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Diversidade e variação morfológica de besouros escarabeíneos no Arquipélago de Santa Catarina, Atlântico sul do Brasil

Florianópolis
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Orientadora: Prof.ª Dr.ª Malva Isabel Medina Hernández

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Eloisa Alves de Sousa

Diversidade e variação morfológica de besouros escarabeíneos no Arquipélago de Santa Catarina, Atlântico sul do Brasil

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

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

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Prof.ª Dr.ª Malva Isabel Medina Hernández
Orientadora

Florianópolis, 2022.

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Avançar na ciência é elaborar novos padrões de pensar, que definirão por sua vez os modelos e os experimentos. Fácil de dizer, difícil de fazer. (WILSON, 1994)

RESUMO

As ilhas reúnem padrões e processos ecológicos, em níveis populacionais e de comunidades, que podem ser delimitados e melhor compreendidos devido às suas condições ambientais e de isolamento específicas. Neste contexto, a biogeografia de ilhas propõe relações entre a colonização de espécies e fatores como área e isolamento das ilhas, enquanto a ecologia de metacomunidades incorpora a existência de fatores como a seleção de espécies e de deriva ecológica em uma escala regional para se pensar a estruturação de comunidades em nível local. Partindo deste arcabouço as hipóteses deste trabalho são: 1) o isolamento faz com que as populações de ilhas menores e mais isoladas apresentem menor probabilidade de chegada de colonizadores, estando mais sujeitas à vicariância refletida em diferenças morfológicas corporais; 2) os fatores ambientais similares nas ilhas fazem com que os fatores geográficos sejam os principais estruturadores da diversidade nessas ilhas. Este trabalho está estruturado em dois capítulos e tem os seguintes objetivos: 1) investigar a existência de variações morfológicas nas populações do besouro escarabeíneo *Canthon rutilans cyanescens* residentes nas ilhas do Arquipélago de Santa Catarina e no continente próximo; e 2) entender quais fatores geográficos e ambientais influenciam a diversidade de besouros escarabeíneos em comunidades de ilhas costeiras de um mesmo arquipélago. Para isto, foram realizadas coletas padronizadas de escarabeíneos, de dados ambientais (vegetação e temperatura) e de fatores geográficos (área e isolamento) em sete ilhas do Arquipélago de Santa Catarina e no continente próximo entre dezembro de 2020 e abril de 2021. No primeiro capítulo, comparou-se o tamanho do corpo de *C. rutilans cyanescens* por meio de uma Análise de Variância e comparou-se a forma do corpo por meio de análises de morfometria geométrica, testando a diferença de forma das diferentes populações através de uma Análise Discriminante com Validação Cruzada, seguida por uma Análise de Variáveis Canônicas para visualização das populações no espaço morfométrico. No segundo capítulo, comparou-se a diversidade alfa e calculou-se a diversidade beta das comunidades, realizando uma análise de partição da mesma. Além disso, gerou-se um Modelo Linear Generalizado tendo como variável resposta a riqueza de escarabeíneos e como variáveis explanatórias: área da ilha, isolamento da ilha, estrutura da vegetação e temperatura do solo. O tamanho corporal foi menor para a população da Ilha Ratones Grande do que para as populações das áreas continentais (Governador Celso Ramos), da Ilha Dona Francisca e da Lagoa do Peri na Ilha de Santa Catarina. Também se observou que a forma do corpo da população da Ilha do Campeche é diferente da população da Ilha do Arvoredo e da população da Ilha de Dona Francisca, com o corpo levemente ovalado, com uma região dorsal maior e o abdome retraído em seus indivíduos. Em relação à diversidade, a riqueza de espécies de escarabeíneos foi positivamente relacionada ao tamanho das ilhas, sendo semelhante para as comunidades das áreas continentais e das áreas da maior ilha estudada, a Ilha de Santa Catarina. A dissimilaridade da diversidade entre as ilhas se deu principalmente por conta do aninhamento de espécies, indicando que as espécies encontradas em ilhas menores são um subconjunto das espécies encontradas nas ilhas maiores e no continente. Assim, os resultados dos dois capítulos nos levam a considerar a hipótese de que as espécies encontradas nas ilhas tenham permanecido lá desde a formação destas ilhas depois do Último Máximo Glacial e que o número de espécies em cada ilha foi diminuindo devido às dinâmicas internas de competição por recursos, de acordo com o tamanho da área destas. O isolamento geográfico e a ausência de conectividade entre as populações explicariam o porquê de algumas ilhas apresentarem populações com morfologia distinta.

Palavras-chave: Biogeografia de ilhas. Ecologia de comunidades. Morfometria geométrica. Scarabaeinae. Tamanho corporal.

ABSTRACT

Islands gather ecological patterns and processes, at population and community levels, that may be delimited and better understood due to their specific environmental and isolation conditions. In this context, island biogeography proposes relationships between species colonization and factors such as area and island isolation, while metacommunity ecology incorporates the existence of factors such as species selection and ecological drift on a regional scale to think about the structuring of communities at the local level. Based on this framework, the hypotheses of this work are that: 1) isolation causes populations of more isolated and smaller islands to have a lower probability of arrival of colonizers, being more subject to vicariance reflected in body morphological differences; 2) similar environmental factors in the islands of the archipelago make geographic factors the main structuring factors of diversity in the islands. This work is structured in two chapters and has the following objectives: 1) to investigate the existence of morphological variations in the populations of the dung beetle *Canthon rutilans cyanescens* residing on the islands of the Santa Catarina Archipelago and on the nearby continent; and 2) understand which geographic and environmental factors influence the diversity of dung beetles in communities on coastal islands of the same archipelago. For this, standardized collections of dung beetles, environmental data (vegetation and temperature) and geographic factors (area and distance) were carried out on seven islands of the Santa Catarina Archipelago and on the nearby mainland between December 2020 and April 2021. In the first chapter, the body size of *C. rutilans cyanescens* was compared by an Analysis of Variance (ANOVA) and the body shape was compared by geometric morphometric analyses, testing the difference in shape of the different populations through a Discriminant Analysis with Cross Validation, followed by a Canonical Variable Analysis (CVA) to visualize the populations in the morphometric space. In the second chapter, the alpha diversity was compared, and the beta diversity of the communities was calculated, followed by a beta diversity partitioning analysis. In addition, a Generalized Linear Model (GLM) was calculated with the response variable of dung beetle richness and as explanatory variables island area, island isolation, vegetation structure and soil temperature. Body size was smaller for the population of the Ratones Grande Island than the populations of the continental areas (Governador Celso Ramos), Dona Francisca Island and the site of Peri in Santa Catarina Island. It was also observed that the body shape of the population of Campeche Island is different from the population of Arvoredo Island and the population of Dona Francisca Island, with a slightly oval body, with a larger dorsal region and a retracted abdomen in their individuals. In terms of diversity, dung beetle species richness was positively related to the size of the islands, being similar for the communities of the mainland areas and the areas of the largest studied island, Santa Catarina Island. The dissimilarity of the diversity between the islands was mainly because of nestedness, indicating that the species found on smaller islands are a subset of the species found on the larger islands and on the mainland. Thus, together, the results of the two chapters lead us to consider the hypothesis that the species found on the islands have remained there since the formation of these islands after the Last Glacial Maximum and that the number of species on each island has been decreasing due to internal dynamics of competition for resources, according to the size of their areas. Geographic isolation and lack of connectivity between populations are likely explanations for why some islands have populations with distinct morphology.

Keywords: Island biogeography. Community ecology. Geometric morphometric. Scarabaeinae. Body size.

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APRESENTAÇÃO

Estudos em ecologia se preocupam em compreender os padrões e processos que estruturam a biodiversidade ao longo do planeta, utilizando análises em diversas escalas de organização biológica, espaço e tempo. Nesse contexto, as ilhas reúnem dinâmicas de comunidades e de populações sob isolamento geográfico que servem de modelo para se testar teorias evolutivas, biogeográficas e ecológicas (Vitousek 2002). Uma das teorias ecológicas que mais contribuiu com os estudos sobre a estruturação das comunidades e a conservação da biodiversidade foi a Teoria da Biogeografia de Ilhas de MacArthur & Wilson (1967), onde se prevê um equilíbrio dinâmico das taxas de imigração e extinção em ilhas. Esta teoria relaciona a influência do contexto geográfico com a dinâmica de colonização e extinção de espécies, prevendo que a riqueza de espécies depende tanto do isolamento, que controla a taxa de imigração de organismos vindos do continente, quanto de sua área disponível, que controla a taxa de extinção de espécies na ilha.

O desenvolvimento da Teoria de Biogeografia de Ilhas permitiu sua aplicação em áreas como ecologia da paisagem, metapopulações e metacomunidades, pensando a dispersão entre ilhas ou manchas e propondo mudanças nas taxas de colonização e extinção ao longo do tempo via processos estocásticos. A ecologia de metacomunidades surge como um novo nível hierárquico de organização da biodiversidade que estuda os padrões e propriedades regionais emergentes da integração das comunidades (Holyoak et al. 2005), reunindo em uma mesma estrutura conceitual os processos de dispersão, filtragem ambiental, interações bióticas e deriva ecológica (Leibold et al. 2004, Vellend 2010). Podendo ser definida como um conjunto de comunidades locais ligadas pela dispersão de espécies que potencialmente interagem entre si (Leibold et al. 2004), a organização de uma metacomunidade pode ser descrita dentro de um *continuum* de comunidades conectadas por diferentes combinações de processos regionais. Este *continuum* parte da alocação de espécies (*species sorting*), onde as dinâmicas internas de competição e características de nicho das espécies são importantes e se encerra no modelo neutro (*neutral*) onde a deriva ecológica e os processos estocásticos de dispersão são mais importantes do que os processos determinísticos de seleção de espécies, tendo ainda, a dinâmica de manchas (*patch dynamics*) e o efeito de massa (*mass effect*) como variações intermediárias onde a dinâmica interna de seleção de espécies e a dispersão são consideradas com diferentes pesos em seus modelos (Leibold et al. 2004; Cottenie 2005). Estes quatro modelos de metacomunidades não são mutuamente exclusivos, podem ocorrer em uma mesma metacomunidade através de um balanço entre seus processos (Leibold et al. 2004, Chase and Bengtsson 2010) e são úteis para se acessar a origem e manutenção da variação da diversidade entre comunidades pois atribuem pesos diferentes para a importância das limitações de dispersão, heterogeneidade ambiental, interações bióticas e abióticas na coexistência local das espécies (Gianuca et al. 2013). A variação nestes arranjos regionais de metacomunidades onde as comunidades estão inseridas têm influência sobre os padrões de montagem ou estruturação de comunidades locais e sobre as populações que constituem cada uma destas comunidades (Leibold et al. 2004).

Os padrões de diversidade de espécies numa escala regional, compartilhada por várias comunidades, podem ser explicados pelo *pool* regional de espécies, pela capacidade de dispersão ou colonização destas e pelos filtros ambientais e abióticos pelos quais as espécies precisam passar na região para chegar a uma determinada localidade (Mittelbach and Schemske 2015). Já os padrões de diversidade em escala local, na escala de uma mesma comunidade, são um reflexo do nicho realizado das espécies, limitado tanto pelas barreiras geográficas e habilidades de colonização de cada espécie, quanto pelos filtros ambientais do local em questão (Hutchinson 1957, Soberón 2007, Mittelbach and Schemske 2015), levando em conta ainda os eventos de interações entre espécies, como a competição ou a coexistência produto da partição de nicho, assim como as interações mutualísticas e relações tróficas. Desta forma, a ocorrência de espécies em ilhas pode estar associada à capacidade destas se dispersarem através do mar que circunda as ilhas e que atua como um filtro ambiental.

O oceano se apresenta como uma barreira à dispersão em diferentes graus, que varia de acordo com os táxons, assim, indivíduos que se movimentam por locais com diferentes habitats ou a maiores distâncias podem possuir características distintas de indivíduos que não realizam tal dispersão (Da Silva and Hernández 2015). Além disso, a dispersão nem sempre se dá de forma ativa, uma vez que também existem eventos de dispersão passiva, nos quais o indivíduo é dispersado por agentes externos para longe do seu habitat natural (Scholtz et al. 2009, Lee et al. 2015). Assim, os eventos de dispersão ativa de espécies em ilhas estão relacionados, principalmente com as suas habilidades de dispersão. Já os casos de dispersão passiva de animais em ilhas estão essencialmente relacionados com eventos de deriva ecológica, ou seja, com a probabilidade de chegada de fontes de dispersão na ilha (e.g. objetos flutuantes), que por sua vez, está associada ao tamanho e o isolamento de cada ilha. Em comunidades de ilhas continentais, a vicariância pode explicar a variação morfológica de populações que vivem nas ilhas e apresentam características distintas de sua população de origem. A vicariância encontrada em ilhas costeiras sob isolamento, ou seja, ilhas que já tiveram uma conexão pretérita com o continente e não recebem colonizadores com frequência pode culminar até mesmo na formação de espécies relictas ou paleo-endêmicas para a biota originalmente compartilhada com o continente (Gillespie and Roderick 2002, Brown and Lomolino 2006). Desse modo, as populações insulares podem apresentar variação marcante em forma e tamanho do corpo, atributos facilmente reconhecíveis e mensuráveis, que podem ser desencadeados a partir de condições de isolamento geográfico.

