNITY DECONSTRUCTION APPROACHES

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> “Nature is not cruel, only pitilessly indifferent. This is one of the hardest lessons for humans to learn”.
>
> (Richard Dawkins)

Scale-dependence of processes structuring dung beetle metacommunities using functional diversity and community deconstruction approaches

Abstract

Community structure is driven by mechanisms linked to environmental, spatial and temporal processes, which have been successfully addressed using metacommunity framework. The relative importance of processes shaping community structure can be identified using several different approaches. Two approaches that are increasingly being used are functional diversity and community deconstruction. Functional diversity is measured using various indices that incorporate distinct community attributes. Community deconstruction is a way to disentangle species responses to ecological processes by grouping species with similar traits. We used these two approaches to determine whether they are improvements over traditional measures (e.g. species composition, abundance, biomass) for identification of the main processes driving dung beetle (Scarabaeinae) community structure in a fragmented mainland-island landscape in southern Brazilian Atlantic Forest. We sampled five sites in each of four large forest areas, two on the mainland and two on the island. Sampling was performed in 2012 and 2013. We collected abundance and biomass data from 100 sampling points distributed over 20 sampling sites. We studied environmental, spatial and temporal effects on dung beetle community across three spatial scales, i.e., between sites, between areas and mainland-island. The γ-diversity based on species abundance was mainly attributed to β-diversity as a consequence of the increase in mean α- and β-diversity between areas. Variation partitioning on abundance, biomass and functional diversity showed scale-dependence of processes structuring dung beetle metacommunities. We identified two major groups of responses among 17 functional groups. In general, environmental filters were important at both local and regional scales. Spatial factors were important at the intermediate scale. Our study supports the notion of scale-dependence of environmental, spatial and temporal processes in the distribution and functional organization of Scarabaeinae beetles. We conclude that functional diversity may be used as a complementary approach to traditional measures, and that community deconstruction allows sufficient disentangling of responses of different trait-based groups.

Introduction

Community ecology has advanced greatly in recent decades with the understanding that local species diversity is jointly affected by ecological processes operating at different spatial scales [1-3]. This occurs because environmental variables that shape communities differ in their range of variation across spatial scales [4, 5]. The study of the relative importance of ecological processes across different spatial scales in driving local communities is an issue of metacommunity theory [6, 7]. The term ‘metacommunity’ currently refers to a set of communities connected by dispersal of potentially interacting species [6].

Four theoretical models have been proposed to characterize mechanistic processes operating in metacommunities: species sorting, patch dynamics, mass effects and neutral model [2, 6, 7]. These models consider two main issues: whether and how species respond to changes in environmental conditions, and whether species dispersal ability is limited, efficient or high [7, 8]. In heterogeneous environments, differences in local communities caused by environmental filters (e.g., quality and resources) and/or interactions between species characterize a metacommunity guided by species sorting [6]. High dispersal of individuals in heterogeneous environments from source to sink areas may rescue populations in harsh environments (i.e., mass effects) [9]. In a homogeneous environment, competition-colonization trade-offs predict that better competitors should exclude better colonists (i.e., patch dynamics) [6]. In an environment with similar environmental conditions, a neutral metacommunity would be composed of individuals of different species that are similar in their competitive ability, dispersal and fitness; in this case speciation, extinction and dispersal limitation drives variation in local community composition [10]. Mass effects and patch dynamics may be special cases of species sorting, and metacommunities can be neutral or guided by species sorting with limited (patch dynamics, sensu [6]), efficient (species sorting, sensu [6]) and high (mass effects, sensu [6]) dispersal [8]. However, a metacommunity may be structured by more than one paradigm [6], and mechanisms may have greater or lesser importance depending on spatial scale [4]. A key issue is to understand the relative roles of environmental and spatial processes [8].

Temporal turnover may be useful for identifying key processes structuring local communities, although different organisms may respond differently depending on the temporal scale used [11]. This process in species abundance may have a crucial role in ecosystem functioning [12], and needs to be taken into account when assessing environmental effects on biological communities at different spatial scales. Thus, the main goal of metacommunity theory is to explain how the interaction between species dispersal ability and local dynamics influences the structure of biological communities [13].

Over the last few decades, ecologists have developed a variety of ways to measure diversity [14-21] for the purpose of understanding the ecological processes that create and sustain the diversity of biological communities [14]. Spatial and/or temporal variation in the composition and abundance of species between different sites (β diversity) produces a direct link between diversity at the local scale (α diversity) and the species pool at the regional scale (γ diversity) [22, 23]. The importance of spatial processes has become increasingly clear in recent decades due to greater understanding of how environmental heterogeneity and species dispersal ability vary over space, thus promoting differential structuring of local communities depending on scale.

In addition to studies of variation in species composition and abundance, alternative ecological methods have recently been used to investigate community structure. Among them is functional diversity based on species traits [24]. A trait is a measurable variable with the potential to affect the performance and fitness of a species [25]. The trait can be physical, biochemical, behavioral, and phenological or temporal, and in this sense, a species would consist of sets of individuals sharing similar traits [25, 26]. Traits determine when and where species can exist and how they can interact with individuals of other species [26]. Species with similar responses to the environment or similar effects on key ecosystem processes form functional groups [27]. Further, the sets of traits contained within species functional groups may be related to environmental characteristics [28]. Functional diversity is the component of diversity that has the potential to affect the functional dynamics of the ecosystem [29, 30], as well as ecosystem services and processes [31-34]. The functional traits approach also provides a means by which to test the mechanisms driving biological communities, because these mechanisms influence the fitness of the species via the traits they possess [24]. Thus, diversity measures that incorporate species traits may provide novel information on community structure and dynamics and ecological processes beyond what can be determined from the traditional measures generally used in ecology and conservation studies (e.g., composition, abundance and species richness) [26].

Community deconstruction is another method gaining in popularity [35-38], which partitions species-by-site data into subgroups based on species traits. This enables categorizing species into homogenous groups, which can facilitate interpretation of causal mechanisms for species patterns observed in nature [39]. For example, generalist and/or common species generally exhibit broad environmental tolerance while specialist and/or rare species have a specific or narrow tolerance to environmental variation [35, 37]. In general, studies on metacommunities do not distinguish between species and groups of species, even though responses to the environment and population dynamics may be distinct between these organizational levels (e.g., dispersal ability, environmental tolerance) [35]. This approach can also be expanded to other sets of species characteristics that influence life history, such as dispersal mode and body size [38]; this information may provide a better understanding of the relative importance of community structuring processes, particularly for some species groups. Furthermore, the use of these approaches may aid our understanding of scale-dependence of some ecological processes, and may help to determine whether the new methods contribute to our understanding of community structure and the various processes involved.

The objective of this study is to identify the relative importance of environmental, spatial and temporal processes in structuring dung beetle communities at three spatial scales in a mainland-island scenario in Atlantic Forest in southern Brazil, using functional diversity and community deconstruction approaches. As different indices of functional diversity take into account different aspects of communities such as species richness, abundance and evenness [24], we expect that they can serve as a proxy to test the effects of different ecological processes on biological community structure. Deconstructing the entire community using species traits, we expect to find different responses of these groups to different ecological processes [35]. The Atlantic Forest, one of the world’s biodiversity hotspots, is the most endangered Brazilian ecosystem [40], with only roughly 12% of its original size remaining, which is highly fragmented with a high degree of isolation, and with areas mostly in intermediate successional stages [41]. Due to the discontinuous distribution of fragments, the Atlantic Forest offers an interesting model system for the study of ecological processes structuring communities at different spatial scales. Dung beetles

(Coleoptera: Scarabaeinae) are excellent model systems for such studies [42, 43], due to ease of sampling with standardized, efficient and inexpensive protocols [44], wide distribution, and high species richness and abundance in tropical regions [45]. These insects respond quickly to anthropogenic environmental changes (e.g., destruction, fragmentation and isolation of forests) with notable changes in species composition, richness, and abundance, and in functional guild proportions [46-50]. Moreover, their diversity is correlated with other taxa, including mammals [48, 51, 52] and are involved in several ecological services such as nutrient cycling, bioturbation (i.e., the displacement and mixing of soil and sediment by animals or plants), secondary seed dispersal and parasite control [53]. Several dung beetle species that inhabit forests avoid distribution into open areas [54-56], and this behavior influences dispersal and colonization when the matrix is inhospitable. Although knowledge of dung beetle dispersal ability is generally scarce, some studies suggest that factors such as sex, body size and perching behavior are related to the movement capacity of these insects [57-59].

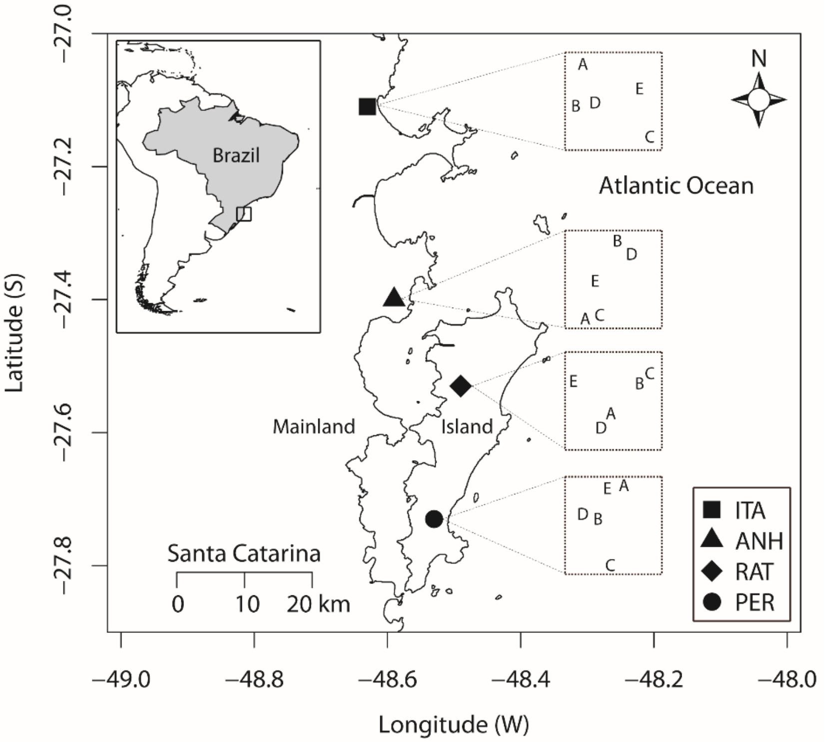
We sampled dung beetle communities at 20 sampling sites divided into four large areas of Atlantic Forest, two on the island and two on the mainland in Santa Catarina, southern Brazil, during the summers of 2012 and 2013. The sampling design is hierarchical and the landscape discontinuous, thus it was possible to access the effect of different ecological processes (i.e. environmental filters, spatial structuring and temporal turnover) on dung beetle community structure at three different spatial scales (i.e., sites, areas, mainland-island). We used indices of functional diversity and also deconstructed the community into groups of species with similar traits to test the following hypotheses: (i) dung beetle beta diversity will increase with spatial scale; environmental filters will be most important at a local scale while spatial processes will be most important at larger scales due to the dispersal limitation; (ii) functional diversity will have a similar response to the effects of different ecological processes across spatial scales as do traditionally used metrics (e.g., species composition, abundance, biomass); (iii) the deconstruction of community into groups of species with similar traits will show different responses according to each functional group. We anticipate that trait-dependence will render some functional groups more sensitive to environmental filters (e.g., rare, specialist, diurnal species), and others more sensitive to spatial effects (e.g., common, generalist, nocturnal species) [60]. Overall, these relatively recent approaches will increase the explanatory power of the models and hence, our understanding of the primary mechanisms involved in the structuring of biological communities.

Material and methods

Study area

The study sites consisted of four large Atlantic Forest areas in Santa Catarina state, southern Brazil, two on the mainland (both on the east coast) and two on the island of Santa Catarina (municipality of Florianópolis) (Fig. 1). The island of Santa Catarina has a total land area of 424.4 km² (54 km north-south, maximum of 18 km wide) and the distance between the mainland and the island varies greatly (minimum 500 m, maximum ~10 km). On the mainland, one study area lies within the Environmental Protection Area of Anhatomirim in Governador Celso Ramos city (ANH, 27º25’1”S, 48º34’25”W), and the other in a Permanent Protection Area in the municipality of Itapema (ITA, 27º05’13”S, 48º35’54”W). On the island, one study areas lies within the Lagoa do Peri Municipal Park (PER, 27°43’30”S, 48°32’18”W) and the other in the Permanent Protection Area of Ratones (RAT, 27°31’52”S, 48°30’45”W). According to the Brazilian Forest Code (Law nº. 12.651/2012), permanent protection areas are sites with characteristics that have the environmental function of preserving water, biodiversity resources, and landscape and geological stability, and for facilitation of floral and faunal gene flow. All sites sampled are near the Brazilian Atlantic coastline, and have dense rain forest vegetation [61] within the Atlantic Forest biome, with various levels of vegetation succession. According to the Köppen classification, the climate in the eastern region of Santa Catarina is Cfa, humid subtropical (mesothermal) with no dry season and hot summers (mean 25°C), and well distributed rainfall throughout the year (app. 1,500 mm annually) [61]. The distance between sites is as follows: PER and RAT, 21 km; PER and ANH, 34 km; PER and ITA, 71 km; ANH and RAT 13.5 km, ITA and RAT, 50 km; ANH and ITA, 37 km. Sampling site altitude ranged between 28 and 265 m.

Fig. 1. Map of the four areas and schematic distribution of sites sampled (represented by letters A-E, unscaled distribution) in eastern Santa Catarina, southern Brazil. ANH: Environmental Protection Area of Anhatomirim; ITA: Permanent Protection Area of Itapema; PER: Lagoa do Peri Municipal Park; RAT: Permanent Protection Area of Ratones. Reprinted from [5] under a CC BY license, with permission from Pedro G. da Silva and Malva I. M. Hernández, original copyright 2014 (see S3 Fig.). Figure is similar but not identical to the original image.



Dung beetle sampling

We sampled Scarabaeinae dung beetles using baited pitfall traps made with plastic containers (15 cm diameter x 20 cm depth) buried with the top edge at ground level, allowing beetles to fall in. The traps were protected against rain using a small sheet supported by wooden sticks, placed approximately 10 cm above the trap to prevent overflow. A mixture of water and neutral detergent (300 ml) was added to each container to retain trapped beetles. Human feces and rotting flesh (aged in plastic containers at room temperature three days prior to sampling) were used as bait to attract dung beetles to attract both coprophagous and necrophagous species. Approximately 30 g of each bait type was wrapped in thin cloth and tied in the central part of the rain protection above the traps, preventing the insects from handling the baits. Collected beetles were sorted and dried in an oven (60°C for 72 h), then weighed on a precision balance (0.0001 g). Specimens were identified to species level by expert taxonomists (Dr. Fernando Vaz de Mello, Universidade Federal de Mato Grosso, Cuiabá, Brazil and Dr. David Edmonds, Marfa, Texas, USA) and deposited in the Entomological Collection of the Centro de Ciências Biológicas at the Universidade Federal de Santa Catarina, Brazil. Type specimens were donated to the taxonomic experts for future reference.

The permission to collect dung beetles was issued by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/MMA, permit #32333-3 to MIMH) and Fundação do Meio Ambiente (FATMA-SC). The field study did not involve endangered or protected species. Dataset S1 provides the database of values for abundance and biomass of dung beetle species across the study sites.

