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LANDSCAPE EFFECTS ON BIODIVERSITY ARE CONTEXT DEPENDENT – INSULARIZATION DRIVES PHYSIOLOGICAL CONDITION OF AMAZONIAN DUNG BEETLES

MANAUS, AMAZONAS

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Ao 01 dia do mês de setembro do ano de 2023, às 12:h30min, via videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o Dr. **Víctor Arroyo-Rodriguez**, da Universidad Nacional Autónoma de México – UNAM, o Dr. **José Daniel Rivera Duarte**, da Universidad Nacional Autónoma de México – UNAM e o Dr. **Filipe Machado França**, da Universidade de Bristol, tendo como suplentes o Dr. Rodrigo Felipe Rodrigues do Carmo, da Universidade Federal Rural de Pernambuco – UFRPE e o Dr. Lucas Ramos Costa Lima, da Universidade Estadual do Piauí – UESPI, sob a presidência do orientador, a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **LEONARDO VILAS-BÔAS M.P. DE CERQUEIRA**, intitulado: **"LANDSCAPE EFFECTS ON BIODIVERSITY ARE CONTEXT DEPENDENT– INSULARIZATION DRIVES PHYSIOLOGICAL CONDITION OF AMAZONIAN DUNG BEETLES"**, orientado pelo Dr. Renato Portela Salomão, da Universidad Nacional Autónoma de México – UNAM e coorientado pelo Dr. Daniel Matías González Tokman, do The Institute of Ecology – INECOL .

Após a exposição, o(a) discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

[X] APROVADO (A) [ ] REPROVADO (A)

[X] POR UNANIMIDADE [ ] POR MAIORIA

Nada mais havendo, a presente ata foi lida, lavrada e assinada pelos membros da Comissão Examinadora.

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Sinopse:

O estudo avaliou o efeito da insularização sobre a condição fisiológica de besouros rola bosta. Mais especificamente, se avaliou o efeito do tamanho, forma e isolamento das ilhas, bem como a proximidade, cobertura florestal e área proporcional de floresta de dossel fechado sobre o tamanho corporal, massa muscular, massa lipídica e peso total de besouros rola bosta. Analisamos os efeitos da insularização em diferentes escalas espaciais e sobre as escalas biológicas de assembleia e espécie.

Palavras chaves: Fragmentação de hábitat, hidroelétrica, ecologia de paisagem, impacto ambiental, ilhas.

Para o meu querido sobrinho ou sobrinha,

Mesmo antes vir ao mundo, saiba que já ocupas um lugar especial em meu coração. Que você cresça em meio a um ambiente repleto de amor, conhecimento e sabedoria. Que nunca lhe falte a curiosidade para questionar, a coragem para buscar respostas e a compaixão para se importar com o próximo. Que este estudo seja apenas o início de uma jornada repleta de aprendizado e realizações para você.

Com muita expectativa,

Titio Léo.

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A todos os participantes e colaboradores que gentilmente dedicaram seu tempo e conhecimento para contribuir com esta pesquisa, minha sincera gratidão. Sem a participação de vocês, este estudo não seria possível, e espero que os resultados aqui obtidos possam retribuir de alguma forma à sociedade o que generosamente foi compartilhado.

Ao INPA e todas as instituições de ensino em que pude participar, além de todos os profissionais envolvidos, obrigado por proporcionarem um ambiente propício ao aprendizado e à pesquisa, nutrindo o desejo constante pelo saber.

Por fim, como um lembrete, dedico esta dissertação a mim mesmo. Foram muitos desafios ao longo do percurso, mas acreditei em minha capacidade e superei limites. Que este trabalho seja uma inspiração para enfrentar novos desafios e jamais cessar o desejo de aprender e crescer.

Que este estudo possa contribuir, mesmo que modestamente, para a ampliação do conhecimento em nossa área, e que seja útil para futuras pesquisas e nas mentes daqueles que, assim como eu, buscam compreender o mundo.

Com muito carinho,

Leo.