Pesquisas em ilhas são de grande relevância para o estudo da biodiversidade, já que os ecossistemas insulares abrigam mais de 20% das espécies de vertebrados e plantas terrestres, apesar de ocuparem apenas 5% da área terrestre global, e são ambientes altamente ameaçados, com grande ocorrência de espécies endêmicas (Courchamp et al. 2014). Sabe-se que as mudanças no nível do mar ocasionadas pelo último ciclo glacial, durante o Pleistoceno, provocaram alterações na dinâmica de ilhas, seja de clima, altitude, área e isolamento, afetando sua conectividade, fontes de espécies e ritmos de colonização (Fernández-Palacios 2016). As mudanças climáticas previstas para o Antropoceno e seu consequente aumento do nível do mar também tem potencial para influenciar o clima, a altitude e a dinâmica das ilhas, podendo modificá-las ou extingui-las, e até mesmo alterar os processos ecológicos que mantêm a biodiversidade atual nestes ambientes. Desta forma, para embasar ações de conservação e fornecer argumentos científicos para o planejamento de políticas públicas e criação de unidades de conservação, faz-se necessário entender como os padrões atuais de diversidade variam nas ilhas, tanto na escala biogeográfica como de metacomunidades e de populações, elencando quais fatores e processos estão envolvidos.

Ilhas costeiras, ou continentais, são ilhas que fazem parte da plataforma continental, mas que se encontram cercadas pelo mar em virtude de processos de insularização recente devido ao aumento do nível do mar após o último período glacial (Ali 2018). Por conta desta separação recente, as comunidades biológicas nestas ilhas tendem a ser semelhantes ao continente próximo (Gillespie and Roderick 2002, Ali 2017) e tal característica nos permite entender quais fatores estão relacionados com a estruturação da diversidade nestes locais. Neste cenário, o Arquipélago de Santa Catarina é um conjunto de ilhas costeiras que inclui a Ilha de Santa Catarina e mais 25 ilhas que a circundam. Estas ilhas estiveram conectadas ao continente devido ao recuo do nível do mar durante o Último Máximo Glacial, há cerca de 10 mil anos, (Klein et al. 2006, de Mahiques et al. 2010) e atualmente, não ultrapassam 14 Km de distância do continente. Com exceção da Ilha de Santa Catarina, as ilhas do arquipélago, em geral, são ilhas pequenas, menores do que 20 ha.

Os besouros escarabeíneos (Coleoptera: Scarabaeidae: Scarabaeinae) respondem rapidamente a alterações no habitat, como destruição, fragmentação e isolamento, através de mudanças na estrutura de suas comunidades e na organização de suas guildas alimentares (Klein 1989, Halffter et al. 1992, Halffter and Favila 1993, Gardner et al. 2008, Hernández and Vaz-de-Mello 2009). Além disso, por habitarem o solo, os escarabeíneos têm a sua distribuição influenciada por características do solo como a temperatura do solo, o tipo de solo e cobertura vegetal. Estes insetos oferecem vantagens para estudos de diversidade em ilhas por serem de fácil coleta com baixo custo associado, são compatíveis com o uso de protocolos padronizados e suas espécies são de fácil identificação em campo (Gardner et al. 2008). Os besouros desta subfamília são copronecrófagos e usam fezes de mamíferos e carcaça de animais como recurso primário para alimentação e nidificação (Halffter and Matthews 1966). As fezes ocorrem em manchas que são determinadas pela distribuição dos animais que as produzem, caracterizadas por serem recursos efêmeros que podem rapidamente ser removidos ou desidratados (Scholtz et al. 2009). Assim, a estrutura das assembleias de escarabeíneos é fortemente influenciada pela competição por recurso alimentar (Halffter 1991). Apesar da forte competição enfrentada pelas espécies do grupo, diferenças na preferência alimentar, no período de atividade e nas formas de alocação de recursos podem favorecer a alta coexistência de espécies destes besouros (Hanski and Cambefort 1991, Hernández et al. 2019).

Desse modo, a partir da Teoria da Biogeografia de Ilhas e da Teoria de metacomunidades, considerando o Arquipélago de Santa Catarina como cenário e os besouros escarabeíneos como grupo focal, esta dissertação buscou entender os fatores que influenciam a diversidade de espécies em ilhas costeiras e no continente próximo, em diferentes escalas (local e regional), investigando quais são os processos que explicam os padrões de diversidade em comunidades, além de características das populações de besouros escarabeíneos nas ilhas. O trabalho está estruturado em dois capítulos: o primeiro capítulo busca verificar a existência de variações morfológicas entre as populações de besouros escarabeíneos que habitam diferentes ilhas costeiras e o continente próximo; e o segundo capítulo busca compreender quais fatores geográficos (isolamento e área da ilha) e ambientais (estrutura da vegetação e temperatura do solo) contribuem para a estruturação das comunidades de besouros escarabeíneos em ilhas costeiras.

OBJETIVOS

Objetivo Geral

O objetivo desta pesquisa foi investigar a existência de variações morfológicas em populações de escarabeíneos presentes nas ilhas do Arquipélago de Santa Catarina e no continente próximo e descrever e comparar a diversidade de besouros escarabeíneos nestas ilhas, buscando entender quais fatores ambientais e geográficos são estruturantes de suas assembleias.

Objetivos Específicos

Capítulo 1: Evidência do efeito do isolamento na diferenciação morfológica de populações de *Canthon rutilans cyanescens* do Arquipélago de Santa Catarina

(1) Comparar o tamanho e a forma corporal das populações presentes nas diferentes ilhas costeiras e no continente próximo.

Capítulo 2: Diversidade de besouros escarabeíneos relacionada à área de ilhas no Arquipélago de Santa Catarina, Atlântico Sul do Brasil

(2) Descrever e comparar a diversidade alfa (de cada ilha) e beta (dissimilaridade entre ilhas) das assembleias de escarabeíneos nas ilhas costeiras do Arquipélago de Santa Catarina;

(3) Investigar os fatores geográficos e ambientais que influenciam a estruturação das assembleias de escarabeíneos.

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CHAPTER 1: EVIDENCE OF THE ISOLATION EFFECT IN MORPHOLOGICAL DIFFERENTIATION OF *CANTHON RUTILANS CYANESCENS* POPULATIONS ON ISLANDS OF THE SANTA CATARINA ARCHIPELAGO

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ABSTRACT

Islands are systems capable to gather isolation conditions that allow the emergence of morphological changes in populations. Several changes in body size and other morphological traits related to the geographic isolation faced by populations have been recorded for insects on islands. The influence of geographic isolation on insular biota can vary according to the history and classification of the islands and the dispersal ability of each species. This study investigated the existence of morphological variations in the populations of the *Canthon rutilans cyanescens* dung beetle from the islands of the Santa Catarina Archipelago and the nearby mainland. For this purpose, standardized samplings of *C. rutilans cyanescens*, on five islands of the Santa Catarina Archipelago and on the nearby mainland took place between December/2020 and April/2021. With geometric morphometric analyses and ten individuals from each population we compared the body size using an Analysis of Variance and the body shape using a Discriminant Analysis with cross-validation test, followed by a Canonical Variable Analysis to visualize the populations in morphometric space. The results show a significant difference in the body size of the different populations. The population of Ratones Grande Island has smaller individuals than the populations of the mainland (Governador Celso Ramos), Dona Francisca Island, and the Peri on Santa Catarina Island. We also observed that the body shape of the population of Campeche Island differs from the populations of Arvoredo Island and Dona Francisca Island, with a slightly oval body, a larger dorsal region, and a retracted abdomen. These results suggest the hypothesis that the species found on the islands have remained there since their formation after the Last Glacial Maximum. Thus, the geographical isolation and the absence of connectivity between the populations would explain why some islands have populations with distinct morphology.

Keywords: Biogeography. Body size. Coleoptera. Dung beetle. Morphometry.

INTRODUCTION

Morphological changes in populations are often found on islands due to their isolation conditions. (Dennison and Baker 1991, Laparie et al. 2010, Senczuk et al. 2014, Alvial et al. 2019). The morphological changes related to the island's isolation are so well documented that they gave rise to the ‘island rule’, a rule describing dwarfism and gigantism on islands, well established for vertebrates, mainly mammals, but which presents few evidence for invertebrates, such as insects (Palmer 2002, Brown and Lomolino 2006). Despite this, several changes in body size and other morphological attributes related especially to the geographic isolation faced by populations have been recorded for insects on islands (Hayashi 1990, Palmer 2002, Camara et al. 2006, Deidun et al. 2011, Lee and Lin 2012, Benítez et al. 2014, Myers et al. 2017).

The influence of geographic isolation on the insular biota may vary according to the history and classification of the islands since the continental or coastal islands are more subject to processes of vicariance and paleoendemism, due to the separation of original populations through changes that create barriers to the dispersal of previously connected populations. On the other hand, volcanic or oceanic islands are more subject to processes of founder effect and neoendemism, where new individuals disperse to previously uninhabited locations, overcoming pre-existing barriers (Gillespie and Roderick 2002, Brown and Lomolino 2006). Geographic isolation is also related to the immigration rates of individuals in an island, causing the increase in isolation to lead to a reduction in the potential for the arrival of new colonizers (MacArthur and Wilson 1967). The immigration rate tends to be higher on nearby islands, such as on continental or coastal islands or even in large archipelagos, whereas in remote islands, such as volcanic or oceanic islands, the arrival of new colonizers decreases dramatically due to the distance of isolation (MacArthur and Wilson 1967, Brown and Lomolino 2006). Thus, the arrival of colonizers may be mainly associated with active dispersal events related to the dispersal ability of species on nearby islands and more associated with stochastic ecological drift events, such as passive dispersal on remote islands.

The sea level decreased during the Last Glacial Maximum about 21,000 years ago and rise again with the end of glaciation (Klein et al. 2006, de Mahiques et al. 2010). These events allowed the occurrence of vicariance processes, allowing many of the islands that currently exist to remain connected to the mainland due to the decrease of the sea level and later to become isolated again, with the emergence of the marine barrier. Within this context, we have the Santa Catarina Archipelago in the southern region of Brazil, which is composed of coastal islands. There are more than 25 islands, most of which with area of less than 20 ha, with exception of the Santa Catarina Island, which has about 40 thousand ha. These islands, previously connected to the mainland due to the sea level decrease during the Last Glacial Maximum, currently do not exceed 14 km from the mainland. Although coastal islands are close to the mainland, the importance of geographic isolation for connectivity between island populations vary according to the dispersal ability of each species or the frequency of passive dispersal events, such as rafting on floating objects (Peck and Kukalova-Peck 1990, Scholtz et al. 2009, Lee et al. 2015).

The effect of geographic isolation related to morphological changes in body size and shape is well documented for different organisms (Dennison and Baker 1991, Silva et al. 2008, Hernández-Salinas et al. 2014, Senczuk et al. 2014, Trevisan et al. 2014, Ober and Connolly 2015, Lazzarotto et al. 2017, Alvial et al. 2019, Ouisse et al. 2020, Jaskuła et al. 2021), including for insects in insular conditions (Palmer 2002, Camara et al. 2006, Laparie et al. 2010, Deidun et al. 2011, Lee and Lin 2012, Benítez et al. 2014, Sazali et al. 2018). Body size and shape are easily recognizable and measurable traits that can be used as proxy of physiological characteristics and life history of organisms (Mercer et al. 2001). Additionally, these traits are associated with important ecological aspects, such as dispersal ability and intra and interspecific competition (Hernández et al. 2011, Da Silva and Hernández 2015a, b).

A well-established way to evaluate body variations between species or populations is the use of geometric morphometry tools, which gather knowledge in geometry, biology, and multivariate statistics to perform comparative analysis of shape and its associations with causes and effects (Bookstein 1991). Within investigations in geometric morphometry, beetles (Coleoptera) stand out as ideal model organisms for presenting an exoskeleton with well-defined structures that facilitate the positioning of anatomical landmarks (Hernández et al. 2011, Alves and Hernández 2017, 2019), and because they are very abundant, easy to collect and identify (Gardner et al. 2008a). In addition, because they present complete metamorphosis, they offer the advantage of being compared only as adult individuals, thus avoiding ontogenetic variations in shape.

The dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are organisms that occur with great diversity and abundance in the Atlantic Forest of Brazil (Da Silva and Hernández 2016, Hernández et al. 2019). Feeding mainly on animal feces and decaying organic matter (Halffter and Matthews 1966, Halffter and Edmonds 1982), usually they do not actively disperse to distances greater than one kilometer within the same habitat (Arellano et al. 2008, Da Silva and Hernández 2015a), and its main foraging strategy is the “sit and wait” behavior, where individuals remain perched on leaves until the odor trail of the food resource is detected (Halffter and Matthews 1966). Such is the case of *Canthon rutilans cyanescens* Harold, 1868, a diurnal and small-sized species (about 1 cm length), which in a marking and recapture study showed an average daily movement rate of 9 m, found at a maximum distance of only 500 meters in two months (Da Silva and Hernández 2015a). Despite this, there are records of passive dispersal for the group, such as that reported by Darwin, who observed a living “*Scarabaeus*", floating at sea about 40 km from the mouth of the Rio da Prata (Peck and Kukalova-Peck 1990, Scholtz et al. 2009) and of González-Vainer (2015), who found many living individuals of the *Canthon bispinus* dung beetle in the sand of a beach at the mouth of the Prata River after a stormy night, indicating that they had been dispersed by the water fluctuation because they were at the high tide line along with many other insects.