Sampling design

Samples were taken at five different forested (hillside) sites within each sampling area. Distance among sites ranged between 300 m to several kilometers within each area. Each site contained five pairs of traps spaced 5-10 m apart, each pair containing both bait types. The pairs of traps were spaced 50 m apart, and were considered one sampling point. The traps remained in the field for 48 h prior to beetle collection. We sampled a total of 100 points in 20 sites distributed among the four areas. The samplings were carried out during the summer of 2012 and 2013 (January and February of both years), because of high temperatures, and it being the period of greatest abundance of dung beetles in southern Brazil [62, 63]. Due to the spatial configuration of our sampling design, the great distance between the four areas, and the effect of spatial discontinuity between the mainland and island, the sampling sites showed a hierarchical distribution. Thus, it was possible to investigate variation in dung beetle communities at three spatial scales (or spatial levels [64]), i.e., mainland-island, between areas, and between sites. A full, detailed description of the sampling design can be found in a previous work [5]. Sites represent the local spatial scale, i.e., the smallest spatial extent in our study that encompasses five sampling points. Areas represent the intermediate spatial scale with five sites per area. Mainland-island represents the regional spatial scale, i.e., the largest spatial extent in our study that encompasses two areas in each one.

Dung beetle traits

Dung beetle species were characterized in terms of four ecological attributes: food relocation behavior (rollers, tunnelers or dwellers), diet (coprophagous, necrophagous or generalist), activity period (diurnal, nocturnal or diurnal-nocturnal) and biomass (see S1 Table). Protocols for trait assignments are described in S1 Appendix. We also obtained additional information on dung beetle traits from the literature and from consultations with experts, when necessary. These characteristics are widely used to identify the functional groups of Scarabaeinae species and each one has a particular impact on the ecosystem functioning [65].

Food relocation behavior and nesting strategy may alter the relative success of larval and adult dung beetles in modified forests due to abiotic and biotic changes [60]. Roller species form the food source into a ball and roll it on the ground to another location for burial. These species may be affected by differences in the physical structure of the forest floor [60] while dwellers (which nest within the food resource at the site of discovery) are more susceptible to environmental and climate changes. Tunneler species build their nests and bury portions of food in tunnels beneath the resource.

Dung beetles have a broad diet, however most species have evolved to consume mammal feces (coprophagy). Others prefer to eat carrion (necrophagy), and some consume decaying plant matter (saprophagy). Some species are trophic specialists, mainly those that eat fruit or fungi [66, 67]. Due to this variety of dietary preferences, differences in habitat structure may alter food availability in ways that impact dung beetle community structure.

Dung beetle activity is associated with daytime temperatures and humidity, and differences in forest structure may negatively influence the level of activity of diurnal species [68]. Diurnal species often have smaller body size [69, 70] while large-bodied species are often nocturnal [71]. Dung beetle biomass in a given community is mainly derived from nutrients obtained from mammal feces [72]. Individually, biomass can be used as a measure of body size. This trait is positively correlated with dung removal and secondary seed dispersal for large-bodied, nocturnal dung beetles [73, 74], an important ecosystem service provided by these insects. Dung beetle size (and biomass) has been positively correlated with sensitivity to modification [46] and fragmentation [75] of tropical forests. Large-bodied dung beetles show advantages in food acquisition [76], with better competitive outcomes [77] and are also associated with high dispersal rates [78]. We used these sets of traits to calculate four indices of functional diversity (see Functional diversity section).

Explanatory variables

We measured 20 environmental variables related to habitat structure, to test their influence on dung beetle community structure. Measurements were performed using the adapted point-centered quarter method [79]. Tree, shrub and soil environmental variables were measured in four quadrants as follows: (1) circumference at breast height, (2) height, (3) top diameter, (4) distance away from the nearest tree to the center of cross, (5-8) same measures for trees up to 10 m distance, (9-12) same measures for shrubs, (13) land slope, (14) canopy cover, (15) percentage of leaf litter cover, (16) percentage of green cover, (17) percentage of exposed soil, (18) height of leaf litter, (19) dry biomass of leaf litter, and (20) altitude. The material and methods used to measure these variables are described in S2 Appendix. See also S2 Table for a summary of environmental measures. Differences in environmental conditions (environmental variables measured) among sampling sites is defined as environmental heterogeneity.

We used a method called Principal Coordinates of Neighbour Matrices [80] to create spatial predictors using the create.MEM.model function [4] for the R 3.1.1 program [81], which is suitable for nested sampling designs [80]. This function produces a set of orthogonal spatial variables in a staggered matrix divided by blocks based on the geographical coordinates, number of blocks (or groups of sites) and sampling sites in each block. Each block represents the hierarchical spatial distribution of the sampling points and different blocks receive a value of zero (0) for each spatial variable created. These variables represent spatial relationships among the sampling sites at different scales, and can be used as explanatory variables for community variation [80]. The spatial variables can also represent spatial structures generated by biotic processes, such as dispersal [82]. Dispersal is expected to be high in closest sites and low when sites are more distant [83].

A dummy variable was used to represent different sampling years. Thus, we were able to test and remove the temporal effect from environmental and spatial models when testing their effects using variation partitioning techniques (see Variation partitioning section).

Data analysis

Diversity partitioning

An approach called ‘true diversity’ [17] has been used to partition diversity into its different components in an additive or multiplicative way [18, 84]. We used the additive partitioning approach ($\gamma = \alpha + \beta1 + \beta2 + \beta3$) to estimate beta diversity at three spatial scales for the entire dataset, different years and deconstruction approach (see Community deconstruction section). Alpha (α) is the average species richness in local communities, while gamma (γ) refers to the total species richness observed in the entire set of samples. Each component of beta diversity refers to different spatial scales: $\beta1$ = between sampling sites, $\beta2$ = between areas, $\beta3$ = between mainland-island. We used abundance data for the hierarchical analysis of diversity partitioning. We also conducted a separate analysis for functional groups (see Variation partitioning section). These analyses were performed in Partition 3.0 program [85] using an individual-based randomization ($N = 999$). We used an algorithm to test whether the observed diversity components could have been obtained by a random distribution of individuals between samples at each spatial scale. The statistical significance is obtained by determining the proportion of null values (created by the randomization procedure) that are greater or smaller than the observed values [85].

Functional diversity

We used dung beetle traits important for ecosystem functioning to calculate functional diversity, such as food relocation behavior, diet, activity period and dry biomass [60, 65, 86]. We calculated four indices of functional diversity: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) [87, 88]. FRic is based on the volume of a multidimensional functional space occupied by the species present in a community, and is measured as a convex hull volume [88]. FEve represents the evenness of species abundance distribution in the functional space [88]. FDiv describes how species abundance is spread within the volume of functional trait space occupied by species [88]. FDis is the average distance of the species to the centroid of all species in the multidimensional trait space [87]. Functional diversity analyses were performed with the dbFD function using the FD package [89] for R 3.1.1 program [81].

Community deconstruction

To assess the effect of the deconstruction of community data we used the variation partitioning procedure (see Variation partitioning section) in different datasets. Based on sets of ecological traits used to calculate the functional diversity, we decomposed the abundance dataset into groups of species. We decomposed the community dataset based on the food relocation behavior (rollers and tunnelers; dwellers are represented by only two species, so we could not use the variation partitioning procedure for this group), diet (coprophages, necrophages and trophic generalists), activity period (diurnal, nocturnal and diurnal-nocturnal), body size (small, medium and large beetles: species with < 10 mg of dry biomass are classified as small, 10-100 mg as medium, and > 100 mg as large [90]).

We also used combinations of food relocation behavior and body size to create new functional groups. Thus, we created four additional groups: large-sized tunnelers, medium-sized tunnelers, large-sized rollers, and medium-sized rollers. Other groups were represented by only one or two species, and thus were not used in the analyses. Combinations of diet and activity period were not used because we expect that these traits are least important for ecosystem functions provided by these beetles. In addition, the majority of dung beetles were attracted to feces (coprophages and trophic generalists) and these resources are both spatially and temporally unpredictable, so the division into trophic categories seems to be less important with respect to ecological functions.

Furthermore, we decomposed the entire metacommunity based on species occurrence to test the prediction that common species are mainly affected by dispersal limitation while rare species are mainly affected by environmental filters [37, 91]. We used the inflection point criterion to define common and rare species [37]. With this approach, we examined a rank abundance curve and used the inflection point of the curve (the region where the curvature changes) to separate common and rare species. We used non-logarithmic abundance values and visually defined the inflection point (see S1 Fig.). Thus, species on the left side were classified as common, and those on the right side as rare.

Variation partitioning

To test the effect of different sets of predictors on community matrix variation (abundance, biomass, functional diversity, and functional groups) we used a partial redundancy analysis (pRDA) [80] to partition the total variation of response matrices into environmental, spatial and temporal fractions. Despite being criticized [92, 93], variation partitioning has been used in the study of metacommunities for a long time (e.g., [35, 37, 83, 94, 95]). The pRDA allows decomposition of the total variation into fractions that indicate the relative importance of pure environmental predictors, pure spatial predictors, pure temporal predictors, shared portions of variation, and unexplained variation [96]. The analyses of community matrices were performed after Hellinger transformation [97]. We tested for a linear spatial trend and found a significant longitudinal and latitudinal trend for dung beetle abundance data (longitude: $F = 22.681$, $P = 0.001$; latitude: $F = 5.509$, $P = 0.001$) and biomass (longitude: $F = 5.412$, $P = 0.001$; latitude: $F = 25.433$, $P = 0.001$). We also found a significant longitudinal trend for dung beetle functional diversity ($F = 4.040$, $P = 0.015$). Thus, all datasets were detrended prior to analyses [80].

For each analysis, a subset of explanatory variables was selected using the forward selection method [98] in order to avoid Type I error and overestimation of the explained variance. This procedure is performed in two steps. First, a model using all explanatory variables is tested, and the analysis continues if the result is significant ($P < 0.05$). After this step, we checked the variance inflation factor (VIF) to identify collinear variables. Variables with higher VIF > 20 were removed [80]. Next, if the result is significant, the selection of variables continues considering the significance level of each explanatory variable, and the adjusted coefficient of multiple determination (R^2_{adj}, or data variation explained by the model) is calculated using all variables (i.e., the full model). If these criteria are not reached, the variables are non-significant and the analysis is terminated. Variable selection was performed separately for spatial and environmental data.

For the functional diversity dataset we conducted a distance-based approach [95] using Euclidean distance, since several functional diversity indices were correlated with species richness. The proportion between the number of species and number of individuals of each functional group can be found in S2 Fig. The analyses were performed using R 3.1.1 software [81] and PCNM and packfor packages [99].

Results

General results

We sampled a total of 5,794 individuals, belonging to 28 species of Scarabaeinae dung beetles (3,004 individuals and 21 species in 2012; 2,790 individuals and 24 species in 2013, see S3 Table). The largest number of individuals was found on the island (N = 3765). The mainland showed the greatest species richness (S = 22). Among areas, Ratones had the largest number of species (20) and individuals (2,438), while Anhatomirim had the lowest values (S = 13, N = 975). Four species (*Dichotomius sericeus*, *Canthon rutilans cyanescens*, *Canthidium* aff. *trinodosum*, and *Deltochilum morbillosum*) accounted for 77% of total dung beetle abundance. Only seven species were shared between all sample sites. Four species (*Dichotomius sericeus*, *Coprophanaeus saphirinus*, *Canthon rutilans cyanescens*, and *Deltochilum multicolor*) accounted for 83% of the total dung beetle biomass.

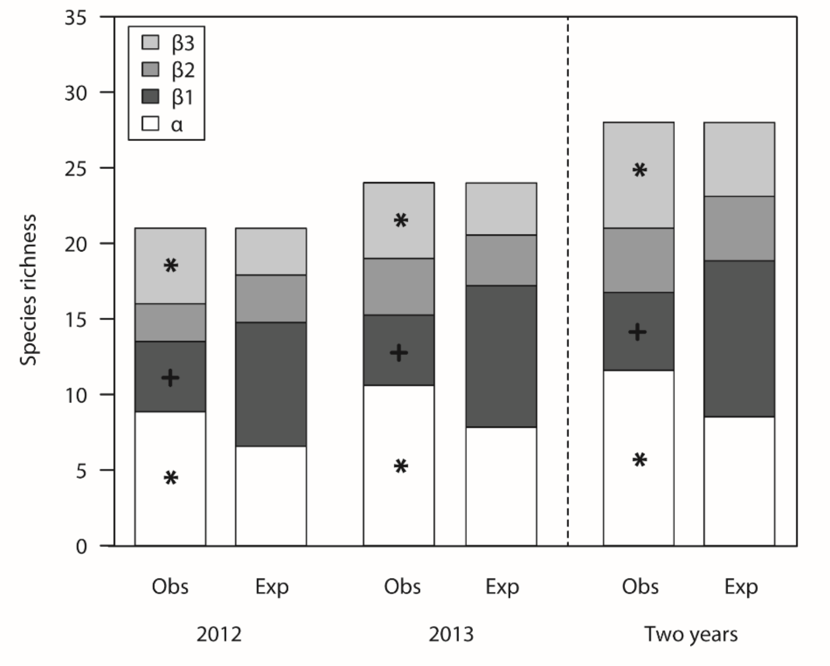
Patterns of beta diversity across spatial scales

The total γ-diversity (over two years) was mainly attributed to β-diversity (Fig. 2). This was a consequence of the increase in mean α-diversity and β-diversity between areas over the years. The total diversity percentage explained by all β-components was 58.6% (57.8% in 2012 and 55.8% in 2013), of which 18.4% (app. five species) was between sites (β1), 15.2% (app. four species) between areas (β2), and 25.0% (seven species) between the mainland and the island (β3). The total α-diversity was higher than expected by chance ($P < 0.05$) and comprised 41.4% of the total dung beetle species richness, with an average of 12 observed species from the total γ-diversity of 28 species.

The α-diversity in 2012 and 2013 was also higher than expected. The contribution of β-diversity was always higher for β3 and β1 components. Only the observed β-diversity between the mainland and the island was higher than expected by chance. The observed β1-component was nearly always half of the expected. Only β-diversity between areas was equal to the expected value, and always had the lowest contribution to β-diversity among hierarchical levels.

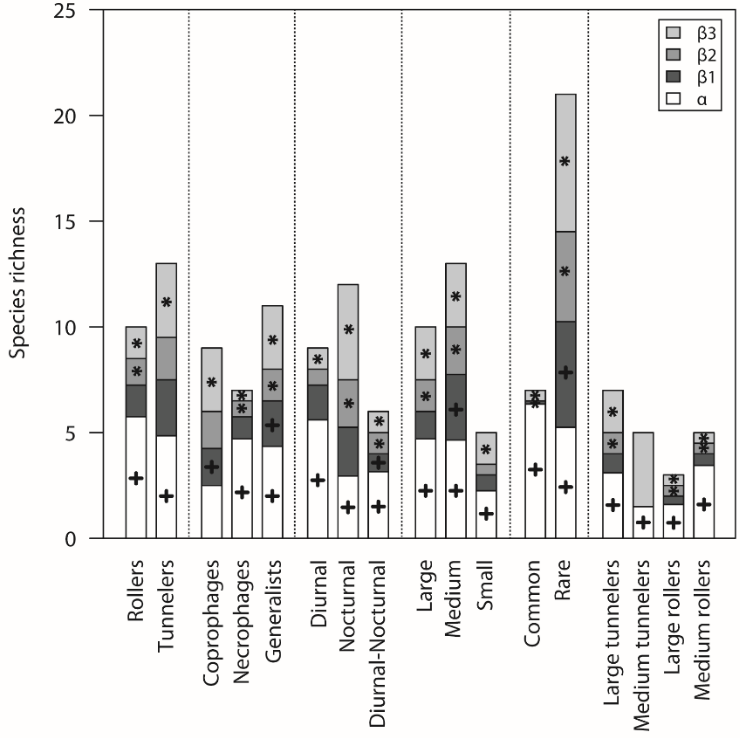
Diversity partitioning of functional groups showed different responses (Fig. 3). Out of 17 groups, seven showed greater α-diversity components compared to β-diversity components. The α-component accounted for 90.7% for common species. Medium-sized rollers, necrophages, diurnal species, rollers, large rollers and diurnal-nocturnal species also had high α-diversity. The α-component, however, was always lower than expected by chance.