RESUMO

A degradação e fragmentação das paisagens naturais em fragmentos isolados ameaçam a manutenção das espécies em ecossistemas antrópicos. A insularização, causada por atividades humanas como a construção de barragens de hidroelétricas, leva à perda e fragmentação de habitats, afetando negativamente a biodiversidade. Neste estudo, focaremos na abordagem fisiológica como uma ferramenta-chave para compreender o impacto da insularização nos organismos. Este estudo avaliou os efeitos da insularização sobre a condição fisiológica de assembleias, utilizando besouros rola bosta como organismos modelo. Nós investigamos a condição fisiológica e o tamanho corporal dos besouros rola bosta na Usina Hidrelétrica de Balbina, localizada na Amazônia Central. O lago desta Hidrelétrica é composto por várias ilhas de tamanhos, formas e distâncias variadas das florestas contínuas. Nós coletamos besouros rola bosta de várias ilhas e áreas contínuas de floresta usando armadilhas de queda. Analisamos os efeitos de diversas variáveis de paisagem, como tamanho, forma, isolamento, proximidade, cobertura florestal e tipo de habitat (ilha ou continente), sobre a condição fisiológica (massa muscular, massa lipídica e peso seco) e o tamanho corporal dos besouros rola bosta. Utilizamos duas abordagens para avaliar o impacto da insularização nos besouros rola bosta: no nível individual e no nível de assembleias. Em escala de assembleia, os resultados indicaram que a cobertura florestal apresentou uma relação positiva com o tamanho corporal dos besouros rola bosta. No entanto, o tipo de habitat não afetou o tamanho ou a massa corporal dos besouros. Quando analizando os efeitos a escala de espécies, respostas contrastantes foram encontradas a depender daespécies analizada. Ilhas maiores tendiam a abrigar indivíduos maiores de certas espécies de besouros rola bosta, como *Deltochilum aspericolle*. Enquanto isso, os indivíduos do continente, como *Dichotomius lucasi* e *Canthon triangularis*, possuíam tamanho corporal maior do que os das ilhas. A proporção de floresta com dossel fechado também influenciou os atributos fisiológicos, com algumas espécies, como *C. triangularis*, apresentando maiores massas de lipídios em paisagens com maior proporção de dossel fechado enquanto *D. aspericolle* e *Dichotomius boreus* apresentando menores massas de lipídios em paisagens com maior proporção de dossel fechado. Este estudo lança luz sobre o impacto da insularização na condição fisiológica e no tamanho corporal dos besouros rola bosta na região Amazônica. As descobertas contribuem para uma melhor compreensão de como a fragmentação e a perda de habitat afetam a biodiversidade em paisagens insulares. Tais informações podem auxiliar no desenvolvimento de estratégias eficazes de conservação para mitigar as consequências adversas da construção de barragens e da fragmentação de habitats na biodiversidade Amazônica.

ABSTRACT

The degradation and fragmentation of natural landscapes into isolated fragments threaten species survival in anthropogenic ecosystems. Insularization, caused by human activities such as the construction of hydroelectric dam reservoirs, leads to habitat loss and fragmentation, negatively impacting biodiversity. In this study, we focus on the physiological approach as a key tool to understand the impact of insularization on organisms. We evaluated the effects of insularization on the physiological condition of assemblages, using dung beetles as model organisms. We investigated the physiological condition and body size of dung beetles at the Balbina Hydroelectric Reservoir in the Central Amazon region. The reservoir comprises numerous islands of varying size, shape, and distance from continuous forests. We collected dung beetles from multiple islands and continuous forest areas using pitfall traps. We analyzed the effects of various landscape variables, including size, shape, isolation, proximity, forest cover, and habitat type (island or mainland), on dung beetle physiological condition (muscle mass, lipid mass, and body dry mass) and body size. We used two approaches to assess the impact of insularization on dung beetles: at the individual and assemblage levels. At the assemblage level, the results indicated that forest cover positively influenced dung beetle body size. However, habitat type did not affect the size or body dry mass of the beetles. When analyzing the effects at the species level, contrasting responses were found depending on the species analyzed. Larger islands tended to harbor larger individuals of certain dung beetle species, such as Deltochilum aspericolle, while mainland individuals, such as Dichotomius lucasi and Canthon triangularis, had larger body sizes than those on islands. The proportion of closed-canopy forest also influenced physiological attributes, with C. triangularis exhibiting larger lipid masses in landscapes with a higher proportion of closed-canopy, while D. aspericolle and Dichotomius boreus showed smaller lipid masses in such landscapes. This study sheds light on the impact of insularization on the physiological condition and body size of dung beetles in the Amazon region. The findings contribute to a better understanding of how habitat fragmentation affects biodiversity in island landscapes. Such information can help develop effective conservation strategies to mitigate the adverse consequences of dam construction and habitat fragmentation on Amazonian biodiversity