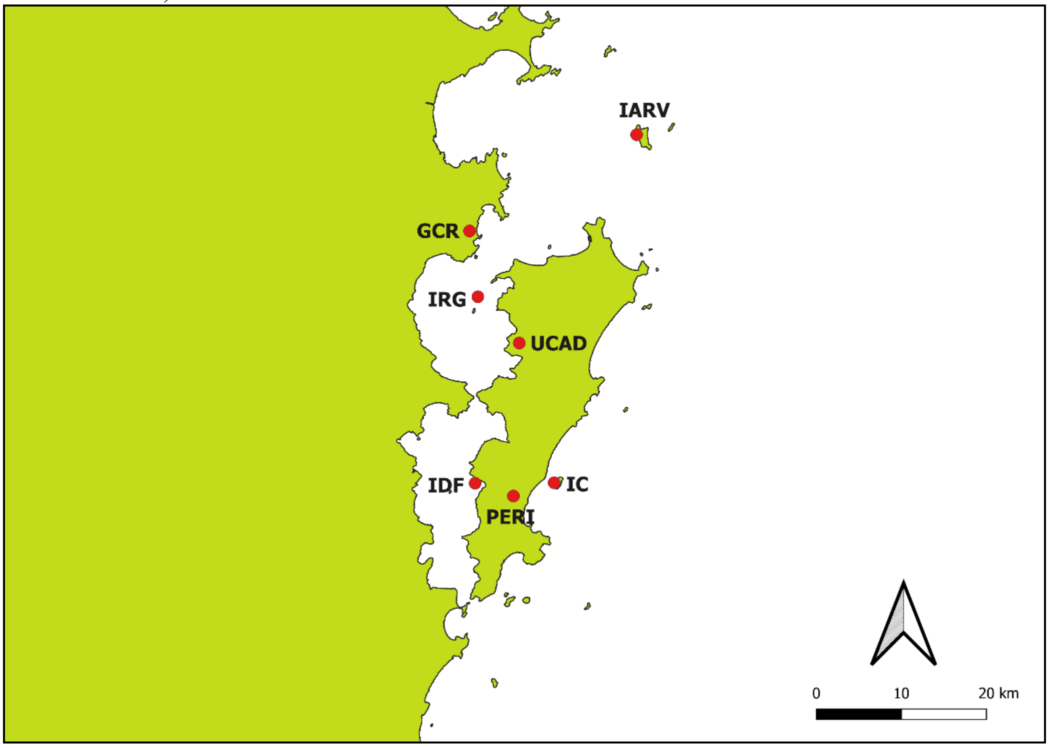
The investigation of the existence of morphological variations, that is, changes in body patterns of size and body shape, in the populations of *Canthon rutilans cyanescens* of the islands of the Santa Catarina Archipelago allows us to test theories related to the geographical isolation between these islands, associated with vicariance processes, because these islands had a direct connection with the mainland during the Last Glacial Maximum and are currently separated from each other by the marine barrier. As the species *C. rutilans cyanescens* does not usually disperse actively over long distances, dispersal events for these islands are expected to be rare and passive, provided mainly by fluctuation in the water or by rafting on logs and other floating objects in floods coming from the mouths of rivers in the region. Thus, the hypothesis of this study is that island populations are subject to vicariance, which is expected to be reflected in morphological differences between populations. Since more isolated islands with smaller coastal areas have a lower probability of arrival of colonizers due to geographical isolation and that less isolated and larger islands have a higher probability of arrival of colonizers, a greater morphological similarity is expected between the populations of more connected islands with a larger surface area and between these and the mainland.

MATERIAL & METHODS

Canthon rutilans cyanescens individuals were collected in a mainland area, Anhatomirim Environmental Protection Area (27°23'48"S, 48°34'2"W) in Governador Celso Ramos – GCR, and in five islands of the Santa Catarina Archipelago that have Dense Ombrophilous Forest vegetation. The island studied were: Santa Catarina Island (42,440 ha), that forming a bay between itself and the mainland, in the Desterro Conservation Unit – UCAD (27°31'50"S, 48°30'46"W), that is in the north 10 km away from the mainland and in the Peri Lagoon Municipal Natural Monument – PERI (27°42'58"S, 48°31'1"O), that is in the south 10.7 km away from the mainland; Ratones Grande Island – IRG (17 ha) situated within the bay, 4.7 km from the mainland and 2.3 km from Santa Catarina Island (27°28'31"s, 48°33'44"W); Dona Francisca Island – IDF (14 ha), also situated within the bay, 6.3 km from the mainland and 0.3 km from Santa Catarina Island (27°41'53"s, 48°33'56"W); Arvoredo Island – ARV (320 ha), the most isolated, situated outside the bay, at a distance of 12.7 km from the mainland and 11 km from Santa Catarina Island (27°16'54"S, 48°22'21"W), and Campeche Island – IC (43 ha), also situated outside the bay, 16 km from the mainland and 1.6 km from Santa Catarina Island (Figure 1.1). These distances were measured in a straight line, counted from the geographic limit of each location to the closest point on the mainland or on Santa Catarina Island. Because they are larger, each site on Santa Catarina Island, UCAD and PERI, as well as the mainland, Arvoredo Island, and Campeche Island, had two sample areas, while the small islands received only one sample area.

Samplings took place from December 2020 to April 2021, except for Arvoredo Island, where they took place from December 2017 to April 2018. In each sample area, standardized dung beetle samplings were performed with 10 traps for live insects, being 5 with domestic dog feces baits (10 g) and 5 with rotten meat baits (10 g). These traps were aligned in a linear transect on the main trail of each island, a few meters away from each other, without showing sample independence from each other. In these areas, a maximum of 10 individuals of *Canthon rutilans cyanescens* were collected per trap and they were sacrificed by freezing and preserved in the Laboratory of Terrestrial Animal Ecology of the Federal University of Santa Catarina (LECOTA/UFSC).

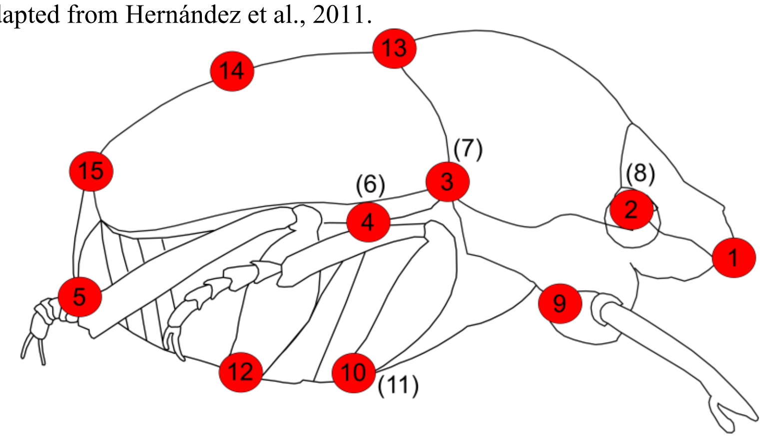
Figure 1.1 – Sampling sites on the mainland: GCR - Governador Celso Ramos; and in the Santa Catarina Archipelago: UCAD – Desterro Conservation Unit, on Santa Catarina Island; PERI – Peri Lagoon Municipal Natural Monument, on Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island, and IDF – Dona Francisca Island.



Ten individuals from each population studied were used for the morphometric analysis and each one of these populations included males and females as equitably as possible (Supplementary Material, Table S1). Photos of the ventral, dorsal, and lateral views of each individual were taken with standardized scale and distances on an Axiocam 105 camera coupled to a Zeiss Stemi 305 stereomicroscope. Based on the work of Hernández et al. (2011), 15 anatomical landmarks were established on the body of individuals, chosen by capturing the morphological variations that describe the body shape of dung beetles on the anteroposterior and ventral-dorsal axis. Each landmark corresponds to a point in space defined by three-dimensional cartesian coordinates (X, Y, Z) that describe geometric positions in space (Bookstein 1991). The landmarks chosen were: 1) anterior margin of the clypeus; 2) eye position; 3) division between the pronotum and the elytra; 4) division between the thorax and abdomen; 5) posterior margin of the abdomen; 9) insertion point of the anterior legs; 10 and 11) insertion points of the medial legs; 12) insertion point of the posterior legs; 13) convergence point between the elytra and pronotum; 14) central point (midline) of convergence between elytra; and 15) posterior margin (along the midline) of the elytra. Points 6, 7, and 8 corresponded to points 4, 3, and 2, respectively, on the opposite side of the body

(Figure 1.2). The anatomical landmarks were captured through the tpsDig2 (Rohlf 2010a) and tpsUtil (Rohlf 2010b) programs.

Figure 1.2 - Anatomical landmarks (red dots) used for building the body shape of *C. rutilans cyanescens* individuals in the side view. Landmarks in parentheses correspond to the same region on the other side of the body. Adapted from Hernández et al., 2011.



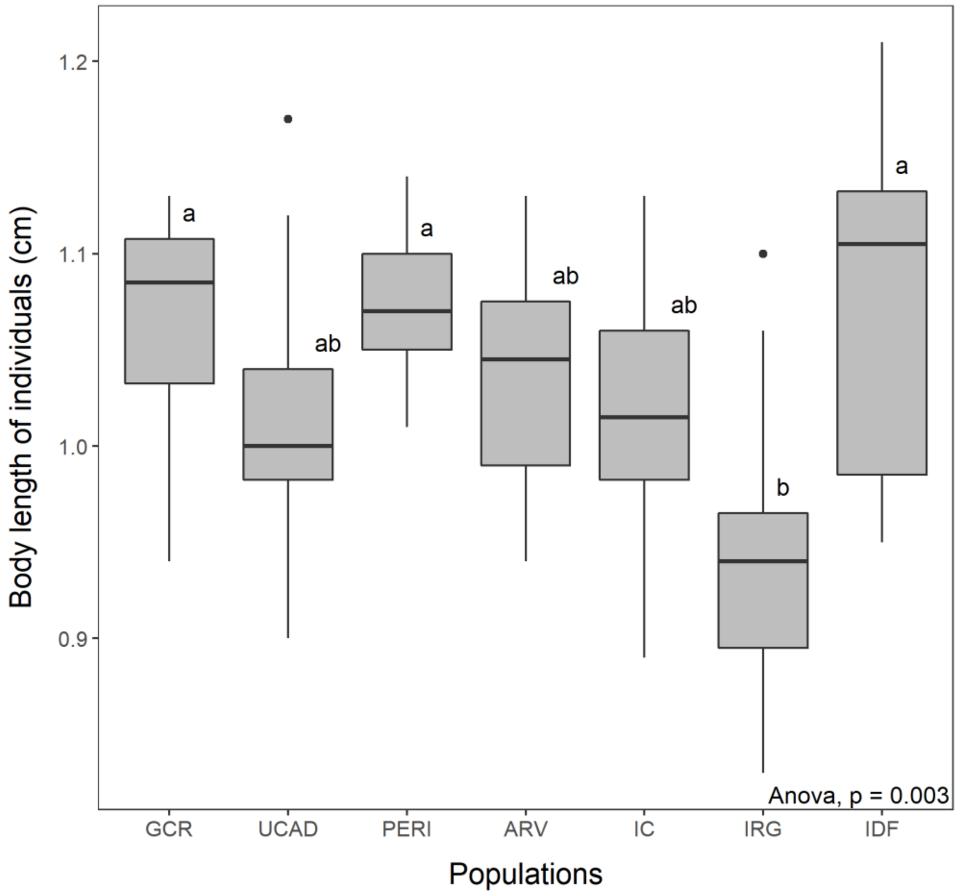
To analyze the variation in body size between populations, the body length of the ten individuals from each population was obtained, measured from the clypeus to the posterior margin of the abdomen from the distance between anatomical landmarks 1 and 5. An analysis of variance (ANOVA) was performed with the length measurements, followed by a Tukey test. To analyze the body shape variation between populations, the cartesian coordinates of each anatomical landmark were subjected to Generalized Procrustes Analysis (GPA), a multivariate analysis consisting of three steps that remove the effects of position, orientation, and size of the analyzed individuals, resulting only in the body shape information. To test the differences in body shape between populations, a Discriminant Analysis (DA) based on Procrustes distances with 1000 permutations was performed, followed by a cross-validation test to verify the reliability of the analysis.

Subsequently, to visualize the position of individuals in the multivariate space and observe the differences between the populations, a Canonical Variable Analysis (CVA) was performed. The GPA and CVA were performed in the MorphoJ program (Klingenberg 2011), while the ANOVAs were performed in the R program, in their specific packages available in version 4.1.2 (R Core Team 2022).

RESULTS

The size of the body of *C. rutilans cyanescens* individuals differed between the populations (ANOVA, $F_{6,63}$=3.75, d.f. =6, p=0.003), and the population of Ratones Grande Island (IRG) has significantly smaller individuals than the populations of the mainland areas (Governador Celso Ramos), Dona Francisca Island, and the site of PERI on Santa Catarina Island (Figure 1.3). The average length of the individuals of Ratones Grande Island was about 0.95 cm (± 0.08), while the populations of Governador Celso Ramos, Dona Francisca Island and PERI presented beetles with approximately 1.07 cm (± 0.07) in length.