Fig. 2. Full hierarchical analysis of diversity partitioning for composition of dung beetles. α = average local diversity, β1 = diversity among sites, β2 = diversity among areas, β3 = diversity among mainland-island. The observed partitions (Obs) are compared with the expected values (Exp) as predicted by the null model based on 999 randomizations. Black star: Exp < Obs, p < 0.05. Black cross: Exp > Obs, p < 0.05.



The highest values of all β-components were found among nocturnal, rare and coprophagous dung beetles. Medium-sized tunnelers, medium-sized, tunnelers, generalists, large-sized tunnelers, large-sized, and small-sized dung beetles also showed higher β-components. In general, the β3-component had the largest values followed by β1-component, with the exception of medium-sized dung beetles. The β3-component accounted for on average 24.2% of the diversity of these functional groups, and was higher than expected by chance for most groups. For medium-sized tunnelers, the β3-component accounted for 70% of the diversity variation. On the other hand, for common species and necrophages it accounted for only 7.1%.

Fig. 3. Full hierarchical analysis of diversity partitioning for community deconstruction approach. Diversity partitioning was analyzed for functional groups of food relocation behavior, diet, diel activity, body size, rarity, relocation behavior and size combined. α = average local diversity, β1 = diversity among sites, β2 = diversity among areas, β3 = diversity among mainland-island. The observed partitions (Obs) are compared with the expected values (Exp) as predicted by the null model based on 999 randomizations. Black star: Exp < Obs, $p < 0.05$. Black cross: Exp > Obs, $p < 0.05$.



Environmental, spatial and temporal effects on community variation

Traditional vs functional diversity measures

Variation partitioning for abundance, biomass and functional diversity showed scale-dependence of processes structuring dung beetle communities using a two-year dataset (Fig. 4). At the regional scale (i.e., mainland-island scale) we found a higher and significant environmental effect, followed by spatial and temporal effects that together accounted for 11.9% of abundance variation at this scale (Fig. 4). Variation partitioning using biomass data showed the same pattern, but with increased spatial and temporal effects (Table 1). The explained community variation was also higher, 14.4% (Fig. 4). For functional diversity, only environmental effects were important, explaining 7.3% of variation at this scale (Table 1).

At the area scale (i.e., intermediate scale), environmental, spatial and temporal models explained significantly variation in abundance (20.7%) and biomass (21.8%) of dung beetles (Table 2, Fig. 4). However, the spatial model was always more important, and the shared fraction also explained a part of total variation for both datasets. At this scale, we found a higher and significant environmental and spatial effect on functional diversity, which alone explained 10% of the data variation. Spatially structured environmental variation also was important for functional diversity at this spatial scale.

At the site scale (i.e., local scale), we found stronger environmental effects on biomass and abundance data (Table 3). Environmental variables explained 8.3% and 8.6% of abundance and biomass variation, respectively. Temporal effects were also important at this scale, but explained only 1% and 1.8% of abundance and biomass, respectively. Spatial effects were not important for any community dataset. For functional diversity, only the environmental model was important at this scale.

Altitude, green cover and greater tree distance were the environmental variables selected to compose the environmental model to explain the variation in abundance data, while altitude, tree height, green cover, tree top distance and greater tree height were selected to explain the variation in biomass data. For functional diversity, the environmental variables selected were altitude, land slope and green cover.

Table 1. Results of the partial redundancy analysis for the abundance, biomass and functional diversity of the dung beetle community, and for functional groups composed of food relocation behavior, diet, activity period, body size, rarity, relocation behavior and size combined at the mainland-island scale.

	*P*GEnv	*P*GSpa	*P*GTem	Env Sel[1]	Spa Sel	Tem Sel	E | S + T			S | E + T			T | E + S		
							R^2_{adj}	F	*P*	R^2_{adj}	F	*P*	R^2_{adj}	F	*P*
Normal approach															
Abundance	**0.001**	**0.001**	**0.002**	ALT, GC, GTD	1, 2	1	0.082	7.072	**0.001**	0.027	3.954	**0.001**	0.010	3.237	**0.001**
Biomass	**0.001**	**0.001**	**0.001**	ALT, TH, GC, TTD, GTH	1, 2, 3	1	0.076	4.474	**0.001**	0.041	4.067	**0.001**	0.018	5.105	**0.001**
Functional diversity	**0.005**	0.297	0.457	ALT, LS, GC	-	-	0.073	6.017	**0.001**	-	-	-	-	-	-
Deconstruction approach[2]															
Rollers	**0.001**	0.250	0.512	ALT, GTD	-	-	0.068	8.207	**0.001**	-	-	-	-	-	-
Tunnelers	**0.002**	**0.001**	**0.010**	ALT, TH, LLB	1, 2	1	0.065	5.808	**0.001**	0.041	5.509	**0.001**	0.012	3.661	**0.009**
Coprophages	**0.043**	**0.010**	0.182	ALT	4, 1	-	0.039	9.200	**0.001**	0.026	3.779	**0.006**	-	-	-
Necrophages	**0.001**	**0.045**	**0.016**	ALT	1, 2	1	0.062	14.375	**0.001**	0.018	2.927	**0.004**	0.012	3.538	**0.004**
Generalists	**0.001**	**0.003**	0.136	ALT, GC, TD	1, 3	-	0.103	8.922	**0.001**	0.030	4.411	**0.002**	-	-	-
Diurnal	**0.001**	**0.030**	**0.008**	ALT	-	1	0.104	24.328	**0.001**	-	-	-	0.015	4.345	**0.002**
Nocturnal	**0.001**	**0.001**	**0.006**	ALT, TD, LLB	1, 3, 2	1	0.055	5.315	**0.001**	0.070	6.460	**0.001**	0.018	5.218	**0.001**
Diurnal-Nocturnal	**0.002**	**0.043**	0.394	ALT, GTD, LL	1	-	0.071	6.108	**0.001**	0.019	5.184	**0.003**	-	-	-
Large	**0.001**	**0.001**	**0.002**	ALT, TH, TTD, GC	1, 2	1	0.080	5.575	**0.001**	0.047	6.322	**0.001**	0.020	5.476	**0.001**
Medium	**0.001**	0.213	0.599	ALT, GTD	-	-	0.078	9.447	**0.001**	-	-	-	-	-	-
Small	**0.026**	**0.033**	**0.047**	ALT, GTH	1	-	0.047	5.962	**0.001**	0.006	2.156	0.102	-	-	-
Common	**0.001**	**0.005**	**0.017**	ALT, GC, GTD	1	1	0.100	8.498	**0.001**	0.012	3.662	**0.002**	0.010	3.119	**0.008**
Rare	**0.012**	**0.001**	**0.009**	ALT, GTBA, GTTD	1	1	0.027	2.852	**0.001**	0.021	5.414	**0.001**	0.009	2.821	**0.008**
Large tunnelers	**0.001**	**0.001**	**0.004**	ALT, TH	1, 2	1	0.055	7.251	**0.001**	0.073	9.312	**0.001**	0.018	5.139	**0.004**
Medium tunnelers	0.219	0.969	**0.001**	-	-	1	-	-	-	-	-	-	0.036	8.510	**0.001**
Large rollers	**0.002**	0.090	0.201	ALT, GTBA	-	-	0.089	10.741	**0.001**	-	-	-	-	-	-
Medium rollers	**0.001**	0.236	0.806	ALT, GTD	-	-	0.085	10.236	**0.001**	-	-	-	-	-	-

*P*GEnv: *P*-values of the global environmental models, *P*GSpa: *P*-values of the global spatial models, *P*GTem: *P*-values of the global temporal models, Env Sel: selected environmental variables, Spa Sel: selected spatial variables, Tem Sel: selected dummy variable, R^2_{adj}: data variation explained by the model, E | S + T: pure environmental model, S | E + T: pure spatial model, T | E + S: pure temporal model. *P*-values lower than 0.05 are indicated in bold.

[1] ALT: altitude; GC: green cover; GTBA: greater tree basal area; GTD: greater tree distance; GTH: greater tree height; GTTD: greater tree top diameter; LL: percentage of leaf litter; LLB: leaf litter biomass; LS: land slope; TD: tree distance; TH: tree height; TTD: tree top diameter.

[2] Food relocation behavior: rollers and tunnelers; Diet: coprophages, necrophages and trophic generalists; Diel activity: diurnal, nocturnal and diurnal-nocturnal; Body size: large, medium and small; Rarity: common and rare; Combined functional groups: large tunnelers, medium tunnelers, large rollers and medium rollers.

Table 2. Results of the partial redundancy analysis for the abundance, biomass and functional diversity of the dung beetle community, and for functional groups composed of food relocation behavior, diet, activity period, body size, rarity, relocation behavior and size combined at the area scale.

	*P*GEnv	*P*GSpa	*P*GTem	Env Sel[1]	Spa Sel	Tem Sel	E | S + T			S | E + T			T | E + S		
							R^2_{adj}	F	*P*	R^2_{adj}	F	*P*	R^2_{adj}	F	*P*
Normal approach															
Abundance	**0.001**	**0.001**	**0.003**	ALT, GC, GTD	13, 4, 5, 10, 6, 1, 12	-	0.047	4.788	**0.001**	0.115	5.053	**0.001**	0.011	3.599	**0.002**
Biomass	**0.001**	**0.001**	**0.001**	ALT, TH, GC, TTD, GTH	5, 4, 6, 10, 13, 1	-	0.045	3.202	**0.001**	0.115	5.728	**0.001**	0.019	5.622	**0.001**
Functional diversity	**0.001**	**0.003**	0.449	ALT, LS, GC	10, 5, 13	-	0.039	3.698	**0.003**	0.027	2.899	**0.003**	-	-	-
Deconstruction approach[2]															
Rollers	**0.001**	**0.001**	0.543	ALT, GTD	1, 13, 4, 6, 5, 14, 10	-	0.043	5.708	**0.001**	0.051	2.640	**0.001**	-	-	-
Tunnelers	**0.001**	**0.001**	**0.017**	ALT, TH, LLB	5, 4, 6, 13, 1	1	0.038	4.235	**0.001**	0.159	9.150	**0.001**	0.013	4.231	**0.005**
Coprophages	**0.037**	**0.020**	0.177	ALT	13, 1	-	0.017	4.593	**0.011**	0.032	4.463	**0.003**	-	-	-
Necrophages	**0.001**	**0.001**	**0.014**	ALT	5, 1, 6, 4, 13, 9	1	0.018	5.116	**0.002**	0.108	5.328	**0.001**	0.012	3.927	**0.004**
Generalists	**0.001**	**0.001**	0.132	ALT, GC, TD	13, 10, 4, 6, 12	-	0.054	5.475	**0.001**	0.106	6.348	**0.001**	-	-	-
Diurnal	**0.001**	**0.001**	**0.007**	ALT	13, 5, 1, 4	1	0.060	15.172	**0.001**	0.054	4.234	**0.001**	0.015	4.630	**0.001**
Nocturnal	**0.001**	**0.001**	**0.006**	ALT, TD, LLB	13, 6, 5, 4, 12	1	0.035	4.190	**0.002**	0.197	11.837	**0.001**	0.019	6.151	**0.001**
Diurnal-Nocturnal	**0.001**	**0.001**	0.355	ALT, GTD, LL	1, 6, 13, 5, 4, 9	-	0.025	2.936	**0.001**	0.097	4.809	**0.001**	-	-	-
Large	**0.001**	**0.001**	**0.003**	ALT, TH, TTD, GC	5, 6, 4, 1, 2, 7	1	0.044	3.876	**0.001**	0.162	8.091	**0.001**	0.021	6.329	**0.001**
Medium	**0.001**	**0.011**	0.597	ALT, GTD	13, 14, 10, 6	-	0.057	7.280	**0.001**	0.029	2.623	**0.003**	-	-	-
Small	**0.030**	**0.002**	**0.048**	ALT, GTH	13, 1	-	0.024	3.719	**0.012**	0.067	8.479	**0.001**	-	-	-
Common	**0.001**	**0.001**	**0.013**	ALT, GC, GTD	13, 5, 4, 10, 1, 6, 9	1	0.060	5.935	**0.001**	0.120	5.352	**0.001**	0.010	3.558	**0.004**
Rare	**0.011**	**0.001**	**0.007**	ALT, GTBA, GTTD	4, 13, 6, 1, 5, 3	1	0.014	1.976	**0.009**	0.056	3.027	**0.001**	0.009	2.930	**0.004**
Large tunnelers	**0.001**	**0.001**	**0.006**	ALT, TH	5, 4, 6, 13	1	0.010	2.286	**0.037**	0.209	15.244	**0.001**	0.019	6.114	**0.001**
Medium tunnelers	0.262	0.574	**0.001**	-	-	1	-	-	-	-	-	-	0.036	8.510	**0.001**
Large rollers	**0.004**	**0.001**	0.192	ALT, GTBA	1, 6, 4, 7, 15	-	0.066	8.871	**0.001**	0.097	5.691	**0.001**	-	-	-
Medium rollers	**0.001**	**0.009**	0.790	ALT, GTD	13, 14, 10	-	0.063	7.980	**0.001**	0.024	2.792	**0.005**	-	-	-

*P*GEnv: *P*-values of the global environmental models, *P*GSpa: *P*-values of the global spatial models, *P*GTem: *P*-values of the global temporal models, Env Sel: selected environmental variables, Spa Sel: selected spatial variables, Tem Sel: selected dummy variable, R^2_{adj}: data variation explained by the model, E | S + T: pure environmental model, S | E + T: pure spatial model, T | E + S: pure temporal model. *P*-values lower than 0.05 are indicated in bold.

[1] ALT: altitude; GC: green cover; GTBA: greater tree basal area; GTD: greater tree distance; GTH: greater tree height; GTTD: greater tree top diameter; LL: percentage of leaf litter; LLB: leaf litter biomass; LS: land slope; TD: tree distance; TH: tree height; TTD: tree top diameter.

[2] Food relocation behavior: rollers and tunnelers; Diet: coprophages, necrophages and trophic generalists; Diel activity: diurnal, nocturnal and diurnal-nocturnal; Body size: large, medium and small; Rarity: common and rare; Combined functional groups: large tunnelers, medium tunnelers, large rollers and medium rollers

Table 3. Results of the partial redundancy analysis for the abundance, biomass and functional diversity of the dung beetle community, and for functional groups composed of food relocation behavior, diet, activity period, body size, rarity, relocation behavior and size combined at the site scale.