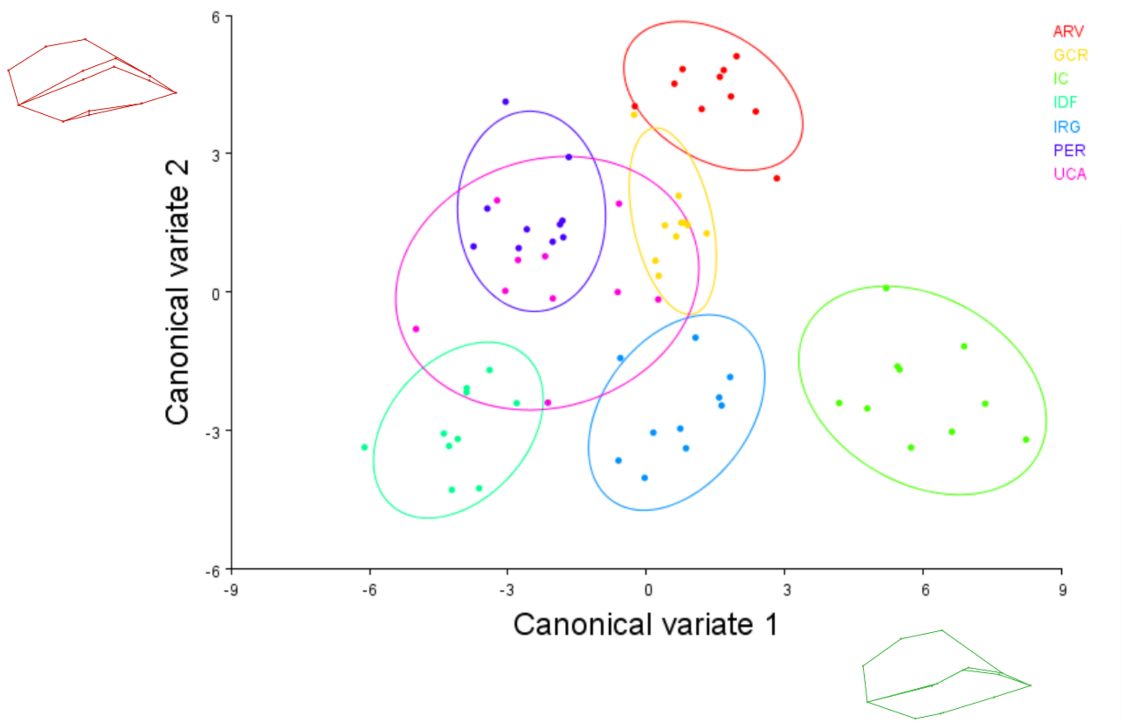
Figure 1.3 - Body length of *Canthon rutilans cyanescens* populations on the mainland: GCR - Governador Celso Ramos; and in the Santa Catarina Archipelago: UCAD – Desterro Conservation Unit, on Santa Catarina Island; PERI – Peri Lagoon Municipal Natural Monument, on Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island, and IDF – Dona Francisca Island.



The body shape of individuals also differed between populations (Procrustes ANOVA, F = 1.19, Pillai trait = 4.41; p < 0.0001). Both the body shapes of the population of Campeche Island (IC) and Arvoredo Island (ARV) differ from each other (AD, p = 0.0025), and the population of Campeche Island differs from the population of Dona Francisca Island (AD, p=0.0296). The population of Campeche Island has a slightly oval body, with a higher dorsal region and a retracted ventral region, differing from both the Arvoredo Island and Dona Francisca Island populations. The cross-validation test indicated that an average of 70% of the individuals in the populations were correctly allocated to their respective populations (Supplementary Material Table S2).

Figure 1.4 reveals the variations in the body shape of populations along two axes of canonical variation (CV1 and CV2), which explained 68% of the observed variations. The first axis of canonical variation explained 41% of the shape variation and represents a gradient between slightly flatter individuals with dorsal landmarks shifted to the center of the body (negative scores) and slightly more oval individuals with the dorsal landmarks (13, 14, and 15) slightly above the intermediate form (positive scores). The second axis of canonical variation explained 27% of the shape variation and represents a gradient of strongly oval individuals due to a widening in the dorsoventral axis, visualized by the landmarks 13 and 14 above the intermediate form (negative scores) for individuals with an anteroposterior axis enlargement and dorsoventral flattening, marked by landmark 15, which represents the posterior margin of the elytra, furthest from the center of the body in individuals of this population (positive scores). Analysis of Variance with scores of canonical variation axes 1 (CV1) and 2 (CV2) with *a posteriori* Tukey's test also confirm the difference between the populations (Supplementary Material, Table S3, S4, and S5).

Figure 1.4 - Position of the *C. rutilans cyanescens* populations in the morphometric space formed by two axes of the Canonical Variable Analysis, from the continent GCR - Governador Celso Ramos (in the center of the figure) and the sampling sites on the islands: UCA – Desterro Conservation Unit, on Santa Catarina Island; PER – Peri Lagoon Municipal Natural Monument, on Santa Catarina Island; ARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island, and IDF – Dona Francisca Island. Ellipses indicate a 90% confidence interval and each point represents an individual from the analyzed population.



Thus, the population of the Campeche Island stands out for its difference in body shape, which presents the largest positive scores on the first axis of canonical variables. Together, the displacement of all landmarks in the population of Campeche Island results in a slightly oval body shape with elevated margin of the head and end of the abdomen, with a higher dorsal region and a retracted ventral region. The population of Arvoredo Island shows its difference in body shape by presenting the largest positive scores in the second axis of canonical variables (positive CV2), indicating a shortening of the body in the posterior region and a flattening of the body in the dorsoventral direction. The displacement of all anatomical landmarks for the Arvoredo Island population results in individuals with a dorsoventrally flattened body with a shortened posterior region and a widening of the anteroposterior axis.

Finally, Figure 1.4 shows that the population of the Dona Francisca Island has a different body shape, presenting the smallest scores in the first and second axis of canonical variation (negative CV1 and CV2), resulting in a wider ventral region in the dorsoventral axis, with a more oval body shape. In addition, these individuals have an enlargement of the body in the anteroposterior axis and dorsoventral axis.

DISCUSSION

In this study, we observed a difference in body size in the population of dung beetles of the species studied on Ratones Grande Island, which presents the smallest individuals among the populations of the islands of the Santa Catarina Archipelago and the adjacent mainland. We also identified differences in the body shape of some isolated populations, such as those of Campeche Island (individuals with expansion in the dorsoventral axis), and Arvoredo Island (individuals with flattening in the dorsoventral axis). Such morphological differences may be related to the ecological drift suffered by the geographical isolation faced by these populations on the islands, corroborating the isolation of these island populations, even on coastal islands close to the mainland (MacArthur and Wilson 1967, Gillespie and Roderick 2002). The difference in size and shape were found for the most isolated islands of the mainland, which meets our hypothesis that predicted the impact of isolation on the morphology of populations.

Geographic isolation allows populations to respond independently to environmental changes and eventually differentiate. This process can even generate new species (Colley and Fischer 2013). The rise in sea level and the consequent isolation of the islands can cause island biotas to changes, which can involve both genetic drift and natural selection and resulting in body changes, which in small populations can be facilitated by inbreeding (Brown and Lomolino 2006, Colley and Fischer 2013). Such morphological changes may be the case of the size difference found for the population of Ratones Grande Island, which is a small island far from possible species sources (4.7 km from the mainland and 2.3 km from Santa Catarina Island). The change in body shape observed in *C. rutilans cyanescens* populations of Campeche Island and Arvoredo Island, the only two islands located outside the bay formed between the mainland and Santa Catarina Island that were sampled, give more strength to our argument of geographical isolation. Campeche Island is about 1.6 km from Santa Catarina Island and 16 km from the mainland, while Arvoredo Island is 12.7 km from the mainland and 11 km from Santa Catarina Island. These distances seem to be enough not to allow a frequent colonization of the islands, leading to the existence of morphological variations associated with the isolation of the islands.

The importance of geographical context for the body variation found has been reported for different organisms (Dennison and Baker 1991, Senczuk et al. 2014, Trevisan et al. 2014, Ober and Connolly 2015, Lazzarotto et al. 2017, Alvial et al. 2019, Ouisse et al. 2020), including in populations of other beetles in insular conditions (Palmer 2002, Laparie et al. 2010, Deidun et al. 2011, Benítez et al. 2014). However, its causal mechanisms remain poorly understood. Often changes in body size and shape for populations under geographic isolation suggest some degree of genetic differentiation and the existence of ecological or evolutionary processes (Camara et al. 2006, Senczuk et al. 2014, Jaskuła et al. 2021). Such changes may involve pronounced population isolation associated with inbreeding, accentuated on smaller islands to genetic drift and natural selection (Colley and Fischer 2013), and may be related to insular climatic and environmental features (Peters 1986, Steenkamp and Chown 1996, Alves et al. 2016).

The wide occurrence of *Canthon rutilans cyanescens* in the islands of the Santa Catarina Archipelago can be attributed the permanence of the species in these locations since the Last Glacial Maximum, about 21,000 years ago, when the sea level decreased (Klein et al. 2006, de Mahiques et al. 2010). In this period, the current islands of the Santa Catarina Archipelago were connected to the mainland portion, with no influence from the geographical barrier of the sea on the distribution of these beetles. With sea level rise during the Middle Holocene (Angulo and Lessa 1997) populations would have been isolated. Thus, the *C. rutilans cyanescens* species found on the islands today may be remnants of periods without geographic isolation. Thus, for this scenario of the Santa Catarina Archipelago, it is possible to identify that, in general, the individuals of the different populations currently occupy different regions of the morphospace, with little overlap between the populations, indicating identifiable morphological differences even from analyzes with a low sample number (ten individuals per population), suggesting the existence of evolutionary or ecological processes. The fact that each population occupies different morphospace regions suggests that the morphological differences found are not due to environmental pressures suffered by the species on the islands, since it would be extremely unlikely that there would be different environmental pressures for these small islands and relatively close to each other environmentally and climatically to the point to take each population to a different position in morphospace.

Dung beetles do not usually actively disperse to distances greater than one kilometer within the same habitat (Arellano et al. 2008, Da Silva and Hernández 2015a), although there are reports of passive dispersal via rafting for this group (Peck and Kukalova-Peck 1990, Scholtz et al. 2009). Thus, this study raises evidence that the dispersal events of dung beetles between the islands of the Santa Catarina Archipelago are extremely rare or non-existent, which may explain the morphological modifications of shape and size found for the *C. rutilans cyanescens* species. To improve the understanding of this study system, we recommend conducting genetic studies to identify whether these phenotypically different populations are also genotypically distinct and to try to understand the mechanisms that caused such differences. With this pioneering research in the Santa Catarina Archipelago, we found evidence that despite the context of coastal islands and short geographic distances, the sea represents an effective barrier for dung beetles, limiting connectivity between their populations.

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SUPPLEMENTARY MATERIAL

Table S1 – Sex ratio of individuals analyzed for each sampled population.

Population	Sex ratio		
	Female	**Male**	**Undefined**
GCR – Governador Celso Ramos	6	4	0
UCAD – Desterro Conservation Unit	4	5	1
PERI – Peri Lagoon Natural Monument	3	3	4
ARV – Arvoredo Island	3	4	3
IC – Campeche Island	6	3	1
IRG – Ratones Grande Island	5	4	1
IDF – Dona Francisca Island	7	3	0

Table S2 – Percentage of correct classification of *C. rutilans cyanescens* populations based on morphology and discriminant analysis.

Population	Allocation value (%)
GCR – Governador Celso Ramos	67
UCAD – Desterro Conservation Unit	65
PER – Peri Lagoon Natural Monument	64
ARV – Arvoredo Island	72
IC – Campeche Island	88
IRG – Ratones Grande Island	73
IDF – Dona Francisca Island	63

Table S3 – Analysis of variance of the first axis of canonical variation (CV1) and of the second axis of canonical variation (CV2) for the shape of the populations studied.

ANOVA CV1					
Source of Variation	**Degrees of freedom**	**Sum of squares**	**Mean squares**	**F statistic**	**p Value**
Body shape	6	660.9	110.2	110.1	$<2^{-16}$
Residuals	63	63.0	1.0		
ANOVA CV2					
Source of Variation	**Degrees of freedom**	**Sum of squares**	**Mean squares**	**F statistic**	**p Value**
Body shape	6	437.9	72.98	72.98	$<2^{-16}$
Residuals	63	63.0	1.00		

Table S4 – Tukey's test for the first canonical axis of shape variation (CV1). Values in bold are significant for the difference in shape between populations.

Teste de Tukey para o CV1				
Sites	Mean difference	p Value	Confidence interval de 95%	
			Inferior limit	Upper limit
GCR-ARV	-0.88	0.44	-2.25	0.48
IC-ARV	4.53	**0.00**	3.17	5.89
IDF-ARV	-5.53	**0.00**	-6.89	-4.17
IRG-ARV	-0.80	0.57	-2.16	0.57
PER-ARV	-3.94	**0.00**	-5.30	-2.58
UCA-ARV	-3.60	**0.00**	-4.96	-2.24
IC-GCR	5.42	**0.00**	4.05	6.78
IDF-GCR	-4.65	**0.00**	-6.01	-3.28
IRG-GCR	0.09	1.00	-1.27	1.45
PER-GCR	-3.05	**0.00**	-4.42	-1.69
UCA-GCR	-2.71	**0.00**	-4.07	-1.35
IDF-IC	-10.06	**0.00**	-11.42	-8.70
IRG-IC	-5.33	**0.00**	-6.69	-3.97
PER-IC	-8.47	**0.00**	-9.83	-7.11
UCA-IC	-8.13	**0.00**	-9.49	-6.77
IRG-IDF	4.73	**0.00**	3.37	6.10
PER-IDF	1.59	**0.01**	0.23	2.95
UCA-IDF	1.93	**0.00**	0.57	3.29
PER-IRG	-3.14	**0.00**	-4.51	-1.78
UCA-IRG	-2.80	**0.00**	-4.16	-1.44
UCA-PER	0.34	0.99	-1.02	1.70

Table S5 – Tukey's test for the second canonical axis of shape variation (CV2). Values in bold are significant for the difference in shape between populations.

Teste de Tukey para o CV2				
Sites	Mean difference	p Value	Confidence interval de 95%	
			Inferior limit	Limite superior
GCR-ARV	-2.72	**0.00**	-4.08	-1.36
IC-ARV	-6.39	**0.00**	-7.75	-5.02
IDF-ARV	-7.24	**0.00**	-8.60	-5.88
IRG-ARV	-6.86	**0.00**	-8.22	-5.50
PER-ARV	-2.51	**0.00**	-3.87	-1.15
UCA-ARV	-4.06	**0.00**	-5.43	-2.70
IC-GCR	-3.67	**0.00**	-5.03	-2.30
IDF-GCR	-4.52	**0.00**	-5.88	-3.16
IRG-GCR	-4.14	**0.00**	-5.50	-2.78
PER-GCR	0.21	1.00	-1.15	1.57
UCA-GCR	-1.34	**0.06**	-2.71	0.02

IDF-IC	-0.85	0.48	-2.21	0.51
IRG-IC	-0.47	0.94	-1.84	0.89
PER-IC	3.88	**0.00**	2.52	5.24
UCA-IC	2.32	**0.00**	0.96	3.68
IRG-IDF	0.38	0.98	-0.98	1.74
PER-IDF	4.73	**0.00**	3.37	6.09
UCA-IDF	3.17	**0.00**	1.81	4.54
PER-IRG	4.35	**0.00**	2.99	5.71
UCA-IRG	2.80	**0.00**	1.43	4.16
UCA-PER	-1.56	**0.02**	-2.92	-0.19

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CHAPTER 2: DIVERSITY OF DUNG BEETLES RELATED TO THE AREA OF ISLANDS IN THE SANTA CATARINA ARCHIPELAGO, SOUTH ATLANTIC BRAZIL

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ABSTRACT

Islands join ecological patterns and processes, at population and community levels, which can be outlined and better understood given their specific environmental and isolation conditions. In this context, island biogeography proposes relationships between species colonization and factors such as island area and isolation, while the ecology of metacommunities incorporates the existence of factors such as species selection and ecological drift on a regional scale to address the community structuring at the local level. This work seeks to understand which geographical and environmental factors influence the diversity of dung beetles in coastal island communities of the same archipelago, with the hypothesis that similar environment across islands turn geographic factors the main drivers of island diversity. For this, dung beetles, environmental data (vegetation and temperature), and geographical factors (area and distance) were collected in a standardized way in seven islands of the Santa Catarina Archipelago and the nearby continent between December/2020 and April/2021. The alpha diversity was compared, and beta diversity of the communities was calculated, followed by a partition analysis. In addition, a Generalized Linear Model (GLM) was calculated with dung beetle richness as the response variable and island area, island isolation, vegetation structure, and soil temperature as explanatory variables. The results show that the richness of dung beetle species was positively related to the size of the islands, being similar for the communities of the mainland areas and the sites located on the largest island, the Santa Catarina Island. The dissimilarity of diversity between the islands was mainly due to nestedness, indicating that the species found on smaller islands are a subset of the species found on the larger islands and mainland. Thus, the results suggest the species found on the islands have remained there since the formation of these islands after the Last Glacial Maximum and the number of species on each island decrease according to islands area variation due to resource amount available in these sites.

Keywords: Biogeography. Community Ecology**.** Insects. Richness. Scarabaeinae.

INTRODUCTION

The Theory of Island Biogeography is quite consolidated in ecology and combines the dynamic balance of colonization and extinction processes with the geographical factors of area and isolation of the island, allowing to predict species richness on a given island (MacArthur & Wilson, 1967). This theory of species equilibrium can be applied in different study contexts and has already supported the development of many hypotheses, concepts, and theoretical structures in ecology, one of them being the organization of the metacommunities framework. The Ecology of Metacommunities highlights the importance of species selection, dispersal, and ecological drift processes that occur at the regional level, that is, at the metacommunity level, but that can influence the assembly of local communities (Holyoak et al., 2005; Leibold et al., 2004). In the metacommunities framework, species selection is related to the characteristics of the species niche, dispersal is related to their dispersal capacity and colonization events, while ecological drift represents stochastic parameters that influence populations within a community and may be linked to stochastic events of colonization and extinction in a region (Chase & Bengtsson, 2010; Vellend, 2010).

Beta diversity describes the change in diversity between different communities in the same region to study species diversity patterns at the regional level. This diversity is evaluated through dissimilarity metrics and can be partitioned into several causal components of dissimilarity, identifying components of species turnover between communities, and nestedness components, where the species of one community are a subset of those contained in another community (Baselga, 2013). A well-documented pattern for beta diversity is the decay of similarity between communities with increasing distance between them (Nekola & White, 1999). This difference can emerge from both stochastic and deterministic processes. In patches with different habitats, beta diversity can arise via deterministic species sorting processes, favoring different species in different environments, while in patches with similar habitats, beta diversity can arise via stochastic processes of extinction, dispersal limitation, or priority effects, common in the model of patch dynamics in metacommunities (Chase & Bengtsson, 2010). On the local scale, species distribution can be seen as a reflection of their niche, limited both by geographical barriers and colonization abilities, as well as by intra and interspecific interactions (Hutchinson, 1957; Soberón, 2007), that is, by environmental and biotic filters (Mittelbach & Schemske, 2015).

Competition for resources is an important factor in community assembly, where competition between species with overlapping niches can lead to competitive exclusion or niche partition. Thus, interspecific competition can result in a decrease in species richness on a given island or in the coexistence of species due to ecological, spatial, or temporal differentiations during resource exploitation (Cadotte et al., 2006; Scholtz et al., 2009). In coastal islands or continental islands, that are part of the continental shelf, the ecological space that houses the species ‘niche of the species is already occupied during connection with the continent, before its insularization. The number of species in these sites decreases after the fragmentation into islands and relict species formation or speciation events may occur if these remain isolated (Gillespie & Roderick, 2002). In this context, in islands with low or no isolation, colonization is associated with the ability of species to overcome the marine matrix that surrounds the islands and acts as an environmental filter or barrier. Dispersal in these cases can be active, with the individual actively moving to another environment, or passive, in which the individual is carried from their original habitat by external dispersal agents, such as rafting on tree trunks or floating objects and and wind currents (Lee et al., 2015; Peck & Kukalova-Peck, 1990; Scholtz et al., 2009).

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are insects unlikely to actively disperse within the same habitat at distances greater than one kilometer (Arellano et al., 2008; Da Silva & Hernández, 2015b). However, there are records of passive dispersal, as reported by Darwin, who saw a living beetle floating in the sea about 40 km from the coast, near the mouth of the Prata River (Peck & Kukalova-Peck, 1990; Scholtz et al., 2009), and Gonzalez-Vainer (2015), who found many living *Canthon bispinus* individuals with other insects of different taxa in the sand of a beach in Uruguay after a stormy night, at the high tide line, indicating that they had been dispersed by the sea. These beetles are known as dung beetles because they feed mainly on animal feces. These insects are distributed mainly in tropical regions where there is high diversity and resource partitioning (Hanski & Cambefort, 1991). Beetles of this subfamily undergo bottom-up control in the regulation of their communities since their food is relatively scarce and ephemeral, resulting in interspecific competition being more important than predation and mortality due to parasitism and diseases (Halffter, 1991). Dung beetle species exhibit different strategies for reallocating food resources (tunneling, rolling, or resident species), different eating habits (coprophages, scavengers, generalists), and different periods of activity (diurnal, twilight, nocturnal) product of selection pressures to reduce competition (Halffter & Edmonds, 1982). Differences in trophic specialization, habitat selection, diel activity, and resource allocation may favor a high coexistence of species, causing them to present high local richness through niche partition (Halffter, 1991; Hanski & Cambefort, 1991; Hernández et al., 2019). Although there are many works on dung beetles, few works seek to understand how the communities of these beetles behave in insular environments, surrounded by the marine or aquatic barrier (Larsen et al., 2005; Qie et al., 2011; Storck-Tonon et al., 2020).

To consider the regional arrangements of island communities, the equilibrium theory of island biogeography brings the dimension of the historical processes of colonization and extinction of species related to geographical characteristics, and the metacommunities framework brings the dimension of regional movements of organisms between the communities contained in islands and the environmental and biotic filters to overcome. The Santa Catarina Archipelago corresponds to a set of more than 25 coastal islands that, during the Last Glacial Maximum, about 21 thousand years ago, were connected to the mainland due to the retreat of the sea level (de Mahiques et al., 2010; Klein et al., 2006). Currently, these islands are up to 14 km from the mainland and are generally small, with < 20 ha. Considering this archipelago and having dung beetles as a focal group, one possibility is that the species may have arrived on the islands by stochastic passive dispersal events, such as rafting on logs in river floods or other floating objects, as has already been documented for the focus group (González-Vainer, 2015; Peck & Kukalova-Peck, 1990; Scholtz et al., 2009), resulting in a connectivity via stochastic events. In this case, the most abundant species on the mainland and on the Santa Catarina Island, local sources of species, would have a higher chance of suffering such passive dispersal events and, once arrived on the islands, the internal dynamics of competition and selection of species, already well documented for the group (Halffter & Edmonds, 1982; Halffter, 1991; Hanski & Cambefort, 1991; Scholtz et al., 2009), would limit the species richness in the islands according to the area of the islands, that is, the amount of resources. Another possibility related with geographic isolation is that the species found on the islands have remained since the Last Glacial Maximum, about 21 thousand years ago, when the current islands were connected with the mainland. This event probably allowed the permanence and wide distribution of species from the mainland areas in areas that currently correspond to the islands of the archipelago (Leite et al., 2016). Subsequently, the islands formed with the reappearance of the geographical barrier represented by the sea, and as the sea level rose, their areas decreased, and the internal dynamics of competition defined the remaining species richness according to the amount of resources available on the islands via vicariance events.

The hypothesis of this work is that, given the islands might have similar environmental conditions, geographical factors are the main drivers of diversity, especially island area, acting as a major diversity driver in the community organization due to the amount resources available limitation. Thus, it is expected that there will be communities with nested pattern of diversity on the islands of the Santa Catarina Archipelago, with a decrease in species richness as island area decreases. Thus, this work seeks to understand which geographical factors (isolation and area) and environmental factors (vegetation structure and soil temperature) contribute to the organization of diversity in dung beetle communities on coastal islands.

MATERIAL & METHODS

Study area

Data collection took place on seven coastal islands of the Santa Catarina Archipelago and on the nearby mainland, both covered with Subtropical rainforest (Dense Ombrophilous Forest). The sampling was carried out on a large island – Santa Catarina Island, with 42,440 ha of area (27°35'49"S, 48°32'58"W); two intermediate islands – Arvoredo Island, with 320 ha of area (27°16'54"S, 48°22'21"W), and Campeche Island, (27°41'51"S, 48°28'1"W), with 43 ha of area; in four small islands - Ratones Grande Island, with 17 ha of area (27°28'31"S, 48°33'44"O"), Dona Francisca Island, with 14 ha of area (27°41'53"S, 48°33'56"W), Anhatomirim Island, with 6 ha of area (27°41'28"S, 48°34'15"W), Laranjeiras Island, with 1 ha of area (27°25'41"S, 48°33'52"W), and on the nearby mainland – Anhatomirim Environmental Protection Area (27°23'48"S, 48°34'2"W) in Governador Celso Ramos municipality that is in a forest patch of approximately five thousand ha (Supplementary Material, Figure S1). Data collection occurred from December 2020 to April 2021, except for Arvoredo Island, which occurred from December 2017 to April 2018. Among the islands of the archipelago, the largest is Santa Catarina Island, with about 500 thousand inhabitants, and is where the state capital, Florianópolis (IBGE, 2021) is located. There, sampling was on two large protected areas: Desterro Conservation Unit (UCAD) in a forest patch of approximately six thousand ha, and Peri Lagoon Municipal Natural Monument (Peri) that is in a forest patch of five thousand ha. Another sampling sites are also protected areas: the Arvoredo Island belongs to the Marine Biological Reserve of Arvoredo, an Integral Protection Conservation Unit; the Anhatomirim Island is inserted within the Environmental Protection Area (APA) of Anhatomirim, which also houses the mainland area studied in this work; the Campeche Island is listed as a National Archaeological and Landscape Heritage by Institute of National Historical and Artistic Heritage (IPHAN); and the Ratones Grande Island, along with the Anhatomirim Island, is under the management of the Fortresses of the Santa Catarina Island of the Federal University of Santa Catarina (UFSC).

Data collection was carried out along a linear transect on the main trail at each site, where sampling areas with five points were located. The points in each sampling area were close to each other, being thus combined in a single sample value. The Santa Catarina Island had four sampling areas (two in UCAD and two in PERI), the mainland and the intermediate islands had two sampling areas, and the smaller islands had only one sampling area. In those sites with two or more sampling areas, they were more than 100 m apart, to ensure sampling independence for dung beetle data (Da Silva & Hernández, 2015b). The geographical factors of area and isolation of islands were obtained in Google Earth Pro. Area was measured from the forest patch of each study site (island or protected area) and isolation was measured from the distance to nearest large landmass (>100 ha) that could be a source of dispersal, in this case, the mainland or the Santa Catarina Island.

Dung beetle data

Standardized collections of dung beetles took place using ten baited pitfall traps for live insects, distributed in pairs at the five collection points in each sampling area. The baits used were: 10 grams of domestic dog feces (five traps), obtained from the Federal University of Santa Catarina Central Bioterium, and 10 grams of rotted pork meat (five traps). Traps were checked after 48 hours of exposure, followed by the collection and identification of individuals in the field using a reference collection with species sampled in the Santa Catarina Island and in the coastal region near the islands. For species record, up to ten individuals of each species were collected per trap for each sampled site and deposited in the Mítia Heusi Silveira Entomological Collection of the Biological Sciences Center (CCB) of the Federal University of Santa Catarina (UFSC). The remaining individuals were identified in the field and returned alive to the same place.