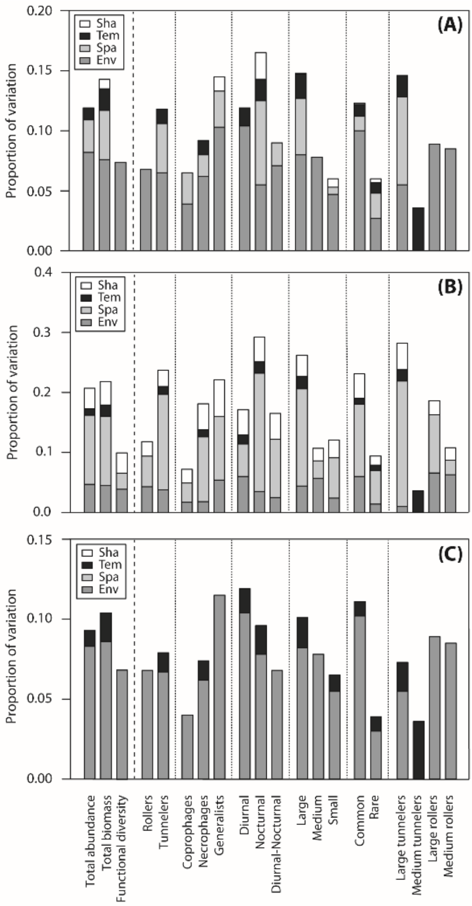
	*P*GEnv	*P*GSpa	*P*GTem	Env Sel[1]	Spa Sel	Tem Sel	E | S + T			S | E + T			T | E + S		
							R^2_{adj}	F	*P*	R^2_{adj}	F	*P*	R^2_{adj}	F	*P*
Normal approach															
Abundance	**0.001**	0.999	**0.004**	ALT, GC, GTD	-	1	0.083	6.996	**0.001**	-	-	-	0.010	3.141	**0.001**
Biomass	**0.001**	1.000	**0.002**	ALT, TH, GC, TTD, GTH	-	1	0.086	4.793	**0.001**	-	-	-	0.018	4.872	**0.001**
Functional diversity	**0.005**	0.968	0.440	ALT, LS, GC	-	-	0.073	6.017	**0.001**	-	-	-	-	-	-
Deconstruction approach[2]															
Rollers	**0.001**	0.959	0.546	ALT, GTD	-	-	0.068	8.207	**0.001**	-	-	-	-	-	-
Tunnelers	**0.001**	0.956	**0.015**	ALT, TH, LLB	-	1	0.067	5.763	**0.001**	-	-	-	0.012	3.500	**0.010**
Coprophages	**0.041**	0.160	0.169	ALT	-	-	0.040	9.373	**0.001**	-	-	-	-	-	-
Necrophages	**0.001**	0.985	**0.009**	ALT	-	1	0.062	14.228	**0.001**	-	-	-	0.012	3.470	**0.006**
Generalists	**0.001**	1.000	0.138	ALT, GC, TD	-	-	0.115	9.649	**0.001**	-	-	-	-	-	-
Diurnal	**0.001**	0.541	**0.006**	ALT	-	1	0.104	24.328	**0.001**	-	-	-	0.015	4.345	**0.003**
Nocturnal	**0.001**	1.000	**0.005**	ALT, TD, LLB	-	1	0.078	6.706	**0.001**	-	-	-	0.018	4.814	**0.002**
Diurnal-Nocturnal	**0.003**	0.988	0.381	ALT, GTD, LL	-	-	0.068	5.832	**0.001**	-	-	-	-	-	-
Large	**0.001**	0.999	**0.002**	ALT, TH, TTD, GC	-	1	0.082	5.506	**0.001**	-	-	-	0.019	5.191	**0.002**
Medium	**0.001**	0.922	0.597	ALT, GTD	-	-	0.078	9.447	**0.001**	-	-	-	-	-	-
Small	**0.022**	0.579	**0.048**	ALT, GTH	-	1	0.055	6.805	**0.001**	-	-	-	0.010	3.070	**0.037**
Common	**0.001**	1.000	**0.008**	ALT, GC, GTD	-	1	0.102	8.590	**0.001**	-	-	-	0.009	3.077	**0.007**
Rare	**0.008**	0.978	**0.013**	ALT, GTBA, GTTD	-	1	0.030	3.055	**0.001**	-	-	-	0.009	2.758	**0.004**
Large tunnelers	**0.001**	1.000	**0.005**	ALT, TH	-	1	0.055	6.900	**0.001**	-	-	-	0.018	4.737	**0.004**
Medium tunnelers	0.267	0.431	**0.001**	-	-	1	-	-	-	-	-	-	0.036	8.510	**0.001**
Large rollers	**0.007**	0.774	0.182	ALT, GTBA	-	-	0.089	10.741	**0.001**	-	-	-	-	-	-
Medium rollers	**0.001**	0.946	0.798	ALT, GTD	-	-	0.085	10.236	**0.001**	-	-	-	-	-	-

*P*GEnv: *P*-values of the global environmental models, *P*GSpa: *P*-values of the global spatial models, *P*GTem: *P*-values of the global temporal models, Env Sel: selected environmental variables, Spa Sel: selected spatial variables, Tem Sel: selected dummy variable, R^2_{adj}: data variation explained by the model, E | S + T: pure environmental model, S | E + T: pure spatial model, T | E + S: pure temporal model. *P*-values lower than 0.05 are indicated in bold.

[1] ALT: altitude; GC: green cover; GTBA: greater tree basal area; GTD: greater tree distance; GTH: greater tree height; GTTD: greater tree top diameter; LL: percentage of leaf litter; LLB: leaf litter biomass; LS: land slope; TD: tree distance; TH: tree height; TTD: tree top diameter.

[2] Food relocation behavior: rollers and tunnelers; Diet: coprophages, necrophages and trophic generalists; Diel activity: diurnal, nocturnal and diurnal-nocturnal; Body size: large, medium and small; Rarity: common and rare; Combined functional groups: large tunnelers, medium tunnelers, large rollers and medium rollers

Fig. 4. Variation partitioning of the whole dung beetle community (abundance and biomass), the set of functional diversity indices and of communities delimited by their food relocation behavior, diet, activity period, body size, rarity, relocation behavior and size combined across three spatial scales: mainland-island (A), areas (B) and sites (C). Env: pure environmental fraction, Spa: pure spatial fraction, Temp: pure temporal fraction, Sha: shared fraction (all other fractions summed). Right portion after dashed line represents the community deconstruction approach.



Deconstructed communities

Variation partitioning of deconstructed communities into species groups with similar traits showed a variety of responses to environmental, spatial and temporal effects (Fig. 4). In general, functional groups from a given category (e.g., relocation behavior, activity period, body size) did not show the same response. We were able to identify four response groups (functional groups with similar responses to environmental, spatial and temporal variables) at the regional scale (Table 1). In the first response group, tunnelers and necrophages, as well as nocturnal, large-sized, common, rare, and large-tunneler species were all influenced by environmental, spatial and temporal models. Environmental effects were more important than spatial and temporal effects for most functional groups, with the exception of nocturnal and large tunneler beetles, which were more influenced by spatial effects. The environmental model explained 10% of the variation for common species. The spatial model was more important for large tunneler species, and explained 7.3% of variation. Among these response groups, nocturnal beetles showed the highest total variation explained value (16.5%). The second response group was formed by functional groups that were only influenced by environmental and spatial models. The environmental model was highest for all functional groups. Trophic generalist species showed the highest total explained value of variation (14.5%) and environmental model accounted for 10.3%. Coprophages, diurnal-nocturnal species and small-sized species were part of this response group.

The third response group was composed of functional groups that were only influenced by environmental variables. Rollers, medium-sized species, large-sized rollers and medium-sized rollers were part of this response group. Among these, large rollers showed the highest explained value of variation (8.9%). The fourth response group was formed by remaining functional groups that showed differential responses to explanatory models. Diurnal beetles were influenced by environmental (10.4% of variation) and temporal (1.5% of variation) factors, while medium-sized tunnelers were influenced only by temporal factors (3.6%).

At the intermediate scale, we found a higher spatial effect for most functional groups (Table 2, Fig. 4). Only diurnal, medium-sized, and medium rollers showed a higher environmental effect. We could find three distinct response groups at this scale. The first response group is formed by functional groups where environmental, spatial and temporal effects were important. Tunnelers, necrophages, diurnal, nocturnal, large-sized, common, rare and large tunneler species were part of this response group. Among these, the spatial model explained 20.9% of large tunneler variation. The greatest amount of variation explained among all models was found for nocturnal dung beetles with 29.2% of the total variation. The second response group was formed by rollers, coprophages, trophic generalists, diurnal-nocturnal species, small, medium and large sized species, and medium-sized rollers, which were influenced only by environmental and spatial models. Only medium-sized and medium-sized roller species showed a higher explained value of variation by environmental models. The third response group was composed of medium-sized tunnelers, which showed different responses. Tunneler species were influenced only by temporal factors (3.6%). At this scale, the shared fraction was very important for most functional groups, showing a large amount of spatially structured environmental variation within the four areas sampled.

At the local scale, only the environmental and temporal models were important for the variation in community data (Table 3, Fig. 4). We could identify two main response groups at this scale: those that are influenced only by environmental variables, and those influenced by environmental and temporal variables. Rollers, coprophages, trophic generalists, diurnal-nocturnal species, medium-sized species, and large and medium rollers were influenced only by environmental variables. Among these, the highest explained value was found for generalist species, where the environmental model accounted for 11.5% of the variation in the data. Both environmental and temporal factors influenced tunnelers and necrophages, as well as diurnal, nocturnal, large-sized, small-sized, common, rare, and large tunneler species. The temporal models always had lower values than the environmental models. Among these response groups, diurnal beetles had the greatest explained value and the environmental model accounted for 10.4% of variation in the data set. The shared fraction was not important at this scale, showing negative values.

Taking into account the responses of functional groups across the three spatial scales studied, we identified the occurrence of two major groups of responses (Table 4). The occurrence of significant temporal effect at any spatial scale was used to separate the two major response groups. Each response group was divided into two subgroups according to the variation in the relative importance of environmental, spatial and temporal models, and a brief summary of the relative importance of explanatory models according to each functional group is provided (Table 4). We found few shared dung beetle species for most functional groups (see S1 Table), which demonstrates support for independence of group responses to environmental, spatial and temporal effects.

The variables that comprised the environmental models differed among response groups. However, altitude was included as a variable in all models. Greater tree basal area, greater tree distance, greater tree height, green cover, leaf litter biomass, percentage of leaf litter, tree distance, tree height, and tree top diameter were the variables that comprised the environmental models, yet they did not show any pattern among the aforementioned groups.

Comparing the responses of different community datasets (functional groups) with abundance response, we found that data on nocturnal, large-sized, large-tunnelers, trophic generalist, and common species, as well as biomass, showed higher explained values of variation than did abundance at the regional scale (Fig. 4). At the intermediate scale, nocturnal, large-sized tunneler, large-sized, tunneler, common, and trophic generalist species and biomass had higher overall explained value of variation than did abundance alone (Fig. 4). At the local scale, the functional groups that had higher explained values than abundance were trophic generalists, diurnal, nocturnal, common, and large-sized species, and biomass (Fig. 4). In general, data on nocturnal species, trophic generalists, large-sized and common species, and biomass showed higher explained values of variation than did abundance at all three spatial scales studied. Large tunnelers also had the highest values at regional and intermediate spatial scales.

Discussion

Our results show that environmental, spatial and temporal processes play different roles in structuring species composition in Scarabaeinae metacommunities. However, the relative importance of these processes depends on spatial scale and the community dataset (or species groups) analyzed. Several ecological processes are scale-dependent, showing spatial and temporal differences from local to continental scales [100, 101], and there is a large body of evidence that supports this claim for several groups of organisms in different ecosystems (e.g., [4, 5, 83, 102, 103]). Besides improving our knowledge of scale-dependence of ecological processes in Scarabaeinae metacommunities, our study was able to identify similar responses of functional groups with different species composition and sets of traits. Our results also show that functional diversity metrics are appropriate for the investigation of different ecological processes over increasing spatial scales.

Table 4. Summary of the relative importance of explanatory models according to the different community datasets, and according to each functional group across the spatial scales studied. Groups were formed by similar responses.

Datasets	Increasing spatial scale			Group[1]/Subgroup	
	Sites	Areas	Mainland-Island		
Abundance	Env + Tem	Spa + Env + Tem	Env + Spa + Tem	-	-
Biomass	Env + Tem	Spa + Env + Tem	Env + Spa + Tem	-	-
Functional diversity	Env	Env + Spa	Env	-	-
Common	Env + Tem	Spa + Env + Tem	Env + Spa + Tem	G2	SG1
Coprophages	Env	Spa + Env	Env + Spa	G1	SG2
Diurnal	Env + Tem	Env + Spa + Tem	Env + Tem	-	-
Diurnal-Nocturnal	Env	Spa + Env	Env + Spa	G1	SG2
Generalists	Env	Spa + Env	Env + Spa	G1	SG2
Large	Env + Tem	Spa + Env + Tem	Env + Spa + Tem	G2	SG1
Large rollers	Env	Spa + Env	Env	G1	SG1
Large tunnelers	Env + Tem	Spa + Env + Tem	Spa + Env + Tem	G2	SG2
Medium	Env	Env + Spa	Env	G1	SG1
Medium rollers	Env	Env + Spa	Env	G1	SG1
Medium tunnelers	Tem	Tem	Tem	-	-
Necrophages	Env + Tem	Spa + Env + Tem	Env + Spa + Tem	G2	SG1
Nocturnal	Env + Tem	Spa + Env + Tem	Spa + Env + Tem	G2	SG2
Rare	Env + Tem	Spa + Env + Tem	Env + Spa + Tem	G2	SG1
Rollers	Env	Spa + Env	Env	G1	SG1
Small	Env + Tem	Spa + Env	Env + Spa	-	-
Tunnelers	Env + Tem	Spa + Env + Tem	Env + Spa + Tem	G2	SG1

Env: pure environmental model, Spa: pure spatial model, Tem: pure temporal model, G: group, SG: subgroup.

[1] G1: response group more influenced by environmental than spatial processes, and not influenced by temporal processes; SG1 (G1): subgroup where spatial effects were important only at the intermediate scale; SG2 (G1): subgroup where spatial effects were important at the intermediate and regional scales, being spatial effects more important than environmental ones at the intermediate scale; G2: response group also influenced by environmental, spatial and temporal processes; SG1 (G2): subgroup where spatial effects were more important than environmental and temporal ones at the intermediate scale, and environmental effects were more important than other at the regional scale; SG2 (G2): subgroup where spatial effects were more important than environmental and temporal ones at the intermediate and regional scales.

Abundance and biomass data were influenced in the same way by different sets of predictors across spatial scales. At the local scale, environmental and temporal predictors were important. Spatial factors were most important at the intermediate scale, i.e. within areas. Contrary to our expectations and consistent with some other studies, there was a greater environmental than spatial effect at larger spatial scales [4]. These results demonstrate that some environmental variables may show a large spatial variation that can affect species distribution both locally and regionally. At intermediate spatial scales, environmental filters were less important, and spatial processes other than dispersal limitation were more important in structuring dung beetle communities.

Dung beetle biomass is mainly derived from nutrients obtained from mammal feces [72]. Biomass can be used as a measure of beetle body size, which is a trait positively correlated with the ecological functions of dung removal and secondary seed dispersal for large-bodied, nocturnal dung beetles [73, 74]. Our results show that abundance and biomass data respond similarly to the ecological gradient, but that biomass showed a higher value explained by sets of explanatory variables than abundance data. The environmental model tested against biomass data had five significant environmental variables, two more than the environmental model tested against abundance data. So, biomass data may be used as a representative measure of species responses when one is trying to describe environmental and spatial effects on ecological functions of dung beetles.