Environmental description

Vegetation structure, vegetation cover, and soil were evaluated at two points of each sampling area, and the soil temperature was measured at each site to describe the environment. A modified quadrant method was used to evaluate vegetation (Brower et al., 1998), where tree height, diameter at breast height (DBH>5 cm), and distance from the first tree to the quadrant point, as a density measure, were measured. The same measurements were performed for the shrubs. In addition, the percentages of canopy cover, bare soil cover, vegetation cover, and leaf litter cover were estimated. Temperature was measured using a datalogger, buried 5 cm deep in the soil, and located near the central trap in a sampling area of each site. This temperature was recorded for 48 hours during the dung beetle collections at each site.

Data Analyses

Data from the same sampling areas of each site were added up, so the sites considered in the data analysis were Governador Celso Ramos on the mainland, UCAD on Santa Catarina Island, Peri on Santa Catarina Island, Arvoredo Island, Campeche Island, Ratones Grande Island, Dona Francisca Island, Anhatomirim Island and Laranjeiras Island. Alpha diversity of the studied sites was compared by generating interpolation/extrapolation curves for species richness (q=0) and for exponential of Shannon Entropy (q=1), using the iNEXT package (Chao et al., 2014). To study beta diversity among sites, a dissimilarity matrix was calculated using the Jaccard Index, followed by a partition analysis, where the dissimilarity matrix was split in turnover and nestedness components (Baselga, 2010). After that, a dendrogram with dissimilarities was constructed using average as agglomeration method with the R package betapart. The environmental variables of vegetation structure were determined by the average of the values obtained per studied site. Highly correlated or redundant variables were first eliminated (Supplementary Material Table S1), keeping only leaf litter cover, canopy cover, distance from the first tree to the quadrant point, height of the first tree, distance from the first shrub to the quadrant point, and height of the first shrub. These variables were inserted in a Principal Component Analysis (PCA), subsequently using the first principal component (PC 1) scores as information of the vegetation structure of each site for other analysis, being that the forested areas have negative scores, and more open areas have positive scores (Table 2.1). Soil temperatures were averaged to obtain a single temperature value per site. In addition, Generalized Linear Models (GLM) with Poisson error structure were generated to identify the influence of different geographical and environmental factors on dung beetle richness. A set of linear models was assembled using all possibly combinations of candidate factors potentially important for dung beetle richness: area, distance, vegetation structure and soil temperature (Table 2.1). Linear correlations were performed between all variables to understand the relationship between them, before inserting them in the models and the models were selected based on the Akaike Information Criterion corrected for small samples (AICc).

Table 2.1 – Input table in GLM with all considered measured variables. Richness – species richness per site; Area – island area; Distance – distance from the nearest large landmass (continent or Santa Catarina Island); Vegetation – scores from a principal component analysis of vegetation structure; Temperature – mean of soil temperature measured at each local during dung beetle collections. CGR - Governor Celso Ramos; UCAD – Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI – Peri Lagoon Municipal Monument on the Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IDF – Dona Francisca Island; IL – Laranjeiras Island.

Site	Richness	Area	Distance	Vegetation	Temperature
GCR	8	5070	NA	-0.88	22.9
UCAD	11	7123	10	-0.58	23.4
PERI	8	4678	9.9	-0.66	23.0
IARV	3	320	11	0.09	23.3
IC	2	29	1.6	0	22.1
IRG	2	14	2.3	-0.23	22.6
IDF	2	10	0.3	0.67	24.6
IL	1	1	0.3	-0.55	24.3
IA	0	1	0.3	2.14	23.3

Additionally, a logistical species-area curve was performed with the R package sars to observe the relationship between species richness and area, the significant variables of the top ranked model. All statistical analyses were performed in the R program in its specific function packages available in R version 4.1.2 (R Core Team, 2022).

RESULTS

A total of 1010 dung beetles belonging to 12 species were recorded, characterizing the regional pool of species (Table 2.2). Only the Anhatomirim Island, an island close to the mainland (300 m) and with 6 ha of area, had no dung beetles. The sites of the Santa Catarina Island (UCAD and PERI) shared the same eight species that also occur on the mainland (GCR), and these sites on the Santa Catarina Island still contains four more species than the mainland. The species found on the intermediate and small islands are a subset of the species that occur on the mainland and on the Santa Catarina Island.

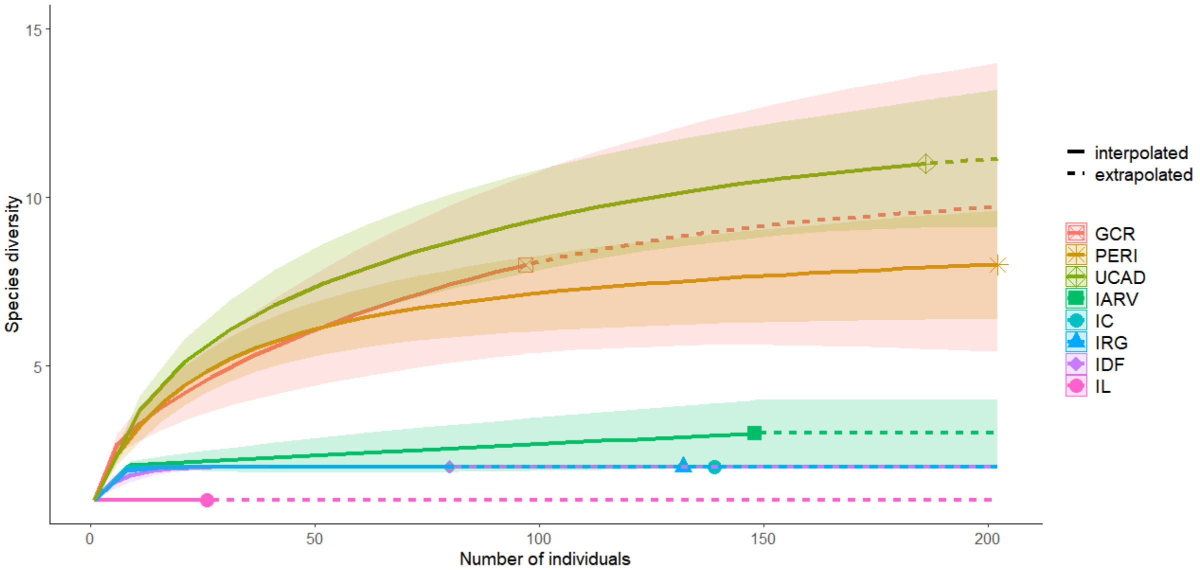
Table 2.2 - Species of dung beetles sampled in the Atlantic Forest of the coast of Santa Catarina, Brazil, from: CGR - Governor Celso Ramos; UCAD – Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI – Peri Lagoon Municipal Monument on the Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IDF – Dona Francisca Island; IL – Laranjeiras Island. The numbers 1 and 2 represent the sampling area at each site, respectively and species are ordered from highest to lowest occurrence. T = Total.

	Mainland			Islands														
Species	GCR			UCAD			PERI			IARV			IC			IRG	IDF	IL
	1	2	T	1	2	T	1	2	T	1	2	T	1	2	T	1	1	1
Dichotomius sericeus	33	1	34	53	73	126	78	72	150	36	23	59	42	32	74	29	69	26
Canthon rutilans cyanescens	12	38	50	13	2	15	11		11	38	50	88	64	1	65	103	11	
Deltochilum morbillosum	1		1	2	9	11	8	2	10	1		1						
Canthidium aff. *trinodosum*	1		1	1	3	4		1	1									
Coprophanaeus saphirinus	6		6	4		4	2	4	6									
Canthon luctuosus				13	5	18	3	1	4									
Deltochilum multicolor	2		2				10	8	18									
Canthidium aff. *lucidum*	2		2	1		1												
Deltochilum rubripenne					2	2	2		2									
Phanaeus splendidulus	1		1		1	1												
Uroxys sp. 1				2		2												
Uroxys sp. 2				2		2												
Abundance	**58**	**39**	**97**	**91**	**95**	**186**	**114**	**88**	**202**	**75**	**73**	**148**	**106**	**33**	**139**	**132**	**80**	**26**
Richness	**8**	**2**	**8**	**9**	**7**	**11**	**7**	**6**	**8**	**3**	**2**	**3**	**2**	**2**	**2**	**2**	**2**	**1**

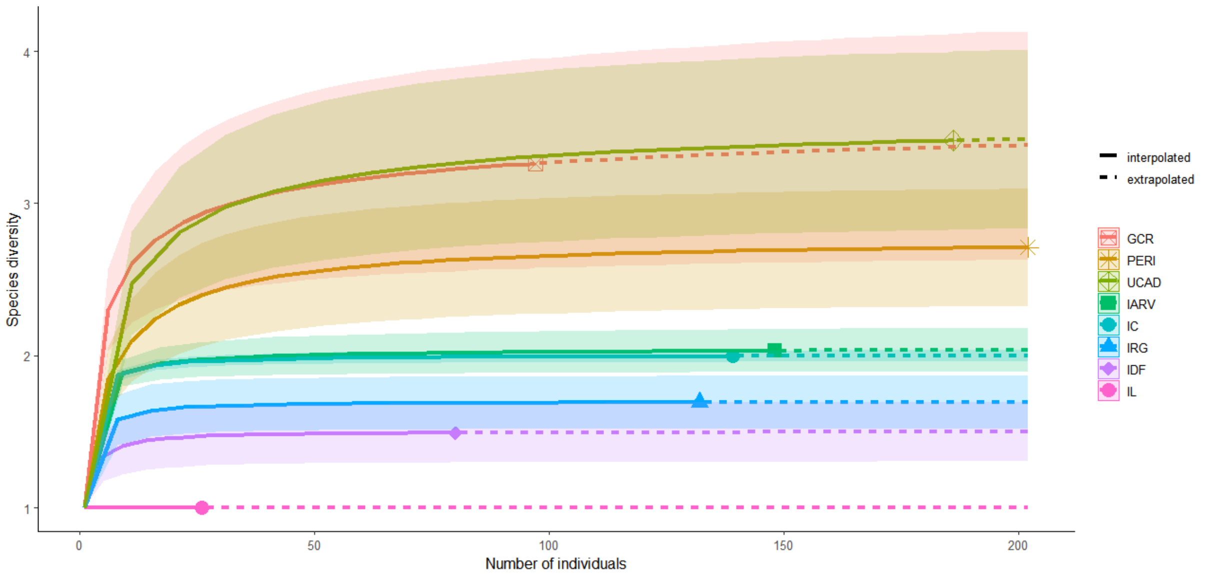
Species richness followed the area of the islands since the mainland and the two sites sampled on the Santa Catarina Island, the largest island studied, had the highest observed species richness, reaching an estimated richness of about ten species, and showing overlapping confidence intervals (Figure 2.1A). Islands of intermediate size had intermediate richness: the Arvoredo Island had three species, the Campeche, Dona Francisca, and Ratones Grande Islands had two species each. Laranjeiras Island, the smallest island of all, had only one species. Sampling effort was adequate to describe the assemblage of dung beetles from the interpolation and extrapolation curves since the curves reach stabilization, except for the mainland (GCR), which likely harbors two more species (Supplementary Material Table S2).

Figure 2.1 – A) Species richness (q=0) and B) diversity measured by the exponential of Shannon Entropy (q=1) found in the collection sites on the mainland: GCR – Governador Celso Ramos; and in the Santa Catarina Archipelago: UCAD – Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI – Peri Lagoon on the Santa Catarina Island; ARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IDF – Dona Francisca Island; IA – Anhatomirim Island; Il – Laranjeiras Island.

A)



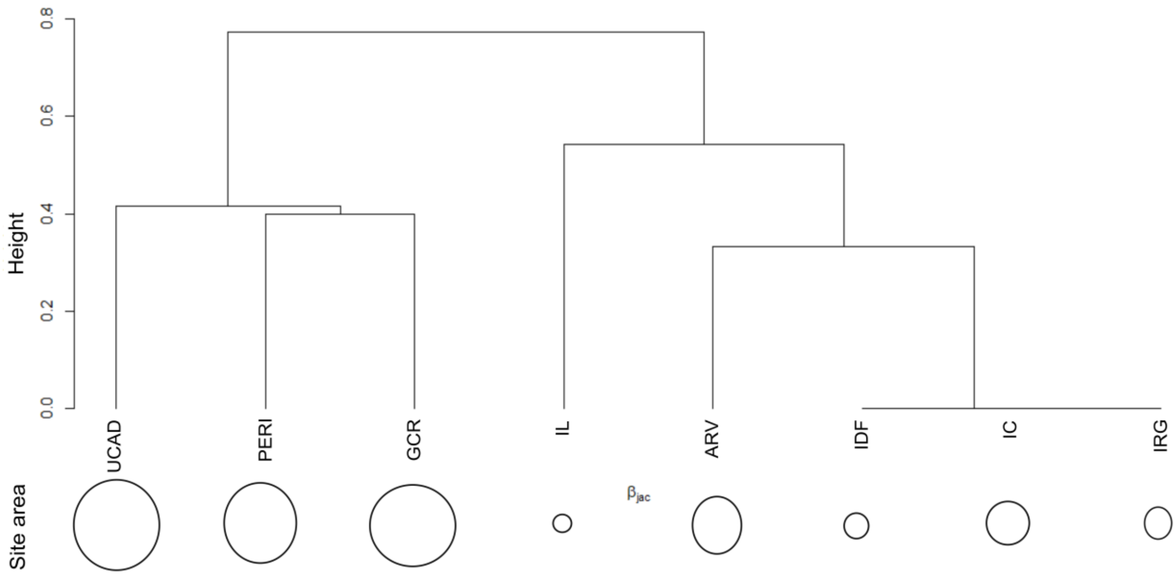
B)



The species *Dichotomius sericeus* and *Canthon rutilans cyanescens* were the most abundant, accounting together for 90% of the total abundance (34% *C. rutilans cyanescens*; 56% *D. sericeus*). *D. sericeus* was found on all islands and on the mainland, being the only species observed on the Laranjeiras Island, and *C. rutilans cyanescens* was found on all other islands and on the mainland. Using the exponential of Shannon Entropy (q=1) as a measure of alpha diversity, thus emphasizing typical species of each assemblage, showed that the areas of the mainland and the Santa Catarina Island have greater diversity, with about three typical species, followed by the Arvoredo and Campeche Islands with two typical species, and the others remaining islands with only about one typical species (Figure 2.1B).