Functional traits and functional diversity measures are increasing among community ecology studies [24]. These approaches have been applied to different biological groups to investigate the relationships between biodiversity and ecosystem processes [29]. Our results showed that a distance-based functional diversity approach responds differently to environmental, spatial and temporal processes compared to traditional measures such as species abundance and biomass. The environmental model was more important than the spatial model, and there was no temporal effect in functional diversity. Environmental effects may be intuitively more important for functional structure than taxonomic structure (see also [104]), and contrary to old ideas (see [105]), functional structure may be spatially structured. At the intermediate spatial scale, the shared fraction was also important, as in other studies [95]. The absence of a temporal effect can be interpreted as a non-significant temporal turnover of functional diversity, which can be explained by the slight increase in β-diversity between years at all spatial scales. As we demonstrated, general patterns of functional diversity can be influenced by environmental and spatial factors [95, 106, 107] that are dependent on spatial scales. Investigation of the importance of environmental and spatial processes in explaining functional diversity across spatial scales is a recent approach [95, 108]. In our study, we did not investigate the response of each functional diversity index because we were attempting to test the use of a set of indices that take into account different features of communities to be used as proxy for traditional measures. We know that different individual functional diversity indices may respond differently to environmental and spatial predictors, and that they may be scale-dependent [39, 95, 106, 109]. We argue that functional diversity is a complementary tool to answer ecological questions [24, 110] regarding species distribution in the metacommunity framework.

Based on our community deconstruction approach, we were able to identify two main robust response groups, each with two subgroups according to their responses to explanatory models at each spatial scale. The two main response groups are formed by functional groups that were influenced only by environmental and spatial patterns at intermediate scales (group 1) and by the three sets of explanatory predictors at higher spatial scales (group 2). Group 1 can be divided into functional groups that showed a higher importance of spatial effects at the intermediate scale (subgroup 1), and those that also showed greater importance of environmental than of spatial effects (subgroup 2). Subgroup 1 was composed mainly of roller groups and medium-sized dung beetles (composed of rollers, tunnelers and dwellers). Subgroup 2 was formed by coprophages, trophic generalists and diurnal-nocturnal dung beetles, and by unrelated groups. Group 2 showed greater environmental than temporal effects at the local scale. It also showed a greater spatial, followed by environmental and temporal effects at the intermediate scale. At the mainland-island scale the environmental effects were higher than spatial and temporal ones. Moreover, the subgroups can be identified by their different responses at the regional scale; subgroup 1 showed a higher environmental effect while subgroup 2 showed a higher spatial effect.

Coprophages and trophic generalists showed higher β-diversity components than necrophages, and in general, the first groups were represented by more species than necrophages. This is a common pattern found in Scarabaeinae communities in Neotropical and Southern Asia regions [111, 112]. Among these groups, trophic generalists showed the highest value of variation explained by environmental and spatial filters. Necrophages differed from the other two groups because they showed a significant temporal turnover at all spatial scales, despite the importance of spatial and environmental effects at higher scales. The temporal turnover in necrophages may be associated with increased abundance of *Canthon luctuosus* and *Coprophanaeus dardanus*, and with decreased abundance of *Coprophanaeus saphirinus* and *Deltochilum rubripenne* at the same sites and at all spatial scales. Mammal feces and carrion were expected to be spatially and temporally unpredictable. However, we expect that dung resources occur more frequently and is more abundant than carrion. Moreover, carrion is also consumed by other organisms such as large birds and also mammals, whereas dung is utilized almost exclusively by a few insect groups, many of them predators of other insects. So, necrophagous beetles may also be responding to temporal effects such as low availability of food resource, which is well recognized to be one of the most important drivers of dung beetle communities (beyond changes in vegetation structure) [42, 46].

Groups based on activity period showed different responses. Activity period of Scarabaeinae beetles is associated with daytime temperatures and humidity, and differences in forest structure may negatively influence the activity of diurnal species [68]. Diurnal species often have smaller body size [69], while large-bodied species are often nocturnal [71]. Diurnal activity may be a limiting factor for species dispersal when climatic conditions are unfavorable. For example, very warm temperatures, low humidity and strong winds can influence the flight capacity of beetles, even within forests [113]. However, our results showed that nocturnal species were more influenced by spatial filters than were diurnal species, mainly at larger spatial scales. Diurnal species were more influenced by environmental than spatial filters. Diurnal-nocturnal species showed an intermediate response between diurnal and nocturnal species. Diurnal beetles showed a high proportion of species richness due to α-diversity (62.2%), while diurnal-nocturnal species showed similar values of α- and β-components. β-diversity components accounted for 75.4% of species richness of nocturnal beetles, which may explain the higher spatial effect on this group, mainly between areas. We expect that species with different sets of ecological traits have different dispersal abilities, and thus they are influenced by environmental and spatial filters differently [5].

Body size in dung beetles is an important trait that can be affected by modification [46], fragmentation [75], and isolation [114] of tropical forests. Large-bodied dung beetles perform better in dung removal and secondary seed dispersal than do small-sized dung species [73, 74] because they are better competitors [76, 77]. Large-sized dung beetles are also expected to be good dispersers [78]. Our results showed that these beetles were very influenced by spatial factors at higher spatial scales, demonstrating dispersal limitation or other spatial mechanisms that limited their spatial distribution. Environmental effects were important at regional scales, and can play an important role in the distribution of these beetles. Large, medium and small-sized dung beetles also showed similar α- and β-component proportions.

Rollers were influenced mostly by environmental filters. Tunnelers were very influenced by spatial factors at the intermediate scale. Rollers showed a higher α-component while tunnelers showed a higher β-component. Using body size and food relocation behavior combined, we found that large tunnelers and medium tunnelers showed higher β-components. However, their responses to environmental, spatial and temporal processes were very distinct. The spatial effect becomes very important for large tunnelers when these traits are combined. Medium-sized tunnelers were only influenced by temporal effects, and only the β3-component was important. This result demonstrates a temporal turnover at the regional scale for this group; environmental and spatial effects were not important. Large rollers and medium rollers showed higher α-component. Spatial effects were important only at the intermediate spatial scale, and mostly for large rollers. Food relocation behavior alone showed no differences in the responses between rollers and tunnelers, however when combined with body size we found different responses between species with distinct sets of traits. The functional group assignment using sets of traits seems to be a more realistic approach for use in community deconstruction. However, this approach may only be feasible when there are a limited number of traits. If we used all measured traits, we would have 22 different groups from 28 species sampled, and most of them would be formed by one to three species. This would preclude the implementation of multivariate analyses and hamper the gathering of species response patterns. The diversity of biological traits originated by ecological, evolutionary and historical processes is one of the characteristics that are associated with the evolutionary success and high diversity of dung beetles [111]. We expect that the high diversity of traits that can be used in studies like ours is shared by the great majority of organisms, and that this approach may be particularly appropriate for groups with higher species richness.

Common and rare dung beetle species showed the same responses to ecological processes across the three spatial scales. However, the explanatory value was much higher for common species at all spatial scales. Our results also showed that common species have a very low β-diversity, while the composition of rare species is strongly dominated by β-diversity in all its components. Assumptions of classical ecological theory and metacommunity framework suggest that common and rare species should respond differently to environmental filters and dispersal limitation [37, 91]. Furthermore, common and rare species are expected to differ in functional traits and environmental preferences. However, our study (see also [37, 91, 115]) showed similar responses across environmental and spatial gradients in common and rare species. These results may have several explanations. First, rare species are expected to exhibit a higher level of environmental specialization, and can be more affected by spatially structured environmental filters than are common species. Second, common and rare species may respond similarly to environmental factors, but in different ways. For example, for both common and rare species the environmental model was formed by three variables, but altitude was the only one shared by both models. Thus, common and rare species may be affected by different environmental filters that are spatially structured in the same way. On the other hand, rare species may be affected by environmental variables that are difficult to measure [37] and are thus 'hiding' the real effect of environmental factors on the group.

Another important factor to be considered is undersampling of species. Species that are considered rare may simply be undersampled due to the inefficient methods. Among dung beetles, many species considered trophic specialists of resources different than those used as bait are typically undersampled, even using standardized and suitable methods. Species rarity is a difficult concept [116] and understanding the mechanisms driving the distribution of rare species is still a challenge in community ecology. Large-scale diversity patterns in aquatic metacommunities can only be well-described using information from common species [115]. Our results indicate the same, but removing rare species does not improve the outcome of analyses when comparing the responses of abundance between rare and common datasets. Species rarity is important in the context of conservation [117] and must be considered when the objective of the study involves the maintenance of biological diversity along ecological gradients, especially anthropogenically altered environmental gradients. However, ecologists should keep in mind that species rarity in disturbed habitats may generate an overestimation of the conservation value of these environments, because the presence of rare species may simply be a sampling artifact [117].

Among the general patterns, we found that environmental effects are prevalent at the local scale, which demonstrates the power of species sorting in local structuring of communities [118]. We also found strong environmental effects on many groups at the regional scale. There is a great body of evidence showing the predominance of environmental filters among aquatic and terrestrial metacommunities [37, 38, 94]. The importance of spatial effects did not follow the increase in spatial scale, and spatial effects were very important at the intermediate spatial scale. This demonstrates that even in the same large forest fragment, the dung beetles “suffer” with dispersal limitation. However, dispersal limitation, if it exists, should be visible at the largest spatial scale studied [4, 102]. Another possibility is that sites close to each other exchange large numbers of individuals and, hence, show mass effects at the intermediate spatial scale (see [83]). We do not have enough data on dispersal of dung beetle species to distinguish between dispersal limitation and mass effect, although the former is more likely due to the greater environmental effect at the local scale and large distance between sites. Thus, Scarabaeinae beetles show a spatially structured community possibly due to the large variation in environmental variables of the sites sampled. These effects are also important at the regional scale, as well as dispersal limitation (or other spatial effect) at intermediate spatial scales, culminating in the greater β-diversity found between the mainland and the island. The temporal effect was also important for the dung beetle community structure, as demonstrated for other groups [119, 120].

The high proportion of the residual fraction is common among metacommunity studies using variation-partitioning methods. A probable cause is that the communities are generally composed of many rare species, which have distributions that are difficult to model [37]. Moreover, snap-shot sampling surveys may yield weak patterns, which are not perfectly structured and may vary in time [110]. Another probable cause is the lack of key explanatory variables, which can be difficult to measure (e.g., biotic interactions) [37]. We measured 20 environmental variables that we expect describe properly the forest structure and environment of the sampling sites. Among the 12 that were selected to compose the different environmental models, the most important variables were altitude, greater tree basal area and green cover. Some of these variables were also related to the distribution of dung beetles in Atlantic Forest fragments in southern Brazil [62, 90]. Altitudinal variation is a common feature in the Atlantic Forest, which is generally composed of mountain chains with different elevations. This feature of the landscape can influence other characteristics of the forest differently, since the land slope was also important for the distribution of functional diversity in our study.

In summary, our study increases evidence of the importance of environmental, spatial and temporal factors acting differently at the local, intermediate and regional spatial scales in Scarabaeinae beetle distribution in Neotropical region. It also highlights that the effect of these processes on species abundance in the Atlantic Forest also changes some aspects of the functional organization of dung beetle communities.

Functional diversity can be used as a complementary, but not substitute, approach to traditional measures of community responses for testing environmental and spatial effects on species distribution. The functional diversity approach may show different responses due to the ecological traits and functional diversity indices used, which will depend on the aim of the study. These new ways of gathering information on different species traits can be used to answer ecological questions about community assembly and ecosystem function [24], which is of great interest in the context of community ecology.

The community deconstruction approach allows us to identify sets of responses for different trait-based groups with distinct species composition. The deconstructive approach was useful to improve our understanding of dung beetle species responses to environmental, spatial and temporal effects. For each functional group category, we must take into account different assumptions to explain the responses, and it seems to be a fruitful way to test other hypotheses (beyond the importance of different processes) in shaping community structure [38]. Studies of metacommunities frequently mix “oranges with apples” [38], i.e., we generally expect that all species in a given community, which are composed of different sets of traits, respond the same way to different processes across different spatial scales, which is simply not true. The community deconstruction approach seems promising for a better understanding of how species respond to environmental and spatial effects in a metacommunity framework.

Supporting Information

S1 Appendix. Protocol for trait assignments. Dung beetle species were characterized in terms of four ecological attributes: food relocation behavior, diet, active period and biomass.
(DOCX)

S2 Appendix. Protocol used to measure the environmental variables. Environmental variables were measured using the adapted point-centered quarter method.
(DOCX)

S1 Dataset. Dataset of abundance and dry biomass of dung beetle species, environmental variables, and geographical coordinates. Samplings were performed in Brazilian Atlantic Forest, Santa Catarina, Brazil using baited pitfall traps from January to February 2012 and 2013.
(XLXS)

S1 Fig. Rank abundance curve of dung beetle metacommunity (two years). Abundances are expressed as the percentage of the total abundance within the metacommunity. The dotted line indicates the inflection point of the curve used to classify the species into common or rare.
(EPS)

S2 Fig. Relation between number of species and number of individual of each functional group of dung beetles.
(EPS)

S3 Fig. Permission letter. Permission request to publish Fig. 1.
(TIF)

S1 Table. Dung beetle traits. Identity and traits for 28 dung beetle species sampled in the Atlantic Forest from southern Brazil. NA: unavailable data. Other: unknown, but different from others.
(XLXS)

S2 Table. Summary of environmental variables. Averages (mean or median, as appropriate), quartiles, minimum and maximum values. 25%: 25 percentile, 75%: 75 percentile; max: maximum recorded for the entire dataset.
(XLXS)

S3 Table. List of Scarabaeine dung beetles species and total captures per years and area. ANH: Environmental Protection Area of Anhatomirim in Governador Celso Ramos (mainland); ITA: Permanent Protection Area of Itapema (mainland); PER: Lagoa do Peri Municipal

Park, Florianópolis (island); RAT: Permanent Protection Area of Ratones, Florianópolis (island). T: total; GT: grand total.
(XLXS)

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Supporting Information

S1 Appendix. Protocols for trait assignments. Dung beetle species were characterized in terms of four ecological attributes: food relocation behavior, diet, active period and biomass.

Species were characterized in terms of ecological attributes: food relocation behavior, diet, diel activity and biomass. Protocols for trait assignments are described below. We also obtained additional information on dung beetle traits from the published literature and personal observations of specialists (Fernando Vaz-de-Mello, Universidade Federal de Mato Grosso, Brazil). Similar approaches were used by other authors [1-3].

Food relocation behavior: Food relocation behavior was assigned following the classification of [4] who categorized dung beetle species as rollers (telecoprids), tunnelers (paracoprids) or dwellers (endocoprids). Rollers build and roll food-balls over the soil until bury them. Tunnelers bury portions of food above or next the resource. Dwellers feed and nest inside or beneath the food source. Additional information was obtained from the published literature [5-11]. When the information was unavailable, we opted to classify the species as the pattern shown by the genera according to several studies with the objective of minimizing the occurrence of NAs in our dataset. Species with different (unknown) patterns of those shown by the group were classified as “Other” (with different numbers at the end to differentiate them).

Diet: Species were categorized as coprophage or necrophage if at least 80% of the individuals were captured in traps baited with human feces or carrion, respectively. Species with similar numbers of individuals in both types of baited trap were considered generalists. Only dung beetle species with more than 10 individuals were assigned to diet categories based in our samplings. Additional information for species with few individuals sampled (< 10) was obtained from the published [10,12,13] and unpublished literature [14-16]. When the information was unavailable, we opted to classify the species as the pattern shown by the genera according to several studies with the objective of minimizing the occurrence of NAs in our dataset.

Diel activity: The dung beetle species were classified according to their period of fly activity in diurnal, nocturnal and diurnal-nocturnal following several authors [2,3,17-23].

Biomass: All individuals of dung beetles were dried at 60°C for 72 h and weighed using a balance accurate to 0.0001 g to obtain the mean dry weight.

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S2 Appendix. Protocol used to measure the environmental variables. Environmental variables were measured using the adapted point-centered quarter method.

The protocol used to measure the 20 environmental variables is described as follows. Measurement was performed using the adapted point-centered quarter method [1] and was chosen for its simplicity and common use in phytosociological surveys [2]. Variables measured: (1) circumference at breast height when diameter at breast height [DBH] > 5 cm), (2) height, (3) top diameter and (4) distance away from the nearest tree to the center of cross, (5-8) same measures for the greater tree distant up to 10 m, (9-12) similar measures for shrubs (circumference at ankle height when DBH < 5 cm and with a minimum height of 1 m), (13) land slope, (14) canopy cover, (15) percentage of leaf litter cover, (16) green cover and (17) exposed soil, (18) height and (19) dry biomass of leaf litter, and (20) altitude. The height of trees and shrubs was visually estimated with a ruler of 4 m length. Circumference and distance were measured with a millimeter tape measure. The percentage of litter, green cover, and exposed soil coverage in each quadrant was estimated in different classes (0-5, 6-25, 26-50, 51-75, 76-95, 96-100%) using a square of 1 m plastic pipes, placed about 20 cm away from the cross. Land slope was obtained at the center of the square using an inclinometer. Litter height was measured using a mm ruler at five points inside the square (near each corner and in the center). A five-inch square was constructed in the center of the 1 m square, and a portion of litter was removed. Litter was later dried in an oven (60°C for 72 hours) and weighed to obtain dry biomass. Using the same classes described above, the percentage of canopy cover was visually estimated using a hollow square of 10 cm side length, placed at a distance of 60 cm from the eye of the observer at a 20° angle in relation to the zenith [2]. Altitude was obtained using a hand-held GPS at ground level. The basal area of trees and shrubs was calculated from the trunk circumference (based on the area of the circle). For each variable, a measure of central tendency was calculated based on the Shapiro-Wilk normality test. Thus, each environmental variable represented a central value (mean or median, as appropriate) of the four measures of each point; this was done to minimize the effects of visual estimation. A subset of the variables analyzed (three basal area, three heights, DBH) is used by the Conselho Nacional do Meio Ambiente (CONAMA), the

Brazilian Council of Environmental issues, to characterize successional stages of Atlantic Forest in the state of Santa Catarina [3].

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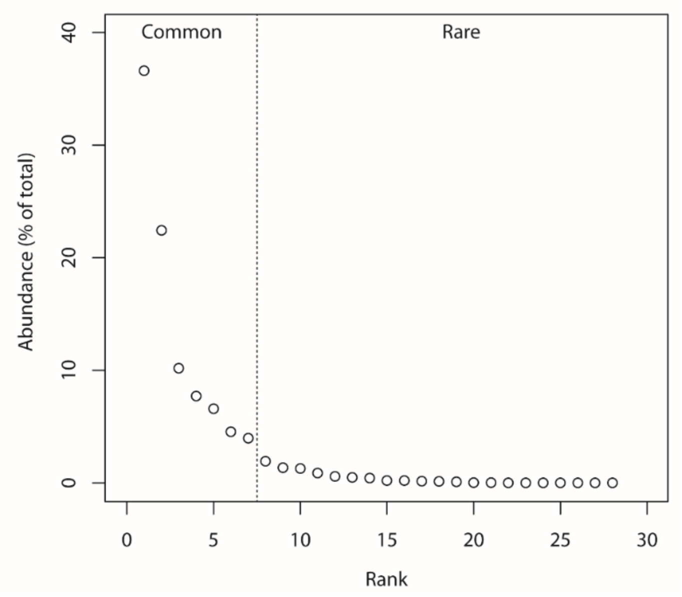
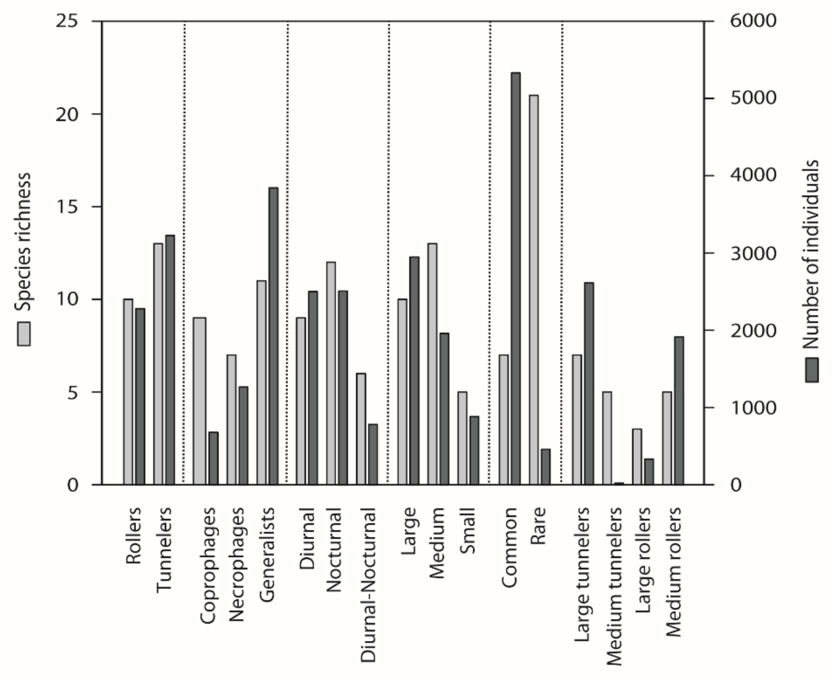
S1 Dataset. Dataset of abundance and dry biomass of dung beetle species, environmental variables, and geographical coordinates. Samplings were performed in Brazilian Atlantic Forest, Santa Catarina, Brazil using baited pitfall traps from January to February 2012 and 2013.

Disponível online somente após a publicação.

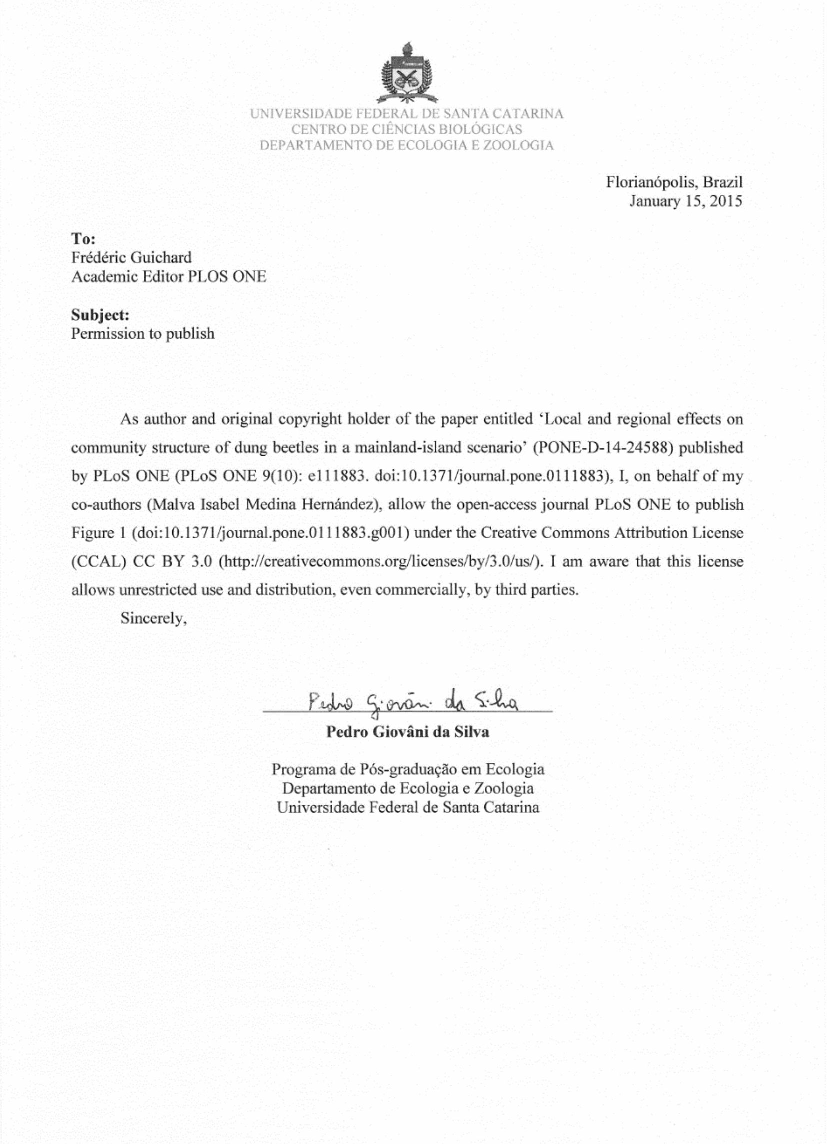
S1 Fig. Rank abundance curve of dung beetle metacommunity (two years). Abundances are expressed as the percentage of the total abundance within the metacommunity. The dotted line indicates the inflection point of the curve used to classify the species into common or rare.



S2 Fig. Relation between number of species and number of individual of each functional group of dung beetles.



S3 Fig. Permission letter. Permission request to publish Fig. 1.



UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
DEPARTAMENTO DE ECOLOGIA E ZOOLOGIA

Florianópolis, Brazil
January 15, 2015

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Subject:
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Sincerely,

Pedro Giovâni da Silva

Pedro Giovâni da Silva

Programa de Pós-graduação em Ecologia
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S1 Table. Dung beetle traits. Identity and traits for 28 dung beetle species sampled in the Atlantic Forest from southern Brazil. NA: unavailable data. Other: unknown, but different from others.

Species	Food relocation habit	Trophic guild	Activity period	Mean biomass (g)
Bdelyrus braziliensis	Other1	Saprophage	NA	0.0115
Canthidium aff. *lucidum*	Paracoprid	Necrophage	Diurnal	0.0268
Canthidium aff. *sulcatum*	Paracoprid	Generalist	Diurnal	0.0228
Canthidium aff. *trinodosum*	Paracoprid	Coprophage	Diurnal	0.0088
Canthon luctuosus	Telecoprid	Necrophage	Diurnal-Nocturnal	0.0118
Canthon rutilans cyanescens	Telecoprid	Generalist	Diurnal	0.0462
Canthonella aff. *instriata*	Telecoprid	Generalist	Diurnal	0.0024
Canthonella catharinensis	Telecoprid	Coprophage	Diurnal	0.0005
Coprophanaeus dardanus	Paracoprid	Necrophage	Diurnal-Nocturnal	0.6227
Coprophanaeus saphirinus	Paracoprid	Necrophage	Diurnal	0.3362
Deltochilum brasiliense	Telecoprid	Generalist	Nocturnal	0.4109
Deltochilum furcatum	Telecoprid	Generalist	Nocturnal	0.2819
Deltochilum morbillosum	Telecoprid	Necrophage	Diurnal-Nocturnal	0.0738
Deltochilum multicolor	Telecoprid	Necrophage	Diurnal-Nocturnal	0.1697
Deltochilum rubripenne	Telecoprid	Necrophage	Diurnal	0.1000
Dichotomius aff. *pygidialis*	Paracoprid	Generalist	Nocturnal	0.0783
Dichotomius assifer	Paracoprid	Coprophage	Nocturnal	0.2212
Dichotomius mormon	Paracoprid	Coprophage	Nocturnal	0.3843
Dichotomius quadrinodosus	Paracoprid	Coprophage	Nocturnal	0.5101
Dichotomius sericeus	Paracoprid	Generalist	Nocturnal	0.1596
Dichotomius sp.	Paracoprid	Coprophage	Nocturnal	0.0688
Eurysternus cyanescens	Endocoprid	Generalist	Diurnal-Nocturnal	0.0469
Eurysternus parallelus	Endocoprid	Coprophage	Diurnal-Nocturnal	0.0442
Ontherus azteca	Paracoprid	Coprophage	Nocturnal	0.0200
Paracanthon aff. *rosinae*	Telecoprid	Generalist	Nocturnal	0.0124
Phanaeus splendidulus	Paracoprid	Coprophage	Diurnal	0.2199
Uroxys sp. 1	Other2	Generalist	Nocturnal	0.0046
Uroxys sp. 2	Other2	Generalist	Nocturnal	0.0023

S2 Table. Summary of environmental variables. Averages (mean or median, as appropriate), quartiles, minimum and maximum values. 25%: 25 percentile, 75%: 75 percentile; max: maximum recorded for the entire dataset.

	Average	Min	Max	25%	75%
Basal area of first tree (cm^2)	111.88	25.08	431.76	55.31	137.59
Height of first tree (m)	9.41	3.18	21.25	7.39	10.98
Top diameter of first tree (m)	4.99	2.67	13.13	3.99	5.5
Distance to first tree (m)	2.29	0.79	3.76	1.84	2.72
Basal area of greater tree (cm^2)	774.68	110.42	2775.06	348.41	880.79
Height of greater tree (m)	15.68	9.25	28.5	12.75	17.66
Top diameter of greater tree (m)	8.31	3.88	16.25	6.75	9.41
Distance to greater tree (m)	5.2	2.03	8.51	4.26	6.14
Basal area of first shrub (cm^2)	5.39	0.61	33.46	2.43	5.93
Height of first shurb (m)	2.55	1.28	5.18	2	3.05
Top diameter of fisrt shrub (m)	1.14	0.5	2.3	0.88	1.35
Distance to first shrub (m)	1.06	0.23	1.83	0.81	1.31
Land slope (º degrees)	20.1	5.5	36.5	15.25	24.5
Leaf litter cover (%)	91.25	50	97.5	85	97.5
Green cover (%)	37.5	2.5	85	15	37.81
Exposed soil (%)	8.75	2.5	50	2.5	15
Height of leaf litter (cm)	3.29	0.98	10.48	2.43	3.83
Canopy cover (%)	91.25	62.5	97.5	85	97.5
Dry biomass of leaf litter (g)	2.66	0.95	7.46	1.81	3.23
Altitude (m)	127.51	28	265	77.5	176

S3 Table. List of Scarabaeine dung beetles species and total captures per years and area. ANH: Environmental Protection Area of Anhatomirim in Governador Celso Ramos (mainland); ITA: Permanent Protection Area of Itapema (mainland); PER: Lagoa do Peri Municipal Park, Florianópolis (island); RAT: Permanent Protection Area of Ratones, Florianópolis (island). T: total; GT: grand total.