Regarding beta diversity, assemblages were clustered in two distinct groups: one consisting of the areas of the mainland and the Santa Catarina Island and the other with the other islands, showing that the communities of the largest island resemble those of the mainland much more than the communities of the smaller islands due to the low richness (Figure 2.2).

Figure 2.2 - Dendrogram based on the Jaccard dissimilarity for the dung beetle assemblages of the islands of the Santa Catarina Archipelago and the nearby mainland: CGR - Governador Celso Ramos; UCAD – Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI – Peri Lagoon Municipal Monument on the Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IDF – Dona Francisca Island; IL – Laranjeiras Island. The circles represent the area of each site studied.



The diversity partition showed that the main component of beta diversity was the species nestedness, except between the mainland and the Santa Catarina Island, where there is a small proportion of species turnover (Table 2.3). Thus, it is possible to conclude that the species found on the smaller islands are a subset of the species found on larger islands and on the mainland.

Table 2.3 - Partition of the beta diversity performed for the dung beetle assemblages of the collection sites on the mainland: GCR – Governador Celso Ramos; and in the Santa Catarina Archipelago: UCAD – Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI – Peri Lagoon Municipal Monument on the Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IDF – Dona Francisca Island; IL – Laranjeiras Island. Null values are represented with a long dash.

Location	Dissimilarity component	IL	IDF	IRG	IC	IARV	PERI	UCAD
GCR	Total	0.9	0.8	0.8	0.8	0.6	0.4	0.4
	Nestedness	0.9	0.8	0.8	0.8	0.6	—	0.2
	Turnover	—	—	—	—	—	0.4	0.2
UCAD	Total	0.9	0.8	0.8	0.8	0.7	0.4	
	Nestedness	0.9	0.8	0.8	0.8	0.7	0.2	
	Turnover	—	—	—	—	—	0.2	
PERI	Total	0.9	0.8	0.8	0.8	0.6		
	Nestedness	0.9	0.8	0.8	0.8	0.6		
	Turnover	—	—	—	—	—		
IARV	Total	0.7	0.3	0.3	0.3			
	Nestedness	0.7	0.3	0.3	0.3			
	Turnover	—	—	—	—			
IC	Total	0.5	—	—				
	Nestedness	0.5	—	—				
	Turnover	—	—	—				
IRG	Total	0.5	—					
	Nestedness	0.5	—					
	Turnover	—	—					
IDF	Total	0.5						
	Nestedness	0.5						
	Turnover	—						

Species richness was positively related to both the area of the islands ($r=0.98$, $p<0.001$) and the distance from the islands ($r=0.78$, $p=0.02$) and was marginally negative related to the vegetation structure ($r = -0.63$, $p=0.07$) (inverse relationship, since negative vegetation values indicate more open or degraded areas). The area and distance of the islands were also positively correlated with each other because largest studied islands are casually farthest from the landmasses. There is no correlation between island area and vegetation structure and temperature was not correlated with any other variables (Supplementary Material Table S2). The GLMs for species richness were tested for all geographic and environmental factors studied and the area of the islands was the most important factor in determining species richness; island distance was also present in two of the top three ranked models (Table 2.4), but in this case it is important to note that the relationship with distance from islands is influenced by the correlation between area and distance from islands.

Table 2.4 – Best approximating generalized linear models of species richness of dung beetles for all studied sites (n = 9). Area – island area; Distance – distance from the nearest large landmass (continent or Santa Catarina Island); Vegetation – scores from a principal component analysis of vegetation structure; Temperature – mean of soil temperature measured at each local during dung beetle collections; df is degree of freedom of model; AICc, Akaike's information criterion corrected for small sample size; ΔAICc, difference between AICc of the top-ranked and current model; *w*AICc is AICc weight; %DE, percentage deviance explained by the model. Models were ranked by AICc.

Model	Intercept	Area	Distance	Vegetation	Temperature	df	AICc	ΔAICc	*w*AICc	%DE
M1	0.6	2.77E-04	—	—	—	2	36.1	0	0.40	82.5
M8	0.2	1.91E-04	0.08	—	—	3	36.5	0.35	0.34	86.8
M2	0.2	—	0.17	—	—	2	37.1	0.99	0.24	63.0
M3	1.0	—	—	-1.33	—	2	42.9	6.72	0.01	59.8
M6	0.4	1.49E-04	0.07	-0.49	—	4	44.7	8.53	0.01	91.1
M7	2.5	1.95E-04	0.08	—	-0.10	4	45.8	9.61	3.00E-03	87.0
M0	1.4	—	—	—	—	1	57.1	20.98	0	0
M4	6.0	—	—	—	-0.20	2	59.8	23.64	0	2.6
M5	1.2	1.51E-04	0.07	-0.49	-0.04	5	63.3	27.19	0	91.2

Alone, the model that included only the area of the islands as an explanatory variable explained 82.5% of the total deviance in the data and was the top ranked model, confirming the important role that the area has in explaining the species richness in these islands ($z=4.793$; $p<0,001$). Soil temperature did not appear in any of the best classified models and the null model was among the worst classified models (ΔAICc > 20), suggesting little influence of stochasticity on the species richness of these islands. A curve representing the species-area relationship ($z=0.34$, $p=0.03$) is available in the supplementary material (Supplementary Material, Figure S2).

DISCUSSION

Our results indicate differences in species richness of dung beetles between the large sites (the mainland and the Santa Catarina Island) and the other islands of the Archipelago, being related to the sites' area (islands and mainland). The Santa Catarina Island presents a pattern of alpha diversity like the mainland and is likely a source of species for the other islands. The size of the islands can be interpreted as a proxy for the amount of resources existing in that location since generalist species, such as those found in this study, can occupy several types of habitats, reaching a balance of species on the island regardless of the diversity of their habitats (Hernández et al., 2019; Hortal et al., 2009). Thus, the amount of resources available on the islands would be the limiting factor of the number of species on each island.

Dung beetle species composition found is consistent with the collections performed by Silva & Hernández (2016) in Governador Celso Ramos municipality (mainland region) and on the Santa Catarina Island. According to Silva & Hernández (2014), the regional species pool for Santa Catarina Island and the mainland is 21 species, being that for collections at the local scale it is expected to find up to 9 species and for collections in more than one location it is expected to find 14 to 16 species, which is in line with the species richness found in this work. The species *C. rutilans* and *D. sericeus* are quite abundant on the mainland and on the Santa Catarina Island, characterizing them as superior competitors in these environments (Da Silva & Hernández, 2015a, 2016; Hernández et al., 2019), which could explain the presence of these two species on the islands in almost all the islands sampled. The great abundance of *C. rutilans cyanescens* and *D. sericeus* meets the data previously collected along the coast of the State of Santa Catarina (Bogoni et al., 2014; Da Silva & Hernández, 2014, 2015b, 2015a, 2016; Hernández et al., 2019). Both species have a different food resource allocation behavior and diel activity: *C. rutilans cyanescens* has a rolling and diurnal behavior, while *Dichotomius sericeus* has a habit of making tunnels and is nocturnal. This indicates that these species have little niche overlap since a strong interspecific competition for resources in communities should lead to resource partition. Thus, these differences in the diel activity and in the resource allocation behavior facilitate coexistence (Halffter & Edmonds, 1982; Halffter, 1991; Hanski & Cambefort, 1991; Scholtz et al., 2009).

The observed stabilization in species richness in the small and intermediate islands, with only two species each, may be due to the exclusive presence of common species on the islands (widely distributed and abundant in the region, see Hernández et al. (2019)), causing less generalist species to be excluded by competition once they arrive there. In addition, the size of these islands has decreased over time due to the rise in the sea level and the current area of these islands may harbor insufficient habitats to support a larger species richness. Thus, the remaining species should be generalist species and better competitors since generalist species are less prone to stochastic extinctions (Cadotte et al., 2006; Kotiaho et al., 2005).

The fact that the area of the islands is the only factor related to the variation of dung beetle richness was expected by our initial hypothesis and corroborates the influence of the area on the species richness proposed by the Theory of Island Biogeography (MacArthur & Wilson, 1967). In contrast, the lack of isolation factor in our top model ranked seems rejects a relationship between isolation and species richness, despite being predicted in the initial hypothesis. This absence of relationship may result from a low variation of the distances of the islands or to the insignificance of the degree of isolation of the islands for the studied focal group. However, studies on continental islands formed by damming in hydroelectric plants show isolation as an important factor for species richness, suggesting dispersal limitation plays an important role in the assembly of dung beetle communities (Qie et al., 2011; Storck-Tonon et al., 2020). Many studies in tropical forests also report dung beetle species richness to be positively correlated with area and negatively related to isolation (Filgueiras et al., 2011; Klein, 1989; Larsen et al., 2005; Nichols et al., 2007). In this work, the significance of the relationship between species richness and isolation in the others models not selected was influenced by the fact that the largest islands studied casually are the most distant islands, which makes it difficult to draw firm conclusions about this relationship when looking only at the models. But more than the insignificance of these distances for the dispersal of individuals in our top ranked model, the absence of a relationship between isolation and richness observed seems to be result of to the type of measure chosen to measure isolation, which were the distances between the islands. These distances would not be related to the species richness if these beetles are not actually dispersing between islands even in the smallest distances, because of the marine barrier, making us to consider that geographic isolation is acting equally for all distances. This would be in line with the evidence of geographic isolation that has already been found for this group in these same studied sites through the existence of morphological variations (Sousa & Hernández, in preparation).

The smallest islands studied, Anhatomirim Island (1 ha of forest patch) and Laranjeiras Island (1 ha of forest patch), are about 300 m away from their species sources, but dung beetles were found only on the Laranjeiras Island. The absence of dung beetles in the Anhatomirim Island can be explained by the environmental filters, which is suggested by a distinct set of environmental conditions from other islands: low canopy cover, large amount of soil covered with either vegetation, or bare soil on the island (Supplementary Material Table S3). The low environmental quality on the Anhatomirim Island can be attributed to its anthropogenic occupation dating back to 1739, with the installation of a fortress, a prison, a telegraph station, and an electricity plant (Tonera & Cruz, 2020), and its consequent low percentage of current forest cover, causing environmental filters to be acting on a local scale, limiting the permanence of dung beetles on this island.

In general, oceanic islands present a low richness of beetles. More isolated islands present impoverished faunas or in altered proportions for beetle families and genera compared to mainland faunas (Gillespie & Roderick, 2002; Halffter & Matthews, 1966; Peck & Kukalova-Peck, 1990). For continental islands, a study conducted with dung beetles 30 years after the formation of islands by the damming of a hydroelectric plant in the Amazon also found impoverished faunas related to geographical isolation (Storck-Tonon et al., 2020). However, the results of our study indicate that the major factor that affects the impoverishment of species in the coastal islands studied is the amount of resources limited by the area of the islands, which historically decreased with the increase in sea level during the Middle Holocene (Angulo & Lessa, 1997; Cooper et al., 2018).

The first hypothesis raised in this work, about island connectivity via stochastic events, would characterize these island communities as a metacommunity governed by stochastic dispersal events and species sorting according to islands area. In a study conducted with dung beetle marking and recapture on the Santa Catarina Island, *C. rutilans cyanescens* and *D. sericeus* had the highest reported abundances but low recapture rates, which may be related to high dispersal rates and wider spatial distributions (Da Silva & Hernández, 2015b). This could explain why we find only the species *C. rutilans cyanescens* and *D. sericeus* in the islands and why the smallest island studied, the Laranjeiras Island, with only 1 ha of area, contains only one species of dung beetle, the species *D. sericeus*, the most abundant species. According to this connectivity hypothesis via stochastic events, the islands with greater surface, that is, with greater area, would have a higher chance of receiving the new species that arrive by rafting and would have more resources so that the species would not be extinct by interspecific competition. This also would explain the presence of three species of dung beetles in Arvoredo Island, with 320 ha, the second largest island sampled and that home to the species *Canthon rutilans cyanescens*, *Dichotomius sericeus*, and *Deltochilum morbillosum*. However, there is evidence for the influence of isolation limiting the connectivity between these islands for the focus group (Sousa & Hernández in preparation), so this hypothesis seems unlikely.