Species	2012				T	2013				T	GT
	ANH	ITA	PER	RAT		ANH	ITA	PER	RAT		
Bdelyrus braziliensis	1				1						1
Canthidium aff. *lucidum*						2	3	6	1	12	12
Canthidium aff. *sulcatum*									1	1	1
Canthidium aff. *trinodosum*	35	25	102	220	382	30	29	17	132	208	590
Canthon luctuosus		3	5	11	19		8	12	12	32	51
Canthon rutilans cyanescens	139	134	128	159	560	158	268	216	98	740	1300
Canthonella aff. *instriata*	1	2	2	3	8	4	8		8	20	28
Canthonella catharinensis									2	2	2
Coprophanaeus dardanus		5			5		29			29	34
Coprophanaeus saphirinus	24	90	58	69	241	17	61	9	54	141	382
Deltochilum brasiliense		1	1	7	9		11	2	3	16	25
Deltochilum furcatum		6			6		73			73	79
Deltochilum morbillosum	40	43	82	76	241	30	64	61	51	206	447
Deltochilum multicolor	35	36	29	23	123	31	36	23	17	107	230
Deltochilum rubripenne	3		19	46	68	8		6	30	44	112
Dichotomius aff. *pygidialis*							4	1	3	8	8
Dichotomius assifer						1				1	1
Dichotomius mormon							2			2	2
Dichotomius quadrinodosus		1			1						1
Dichotomius sericeus	194	33	221	744	1192	185	70	264	410	929	2121
Dichotomius sp.				1	1						1
Eurysternus cyanescens	5				5	7				7	12
Eurysternus parallelus			2	1	3		1	3	2	6	9
Ontherus azteca							1			1	1
Paracanthon aff. *rosinae*			3	1	4				2	2	6
Phanaeus splendidulus	10	1	1	14	26	15	6	14	13	48	74
Uroxys sp. 1			6	102	108			34	121	155	263
Uroxys sp. 2				1	1						1
Number of individuals	487	380	659	1478	3004	488	674	668	960	2790	5794
Number of species	11	13	14	16	21	12	17	14	18	24	28

DISCUSSÃO GERAL

Os resultados demonstraram: (i) associações significativas das espécies de Scarabaeinae com determinadas características ambientais dentro do gradiente ecológico estudado em áreas de Mata Atlântica, sugerindo que mudanças ambientais, sutis e dentro do mesmo tipo de ecossistema, podem ser importantes para determinar a variação espacial das espécies de Scarabaeinae (Artigo I); (ii) efeitos ambientais e espaciais (estes últimos representando a dispersão das espécies) na composição, abundância e biomassa de Scarabaeinae são dependentes da escala de estudo, onde a variação na heterogeneidade ambiental é importante na menor (sítios) e maior escala (continente-ilha), enquanto que o efeito espacial é mais importante em escalas intermediárias, embora também presente na maior escala (Artigo II); (iii) que diferenças na taxa de movimentação entre as espécies de Scarabaeinae parecem relacionadas a diferentes traços ecológicos, sugerindo que pode haver diferenças importantes na capacidade de dispersão das espécies e, consequentemente, na estruturação das comunidades locais (Artigo III); (iv) que a importância dos efeitos ambientais, espaciais e temporais é dependente da escala quando analisada a diversidade funcional e a comunidade desconstruída em grupos de espécies, sendo que grupos formados por diferentes espécies podem apresentar respostas similares a estes efeitos (Artigo IV).

O entendimento da importância da escala espacial na ecologia de comunidades tem aumentado consideravelmente, especialmente nas últimas décadas (MENGE & OLSON, 1990; RICKLEFS & SCHLUTER, 1993). A escala espacial é uma questão chave em estudos ecológicos, pois muitos padrões encontrados nas comunidades e os processos envolvidos na geração destes padrões são dependentes da escala (LEVIN, 1992), exibindo uma variabilidade espacial e temporal da escala local à continental (HUTTUNEN et al., 2014). A escala espacial possui dois componentes: *grain*, que se refere à resolução ou tamanho da unidade amostral, e *extent*, que é o tamanho da região compreendendo todas as unidades amostrais do estudo (WIENS, 1989). Vários estudos têm demonstrado que mudanças em ambos os componentes da escala espacial podem causar mudanças na diversidade beta das comunidades em estudo (GERING & CRIST, 2002; BARTON et al., 2013; HEPP & MELO, 2013). Tais mudanças podem estar relacionadas com a habilidade de dispersão das espécies, que por sua vez podem determinar a extensão espacial na qual os processos ambientais (e.g. *species sorting*) e espaciais (e.g. *mass effects* ou limitação da dispersão) são mais importantes (HEINO et al., 2015b). Além disso, identificar a extensão das escalas onde a estrutura da paisagem possui seu maior efeito nas comunidades (resposta à variação ambiental ou limitação de dispersão) é importante para o entendimento da relação espécie-paisagem (JACKSON & FAHRIG, 2014) e suas consequências para a manutenção da diversidade e funções ecossistêmicas.

O papel da diferenciação de nicho tem sido por muito tempo atribuído como essencial para a manutenção da biodiversidade em diferentes escalas (CHESSON, 2000; CHASE & LEIBOLD, 2003; LEIBOLD & MCPEEK, 2006). Esta diferenciação está fortemente relacionada com a heterogeneidade ambiental e seu efeito na dinâmica populacional e interações entre espécies (CHASE & LEIBOLD, 2003). Algumas espécies podem habitar apenas determinados tipos de hábitats enquanto outras conseguem habitar vários tipos de ambientes, fazendo com que o resultado da interação entre espécies possua maior ou menor peso em diferentes escalas espaciais (LEIBOLD et al., 2004). Além disso, a diferenciação de nicho faz com que a espécie limite sua própria população mais do que a de outras espécies, promovendo a coexistência (CHESSON, 2000), muitas vezes de espécies com nicho semelhante. Os resultados deste estudo mostraram que várias espécies de Scarabaeinae estiveram associadas a determinadas condições ambientais dentro das áreas estudadas de Mata Atlântica, o que gerou os maiores valores de diversidade beta na maior e menor extensão espacial.

A estruturação das comunidades pode ser vista como um contínuo de combinações de mecanismos estabilizadores de nicho e diferenças de aptidão entre espécies (MATTHEWS & WHITTAKER, 2014), onde algumas (ou todas) podem ser consideradas equivalentes (HUBBELL, 2001). A visão anteriormente predominante de que nicho e processos neutros são mutuamente excludentes é uma “falsa dicotomia” (LEIBOLD & MCPEEK, 2006; ADLER et al., 2007) e ignora a possibilidade que os dois tipos de processos atuem juntos e complementarmente na estruturação das comunidades (HUBBELL, 2001). Esta visão permaneceu por muito tempo porque a teoria do nicho tem seu foco principal na escala local e a dinâmica de montagem das comunidades torna-se diferente quando os efeitos regionais são considerados (CHASE & LEIBOLD, 2003; LEIBOLD et al., 2004), levantando duas falsas premissas: (1) de que modelos neutros e de nichos são mutuamente excludentes e (2) que a diferenciação de nicho é importante somente na escala local (LEIBOLD & MCPEEK, 2006). Os resultados deste estudo mostraram que a maior diversidade beta de Scarabaeinae esteve associada à maior extensão espacial onde o principal direcionador da estruturação das comunidades foi a variação nas condições ambientais nesta ampla escala espacial. A heterogeneidade ambiental encontrada dentro de diferentes áreas de Mata Atlântica pode limitar a ocorrência das espécies de Scarabaeinae em um contexto espacial amplo.

A heterogeneidade ambiental proporciona uma variedade de recursos que tornam possível a coexistência entre competidores, a qual poderia não existir em um ambiente homogêneo (LEVIN, 1970; HORN & MACARTHUR, 1972). A coexistência requer que as espécies respondam à heterogeneidade ecológica de diferentes modos, e estas diferenças são geralmente o resultado de *trade-offs* na habilidade das espécies em interagir com diferentes condições e características ambientais (LEIBOLD & MCPEEK, 2006). Além disso, espécies ecologicamente similares são frequentemente mais prováveis de coexistir, especialmente quando há similaridade relacionada aos traços ecológicos que afetam o modo como elas respondem ao ambiente (CHASE & LEIBOLD, 2003; LEIBOLD & MCPEEK, 2006). Estas premissas estão incorporadas no paradigma *species sorting* da teoria de metacomunidades (LEIBOLD et al., 2004; HOLYOAK et al., 2005; LOGUE et al., 2011). Como encontrado nos artigos II e IV, o modelo *species sorting* tem sido atribuído como o mais importante em escalas pequenas (COTTENIE, 2005; SOININEN, 2014). Há, contudo, uma crescente necessidade em separar o papel relativo das interações entre espécies e da heterogeneidade ambiental na explicação do modelo *species sorting* na estruturação das comunidades locais (NOVAK, 2014). Assim como a heterogeneidade ambiental e a dispersão, as interações bióticas são importantes forças estruturadoras das comunidades locais (GRAY et al., 2012; GÖTHE et al., 2013) e seu papel relativo dentro do modelo *species sorting* tem sido pouco investigado, possivelmente pela dificuldade em medir interações bióticas (SIQUEIRA et al., 2012).

A taxa de dispersão também é esperada ser dependente da escala (NG et al., 2009). Porém, seus efeitos podem passar despercebidos porque o comprimento dos gradientes ambientais pode aumentar com o incremento da extensão espacial do estudo (i.e. resolução ou tamanho da região contendo todas as unidades amostrais [WIENS, 1989]) (HEINO et al., 2015a). Em ambientes aquáticos, a importância relativa dos processos ecológicos estruturadores das comunidades locais depende muito da habilidade de dispersão dos organismos (BEISNER et al., 2006; DE BIE et al., 2012; HEINO, 2013; PADIAL et al., 2014). Contudo, a dispersão das espécies pode gerar efeitos mascarados da importância de processos ambientais pelas escalas estudadas (LEIBOLD et al., 2004; NG et al., 2009; WINEGARDNER et al., 2012; HEINO & PECKARSKY, 2014), pois tanto a alta dispersão nas menores escalas (*mass effects*) e a limitação da dispersão nas maiores escalas dissociam as espécies e o ambiente, o que afeta a relação diversidade beta-heterogeneidade ambiental (HEINO et al., 2015a). Dessa forma, o modelo *species sorting* pode ser mais bem distinguido dos demais quando houver uma quantidade intermediária e suficiente de dispersão que permita às espécies acompanhar as mudanças ambientais (HEINO et al., 2015a, 2015b). Os resultados do Artigo III sugerem que várias espécies de Scarabaeinae possuem uma considerável habilidade de movimentação, o que permitiria que elas pudessem rastrear as mudanças ambientais, mesmo que sutis, dentro das áreas de Mata Atlântica.

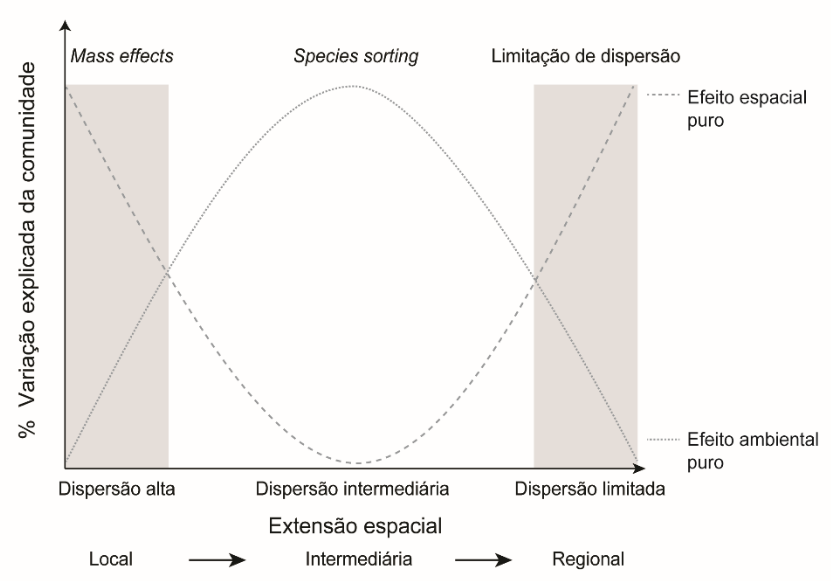
Espera-se que a importância do modelo *species sorting* e da dispersão (limitação ou homogeneização) sejam semelhantes em ecossistemas terrestres tais como ambientes florestais (Figura 4). Contudo, na Mata Atlântica do sul do Brasil a organização das comunidades de Scarabaeinae apresentou um padrão diferente do encontrado para metacomunidades de diferentes organismos aquáticos (e.g. HEINO & PECKARSKY, 2014; HEINO et al., 2015b). Na menor extensão espacial (sítios), não foi encontrado efeito espacial. O efeito espacial foi mais importante do que o ambiental somente na escala intermediária (áreas), mas também foi importante na maior extensão espacial (continente-ilha), embora em menor importância relativa que o efeito ambiental quando considerada a composição, abundância e biomassa de Scarabaeinae (Artigo II). Padrão semelhante foi encontrado para vários grupos de espécies quando a comunidade foi desconstruída (Artigo IV). Como demonstrado no Artigo III, as espécies de Scarabaeinae diferem em sua capacidade de movimentação/dispersão e, dessa forma, o efeito homogeneizador do modelo *mass effects* pode não ocorrer na menor extensão espacial estudada (sítios) devido a maior importância da variação nas condições ambientais e/ou interações biológicas (e.g. competição). Assim, o efeito do modelo *species sorting* parece ser preponderante sobre os efeitos da dispersão na menor e maior extensão espacial. É claro que a extensão espacial total do estudo pode ter incluído diferentes *pools* de espécies, especialmente entre continente e ilha, os quais podem ter sido moldados por diferentes fatores evolutivos (PERES-NETO et al., 2012), incluindo eventos recentes de especiação e efeitos de barreiras geográficas (LEIBOLD et al., 2010), como ocorreu com a elevação do nível do Oceano Atlântico que criou uma barreira entre continente e ilha no sistema estudado. Dissociar o papel de eventos históricos dos processos atuais que moldam as comunidades locais está entre as demandas dos futuros estudos sobre metacomunidades (HEINO et al., 2015b).

A alta importância relativa do efeito espacial em relação ao ambiental encontrada na escala intermediária poderia ser considerada em parte efeito do modelo *mass effects* (HEINO et al., 2015b). Para isso, teríamos de assumir que a distância entre os sítios dentro de cada uma das quatro áreas não limitaria a dispersão das espécies de Scarabaeinae, uma vez que todas fariam parte da mesma área e não haveria barreira à dispersão, o que causaria um efeito homogeneizador das comunidades locais em cada área. A diversidade beta média entre sítios foi a segunda maior, considerando todos os sítios, devido basicamente à presença de espécies ‘raras’. Se considerarmos apenas os sítios dentro de cada área a diversidade beta média é menor, o que pode sugerir efeito do modelo *mass effects* nesta escala espacial. Contudo, o modelo *mass effects* nesta escala não explica o maior efeito do modelo *species sorting* na menor escala espacial. Havendo homogeneização da comunidade na escala intermediária, poderíamos esperar que as comunidades locais de Scarabaeinae também apresentassem um efeito espacial na menor escala, o que não ocorreu. Por outro lado, a elevada dispersão prevista pelo modelo *mass effects* na escala intermediária e a ausência do efeito espacial na menor extensão espacial (i.e. menores distâncias) podem indicar que a menor escala espacial é adequada para permitir dispersão suficiente para que as espécies possam acompanhar as variações ambientais (i.e. *species sorting*) (HEINO et al., 2015b). Elucidar esta questão é uma demanda futura relacionada com a obtenção de dados mais adequados da capacidade de dispersão das espécies de Scarabaeinae, pois a interpretação do efeito do modelo *mass effects* e da limitação da dispersão deve considerar a extensão espacial do estudo e a distância de dispersão dos organismos estudados (HEINO et al., 2015b).

A dispersão dos indivíduos é um traço ubíquo de qualquer espécie (NOVAK, 2014). Espécies com diferentes traços ecológicos podem possuir distinta capacidade de dispersão. A dispersão tem efeitos importantes para a estruturação das comunidades locais, como a diminuição da competição entre espécies aparentadas (HAMILTON &

MAY, 1977) e a potencial chegada de novos alelos (SZULKIN & SHELDON, 2008). Em contrapartida, a variação espaço-temporal do ambiente tem o potencial de afetar a dispersão. A dispersão é requerida para colonizar sítios novos ou vazios devido a extinções locais. A dispersão pode ser limitada ou promovida devido à heterogeneidade espacial dos hábitats em relação à qualidade do hábitat, expressada pela variação na disponibilidade de recurso ou na capacidade de suporte (NOVAK, 2014). Nesse sentido, há uma interação entre a heterogeneidade ambiental e a capacidade de dispersão, a qual tem sido atribuída como uma das principais forças da estruturação e dinâmica das comunidades locais (HEINO et al., 2015a).

Figura 4 – Esquema do papel relativo dos efeitos puramente ambientais e espaciais na organização das metacomunidades. Adaptado de Heino et al. (2015b), modificado e reproduzido com permissão do primeiro autor (Jani Heino).



Apesar da dificuldade na condução de estudos sobre dispersão (Artigo III), mais esforços devem ser direcionados para o entendimento da capacidade de dispersão das espécies de Scarabaeinae. Este não é um problema somente deste estudo, pois vários autores (ver HEINO et al., 2015b) têm tentado quantificar a dispersão de diferentes espécies de organismos de uma metacomunidade através da utilização de armadilhas e enfrentam a dificuldade de replicação espacial e temporal. Além disso, os dados obtidos representam apenas uma ‘fotografia’ da realidade que ocorre durante o processo de dispersão entre comunidades locais. Uma melhor quantificação da dispersão das espécies que compõem uma metacomunidade em substituição aos métodos que usam *proxies* de dispersão (i.e. valores representativos do efeito da distância espacial na dispersão) até então amplamente utilizados (e.g. análises espaciais de autofunções [PERES-NETO & LEGENDRE, 2010] seguidas de análises de particionamento da variação [PERES-NETO et al., 2006]) também é uma demanda urgente, embora de difícil realização, dos estudos de metacomunidades (HEINO et al., 2015b).

Os resultados dos artigos II e III sugerem que a dispersão não é limitada ao longo dos transectos utilizados para amostrar os escarabeíneos dentro dos sítios de Mata Atlântica (escala local). O efeito espacial apresentou maior importância relativa na escala intermediária, seguido da escala regional. Assumindo que as variáveis ambientais mensuradas sejam aquelas que realmente afetam a distribuição dos escarabeíneos e que nenhuma variável ambiental não mensurada (ou mesmo a influência das interações bióticas [SOININEN, 2014]) apresente uma relação positiva com a distância entre os sítios amostrais dentro das quatro áreas de Mata Atlântica (escala intermediária), é possível assumir que a limitação da dispersão é o principal mecanismo estruturador das comunidades de Scarabaeinae. O efeito espacial também apresentou maior importância relativa do que o efeito ambiental ou temporal para alguns grupos de Scarabaeinae na maior escala (e.g. diurnos e tuneleiros grandes).

Um padrão que se destacou (Artigo II e IV) foi a elevada contribuição da maior e menor escala espacial à diversidade beta, assim como destacado em outros estudos (e.g. DECLERCK et al., 2011; BARTON et al., 2013). A diversidade frequentemente varia dentro do sítio amostral (escala local), entre sítios em uma região (escala intermediária) e entre regiões (escala regional ou geográfica) (MENGE & OLSON, 1990). Contudo, a diversidade beta em escalas espaciais intermediárias parece ser menor em relação às outras escalas, sugerindo que a variação local e o *turnover* em largas escalas (ANDERSON et al., 2011) das espécies de Scarabaeinae são determinados pela variação na heterogeneidade ambiental ao longo do gradiente ecológico estudado. É claro que a limitação da dispersão e processos neutros podem se tornar também importantes conforme o aumento da escala ou extensão espacial (DECLERCK et al., 2011), como encontrado para alguns grupos de espécies de Scarabaeinae (Artigo IV).

Os resultados encontrados no Artigo II mostraram que a maior contribuição à diversidade beta foi encontrada na maior escala espacial – continente-ilha, e que a metacomunidade é, em sua maior parte, determinada pela diversidade beta. Os componentes das escalas espaciais podem ser separados por transições abruptas de escala que ocorrem quando um conjunto de padrões e processos ecológicos é substituído por outro conjunto de padrões e processos (GERING & CRIST, 2002). Estas transições podem afetar o balanço entre a diversidade alfa e beta em determinada escala (WIENS, 1989), causando uma dependência, regular ou irregular, entre os componentes de diversidade (alfa, beta e gama) e a escala espacial (GERING & CRIST, 2002). Esta variação dos componentes da diversidade pelas diferentes escalas pode estar relacionada à mudança nos processos ecológicos dominantes como a interação interespecífica, predominante na escala local, e limitação de dispersão e dinâmicas neutras, predominantes em maiores escalas (GERING & CRIST, 2002).

Medidas de diversidade funcional baseadas nos traços das espécies têm crescido bastante em estudos ecológicos (MASON & BELLO, 2013), sendo utilizadas para investigar a relação entre a biodiversidade e processos ecossistêmicos (MASON et al., 2005). A avaliação da resposta conjunta dos índices de diversidade funcional mostrou que a abordagem de diversidade funcional baseada na distância responde diferentemente aos processos ambientais, espaciais e temporais comparada às medidas tradicionais de abundância e biomassa de Scarabaeinae (Artigo IV). O modelo ambiental foi mais importante do que o modelo espacial, e não houve qualquer efeito temporal na diversidade funcional. Na escala espacial intermediária, a fração compartilhada também foi importante, assim como em outros estudos (COLZANI et al., 2013). A ausência de um efeito temporal pode ser interpretada como um *turnover* temporal não significativo na diversidade funcional, o que pode ser explicado pelo aumento moderado da diversidade beta entre os anos em todas as escalas espaciais. Como demonstrado, os padrões de diversidade funcional podem ser influenciados por fatores ambientais e espaciais (LOREAU et al., 2001; HEINO, 2005; COLZANI et al., 2013) que são dependentes das escalas espaciais. A investigação da importância dos processos ambientais e espaciais na explicação da diversidade funcional através de escalas espaciais é uma abordagem recente (COLZANI et al., 2013; STRECKER et al., 2011) e potencialmente promissora.

A abordagem de desconstrução da comunidade tem sido pouco investigada em estudos envolvendo diferentes escalas espaciais. Este método requer informação sobre os traços ecológicos das espécies, dados das comunidades e dos fatores ambientais amostrados em várias localidades (HEINO & PECKARSKY, 2014). Dividir os dados de espécie-por-sítio em subgrupos baseados nos traços das espécies tem permitido categorizar as espécies em grupos homogêneos, o que pode facilitar a interpretação dos mecanismos causais dos padrões das espécies observados naturalmente (HEINO & PECKARSKY, 2014). Os resultados mostraram que vários grupos de espécies baseados em traços ecológicos distintos mostraram respostas similares aos efeitos ambiental, espacial e temporal pelas escalas estudadas, sendo possível identificar a escala de efeito mais importante para os processos investigados. Sem estimativas precisas da escala de efeito, a avaliação empírica adequada da relação entre a escala de efeito dos processos ecológicos e os traços das espécies pode ser prejudicada (JACKSON & FAHRIG, 2014). Espera-se que a utilização da abordagem de desconstrução da comunidade possa contribuir com novas informações sobre as respostas de grupos de espécies semelhantes em traços biológicos ou ecológicos e, assim, melhorar nosso entendimento da importância dos processos estruturadores das comunidades locais (ALGARTE et al., 2014; HEINO & PECKARSKY, 2014; HEINO et al., 2015b).

Dos 17 grupos avaliados, sete mostraram maior componente de diversidade alfa do que de diversidade beta. Naqueles grupos que mostraram maior componente de diversidade beta foi possível identificar que em geral o componente β3 (continente-ilha) foi maior que β1 (sítios), assim como demonstrado pela comunidade como um todo. Contudo, o maior componente de diversidade beta do que alfa não esteve relacionado com maior efeito espacial na resposta dos grupos pelas escalas espaciais. Assim como para a comunidade como um todo, a maioria dos grupos apresentou maior efeito espacial na escala intermediária e alguns grupos (e.g. noturnos e tuneleiros grandes) mostraram também maior efeito espacial na maior escala. Dez grupos apresentaram efeito temporal significativo pelas escalas espaciais, especialmente o grupo dos tuneleiros de tamanho médio. O efeito temporal também foi maior na menor e maior escala.

O processo temporal teve efeito importante nas três escalas espaciais avaliadas, tanto para a abundância como para a biomassa, e também para vários grupos de Scarabaeinae quando a comunidade foi desconstruída (Artigo IV). Em geral, estudos que testam simultaneamente a importância relativa de processos ambientais, espaciais e temporais são incomuns (ANDERSON & GRIBBLE, 1998). Contudo, efeitos temporais têm recebido recentemente maior atenção em estudos envolvendo metacomunidades, demonstrando um importante efeito tanto para a variação na heterogeneidade ambiental em ecossistemas aquáticos (BELLIER et al., 2014) como para o aumento do efeito da dispersão em escala regional na estruturação das comunidades locais (STOFFELS et al., 2015). O efeito temporal foi mais importante na menor escala, tanto para a abundância como para a biomassa, e para vários grupos de Scarabaeinae. Além da importância da estocasticidade demográfica das espécies (HUBBELL et al., 2001), o efeito da dispersão de indivíduos de comunidades vizinhas pode ser fundamental para a estruturação das comunidades locais de Scarabaeinae, uma vez que a heterogeneidade ambiental se manteve a mesma entre os sítios amostrados.

Entender os padrões em termos dos processos que os produzem é a essência da ecologia, sendo a chave para o desenvolvimento dos princípios para o manejo dos ecossistemas (LEVIN, 1992). O entendimento da distribuição da diversidade beta pelas escalas espaciais será crucial para melhorar a teoria e a prática conservacionista (BARTON et al., 2013) frente à crescente transformação dos ecossistemas naturais. A grande influência da atividade humana sobre a diversidade biológica aumentou consideravelmente a demanda para uma maior compreensão dos padrões de diversidade e dos processos ecológicos e evolutivos relacionados aos mesmos (DINIZ-FILHO et al., 2009). Neste cenário, tem havido grande necessidade para o entendimento dos mecanismos direcionadores da estabilidade espacial e temporal dos ecossistemas em escalas espaciais que correspondam às escalas de manejo e conservação (WANG & LOREAU, 2014). O entendimento da importância dos processos ecológicos em diferentes escalas espaciais na fauna de um grupo de organismos que desempenha importantes funções ecológicas – como os escarabeíneos, consiste em um primeiro passo ao encontro desse objetivo crucial.

CONCLUSÕES

Várias espécies de Scarabaeinae estiveram associadas a determinadas características ambientais relacionadas à estrutura florestal da Mata Atlântica ou apresentaram associações com determinada área de estudo amostradas no continente e na ilha, demonstrando a importância da distribuição espacial de áreas de Mata Atlântica com características ambientais espacialmente estruturadas para a manutenção e conservação da diversidade gama de Scarabaeinae.

A importância relativa dos processos ecológicos envolvidos na estruturação das comunidades de Scarabaeinae amostradas em áreas de Mata Atlântica no sul do Brasil é dependente da escala espacial (componente extensão espacial). A heterogeneidade ambiental é o principal direcionador da diversidade beta na escala local (sítios) e regional (continente-ilha), enquanto que efeitos espaciais (*mass effects* e/ou limitação da dispersão) são mais importantes em largas escalas, principalmente na intermediária. O aumento da diversidade beta em escala regional parece ser resultante da limitação na capacidade de dispersão das espécies devido à fragmentação do hábitat e à presença de barreiras geográficas, especialmente entre continente-ilha. Em geral, a composição, abundância e biomassa de Scarabaeinae responderam de forma similar aos efeitos ambientais e espaciais.

Espécies com diferentes conjuntos de traços ecológicos parecem apresentar diferenças na habilidade de movimentação dentro da Mata Atlântica e, consequentemente, podem afetar de forma distinta a estruturação das comunidades locais de Scarabaeinae devido à maior ou menor limitação de dispersão. Ao investigar a movimentação das espécies de Scarabaeinae foi possível investigar o protocolo de distância entre armadilhas de queda utilizadas para a captura deste grupo. A nova distância de 100 m entre pares de armadilhas de queda iscadas é sugerida para substituir os 50 m anteriormente propostos por outros autores na amostragem padronizada de Scarabaeinae em florestas tropicais utilizando-se tanto fezes humanas como carne em decomposição como isca atrativa.

A diversidade gama de Scarabaeinae foi atribuída principalmente à diversidade beta como consequência do aumento nas diversidades alfa e beta entre áreas quando comparadas as amostragens realizadas em 2012 e 2013. Índices de diversidade funcional podem ser utilizados como método complementar, mas não substitutivo, para investigar os efeitos ambientais, espaciais e temporais nas comunidades. Ao desconstruir a comunidade, foi possível identificar dois grandes grupos de respostas entre 17 grupos funcionais avaliados. A diferença entre os dois grupos foi basicamente devido à presença ou ausência de efeito temporal significativo. Em geral, filtros ambientais foram importantes nas escalas local e regional. O efeito temporal, quando significativo, ocorreu nas três escalas espaciais estudadas. Fatores espaciais foram mais importantes na escala intermediária, também suportando a noção de dependência da escala dos processos ambientais, espaciais e temporais na distribuição e organização funcional de Scarabaeinae. Os padrões de respostas apresentados pela metacomunidade de Scarabaeinae na Mata Atlântica do sul do Brasil foram distintos aos padrões frequentemente encontrados para sistemas aquáticos (e.g. HEINO & PECKARSKY, 2014; HEINO et al., 2015a, 2015b).

Futuramente, estudos envolvendo a teoria de metacomunidades deverão incorporar processos ambientais, espaciais e temporais em escalas espaciais diferentes e apropriadas para, além de identificar qual das perspectivas da teoria melhor encaixa-se em determinado sistema, também testar as várias hipóteses que embasam tais paradigmas (e.g. heterogeneidade ambiental, interações bióticas, efeito da alta e baixa dispersão). Além disso, a utilização de abordagens diferentes e complementares poderá auxiliar no entendimento da organização das metacomunidades. Entre as demandas futuras estão: (i) uma melhor identificação da importância da interação entre espécies e a diferenciação desta com efeitos ambientais na escala local, (ii) a identificação de traços ecológicos relacionados à dispersão, quando não for possível quantificar a dispersão, os quais facilitarão a análise e identificação de espécies que potencialmente ocupam guildas distintas de dispersão na escala regional, e (iii) análises da relação entre a capacidade de dispersão e de suportar a competição entre as espécies que compõem a comunidade local. Estas respostas auxiliarão a um entendimento mais robusto e baseado nos processos da estruturação e dinâmica das metacomunidades.

As questões relacionadas às escalas espaciais serão sempre a ‘fronteira final’ na ecologia (LEVIN, 1992). A condução de estudos ecológicos em escalas apropriadas que compreendam gradientes ambientais e os processos de dispersão, além de serem adequadas às escalas de manejo e conservação, é um aspecto crucial e importante de pesquisas sobre biodiversidade. Reconhecer a importância da dependência da escala na geração da variação nos padrões e processos é a chave para o avanço da ecologia (HEINO et al., 2015a).

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