The other hypothesis raised in this work, about geographic isolation and vicariance events since the Last Glacial Maximum, would explain why we found only generalist species on the islands studied, since these generalist species would have remained after sea level rise and these islands formation because they are less subject to stochastic extinctions than the most demanding species (Kotiaho et al., 2005). This hypothesis would characterize these island communities as isolated communities in our spatial scale of study due to lack of connectivity between them and not as a metacommunity. The geographic isolation proposed in this hypothesis is consistent with the presence of the *C. rutilans cyanescens* and *D. sericeus* in the islands, the more abundant and dominating dung beetle species in Santa Catarina coast. Furthermore, this hypothesis is also consistent with the importance of islands area in structuring islands communities, that is, with amount of resources available in these islands that could structuring these communities based on internal dynamics of competition between species or species sorting, as already is well documented for the focus group (Halffter & Edmonds, 1982; Halffter, 1991; Hanski & Cambefort, 1991; Scholtz et al., 2009) or through stochastic extinctions of species with smaller and more susceptible populations. Finally, this hypothesis would also explain the difference in size found in individuals from Ratones Grande Island and body shape in Campeche and Arvoredo Islands (Sousa & Hernández, in preparation), being the hypothesis more consistent with the results of this work.

Our results suggest that dung beetle communities found in the Santa Catarina Archipelago are likely a set of island communities with little or no connectivity, influenced mainly by the island area, and thus, by the number of available resources. Such communities are composed of generalist species with little niche overlap and that represent a subset of the species found on the mainland and on the Santa Catarina Island, which acts as a source area for the other islands of the archipelago. In short, island area is the most important factor for diversity in coastal islands since the isolation probably affect all island equally due to the marine barrier. Thus, small and intermediate islands harbor a low diversity of dung beetles due to their area and, even in coastal islands near the mainland, isolation can influence the diversity of dung beetle communities.

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SUPPLEMENTARY MATERIAL

Table S1 – Correlations of environmental variables sampled on the collection sites on the mainland: GCR - Governador Celso Ramos; and in the Santa Catarina Archipelago: UCAD - Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI - Peri Lagoon Municipal Monument on the Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IA – Anhatomirim Island; IDF – Dona Francisca Island; IL – Laranjeiras Island. Highly correlated variables of bare soil cover and basal area of first shrub were eliminated. Vegetation cover and basal area of first tree variables were also eliminated as they are redundant with the other variables. Variables in bold were the variables kept for the analysis.

Correlations of environmental variables										
-	**Leaf litter cover**	Bare soil cover	Vegetation cover	**Canopy cover**	**First tree distance**	Basal area of first tree	**First tree height**	**First shrub distance**	Basal area of first shrub	**First shrub height**
Leaf litter cover	—	0.43	0.60	0.62	0.31	0.36	0.55	0.15	0.05	0.49
Bare soil cover		—	0.14	0.65	0.39	0.20	0.30	0.83	0.78	0.82
Vegetation cover			—	0.04	0.07	0.15	0.35	0.45	0.16	0.01
Canopy cover				—	0.83	0.22	0.025	0.68	0.36	0.78
First tree distance					—	0.042	0.15	0.53	0.11	0.59
Basal area of first tree						—	0.59	0.30	0.03	0.25
First tree height							—	0.38	0.63	0.28
First shrub distance								—	0.69	0.68
Basal area of first shrub									—	0.73
First shrub height										—

Table S2 – Richness and exponential Shannon Entropy of dung beetle species sampled on the mainland: GCR - Governador Celso Ramos; and in the Santa Catarina Archipelago: UCAD - Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI - Peri Lagoon Municipal Monument on the Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IA – Anhatomirim Island; IDF – Dona Francisca Island; IL – Laranjeiras Island.

Site	Diversity	Observed	Estimator	s.e.	LCL	UCL
GCR	Species richness	8.0	10.2	3.4	8.3	26.9
	Shannon diversity	3.3	3.4	0.4	3.3	4.2
UCAD	Species richness	11.0	11.7	1.3	11.1	18.8
	Shannon diversity	3.4	3.5	0.3	3.4	4.2
PERI	Species richness	8.0	8.5	1.3	8.0	16.4
	Shannon diversity	2.7	2.8	0.2	2.7	3.3
IARV	Species richness	3.0	3.0	0.5	3.0	4.5
	Shannon diversity	2.0	2.0	0.1	2.0	2.2
IC	Species richness	2.0	2.0	0.0	2.0	2.0
	Shannon diversity	2.0	2.0	0.0	2.0	2.0
IRG	Species richness	2.0	2.0	0.0	2.0	2.0
	Shannon diversity	1.7	1.7	0.1	1.7	1.9
IDF	Species richness	2.0	2.0	0.0	2.0	2.0
	Shannon diversity	1.5	1.5	0.1	1.5	1.7
IL	Species richness	1.0	1.0	0.0	1.0	1.0
	Shannon diversity	1.0	1.0	0.0	1.0	1.0

Table S3 – Correlations between all variables measured and inserted in the GLMs. Area – island area; Distance – distance from the nearest large landmass (continent or Santa Catarina Island); Vegetation – scores from a principal component analysis of vegetation structure; Temperature – mean of soil temperature measured at each local during dung beetle collections.

-	p Value				
Correlation coefficient	Richness	**<0.01**	**0.02**	**0.07**	0.68
	0.98	Area	**0.05**	0.13	0.73
	0.78	**0.70**	Distance	0.24	0.63
	-0.63	-0.55	-0.47	Vegetation	0.67
	-0.16	-0.13	-0.20	0.17	Temperature

Table S4 – Environmental variables sampled on the collection sites on the mainland: GCR - Governador Celso Ramos; and in the Santa Catarina Archipelago: UCAD - Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI - Peri Lagoon Municipal Monument on the Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IA – Anhatomirim Island; IDF – Dona Francisca Island; IL – Laranjeiras Island.

Sites	**GCR**	**UCAD**	**PERI**	**IARV**	**IC**	**IRG**	**IDF**	**IA**	**IL**
Leaf litter cover (%)	78.4	69.7	69.4	75.9	81.9	83.8	64.4	58.5	65.6
Bare soil cover (%)	2.5	4.4	4.1	12.8	5.3	4.4	1.3	22.5	5.6
Vegetation cover (%)	19.1	25.9	26.6	28.8	13.5	11.9	34.4	19.0	29.4
Canopy cover (%)	93.8	87.5	87.2	86.6	85.6	84.6	76.3	68.1	88.8
Leaf litter height (cm)	6.8	3.2	5.8	NA	2.1	3.8	6.6	1.9	5.3
First tree distance (m)	2.2	2.1	1.7	2.3	2.3	2.7	3.2	3.2	2.0
Basal area of first tree (cm^2)	270.3	316.5	215.2	106.4	274.7	98.2	193.5	322.1	168.8
First tree height (m)	11.8	14.2	12.1	6.1	8.3	8.3	11.9	10.9	11.9
First shrub distance (m)	0.7	1.3	0.7	1.5	1.8	1.4	0.9	2.5	0.9
Basal area of first shrub (cm^2)	3.4	3.3	7.0	13.1	9.4	3.7	2.6	11.8	3.3
First shrub height (m)	2.5	1.8	2.7	3.3	3.0	2.1	3.1	4.7	2.3

Figure S1 – Sample sites on the mainland: GCR – Governador Celso Ramos; and in the Santa Catarina Archipelago: UCAD – Desterro Environmental Conservation Unit on the Santa Catarina Island; PERI – Peri Lagoon Municipal Monument on the Santa Catarina Island; IARV – Arvoredo Island; IC – Campeche Island; IRG – Ratones Grande Island; IA – Anhatomirim Island; IDF – Dona Francisca Island; IL – Laranjeiras Island.

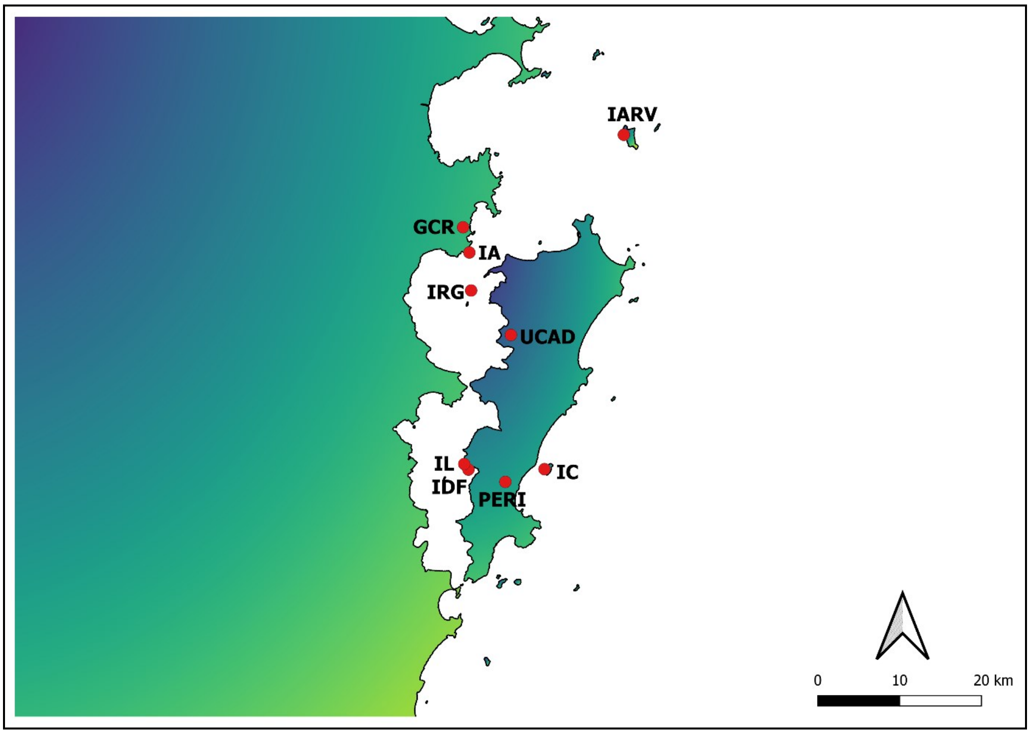
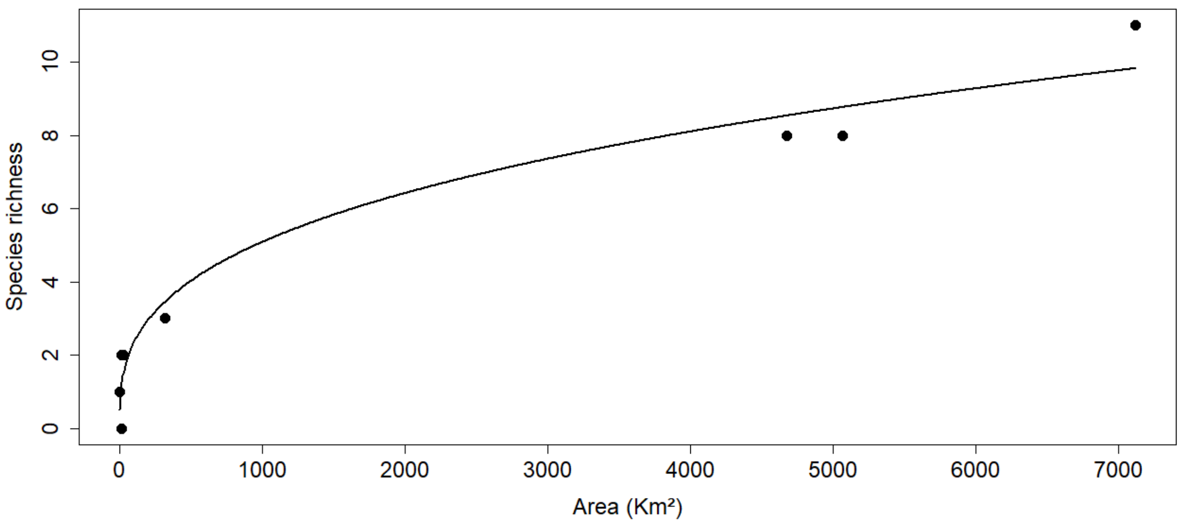


Figure S2 – Logistical species-area curve representing observe the relationship between species richness and area (z=0.34, p=0.03), the significant variables of the top ranked GLM. The sites represented are the mainland Governador Celso Ramos and the Santa Catarina Archipelago: Desterro Environmental Conservation Unit on the Santa Catarina Island; Peri Lagoon Municipal Monument on the Santa Catarina Island; Arvoredo Island; Campeche Island; Ratones Grande Island; Anhatomirim Island; Dona Francisca Island; Laranjeiras Island.



CONCLUSÃO GERAL

A partir do estudo dos besouros escarabeíneos no Arquipélago de Santa Catarina e no continente próximo é possível concluir que mesmo em ilhas costeiras próximas há isolamento suficiente para gerar modificações morfológicas de populações, evidenciadas pelas diferenças de tamanho e forma corporal encontradas para diferentes populações da espécie *Canthon rutilans cyanescens* nas ilhas do arquipélago. Além disso, concluímos que a área das ilhas é o principal fator estruturante da riqueza de espécies de escarabeíneos nestes locais devido à competição por recursos, uma vez que o isolamento afeta todas as ilhas igualmente devido à barreira marinha e que, de modo geral, as ilhas do arquipélago apresentam uma baixa riqueza e diversidade de escarabeíneos, possivelmente limitada pela quantidade de recursos alimentares disponíveis.

Assim, as evidências apresentadas neste trabalho reforçam a hipótese de que a ocorrência dos besouros escarabeíneos nas ilhas do Arquipélago de Santa Catarina se dá por conta da permanência destes insetos desde o período que antecede a formação destas ilhas, possivelmente durante o Último Máximo Glacial e modificadas ao longo do tempo por pressões de interações competitivas entre espécies.

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