SUMÁRIO

INTRODUÇÃO GERAL

A degradação e divisão de paisagens previamente continuas têm efeitos significativos na sobrevivência e persistência das populações de espécies que habitam esses ecossistemas (Thomas, 2000; Chase et al., 2020). A fragmentação de habitats é um tema amplamente estudado em matrizes terrestres, como plantações, pastagens e áreas urbanas (por exemplo, Williams et al., 2006; Didham, 2010; Liu et al., 2016). No entanto, a compreensão das dinâmicas de fragmentação em matrizes não terrestres ainda é um campo de pesquisa pouco explorado (por exemplo, Benchimol & Peres, 2015). A insularização devido a atividades antrópicas corresponde ao processo de perda e fragmentação de habitats imersas em matrizes aquáticas, representa uma ameaça contínua para a biodiversidade global (Krauss et al., 2010). Atividades humanas como a construção de barragens hidrelétricas, diminuem a disponibilidade de recursos e interrompem processos ecológicos essenciais devido à criação de paisagens fragmentadas (Didham, 2010). A presença de corpos de água, como rios ou lagos, atua como uma barreira intransponível para a maioria das espécies terrestres, impossibilitando a movimentação de indivíduos entre os fragmentos, o que intensifica os desafios enfrentados por essas populações (Benchimol & Peres, 2015). Essa realidade torna os locais insularizados em paisagens fragmentadas únicas, que podem servir como um aproximação para compreender dinâmicas de perda e/ou fragmentação de ambientes naturais e suas consequencias sobre a biodiversidade. Além disso, a análise da dinâmica de insularização pode ajudar a identificar os pontos críticos onde as intervenções de conservação são mais urgentes e necessárias para preservar a diversidade biológica e os serviços ecossistêmicos essenciais para a sustentabilidade do planeta.

A avaliação dos processos ecológicos em diferentes escalas biológicas proporciona uma visão mais completa e abrangente da dinâmica dos ecossistemas (Start et al., 2019). Ao analisar as respostas das espécies à mudanças ambientais, pesquisadores têm utilizado diferentes abordagens com o objetivo de entender distintas facetas das dinâmicas ecológicas em paisagens antrópicos (Wellnitz et al., 2001). A análise em nível de espécies individuais fornece uma compreensão mais detalhada, enquanto a observação em grupos de espécies oferece uma visão mais ampla das interações ecológicas (Laforge et al., 2016; Pecher et al., 2010). Dentre as diversas abordagens, estudos de condição fisiológica emerge como essencial para compreender como os organismos se adaptam e respondem às mudanças nos habitats (Buckley et al., 2011; Cooke et al., 2013). Através do estudo de atributos fisiológicos específicos, como a massa de lipídios, massa muscular e peso corporal, os pesquisadores podem obter informações valiosas sobre as estratégias de sobrevivência, comportamento de interação intra e interpopulacional, e respostas ao ambiente em nível de indivíduos e assembleias (França et al., 2016; Salomão et al., 2018, 2020). Além disso, a condição fisiológica dos organismos tem implicações diretas no comportamento das espécies e nos serviços ecossistêmicos que elas fornecem (Adolph, 1990; Amundrud & Srivastava, 2015; Servín-Pastor et al., 2021; Salomão et al., 2021). A integração de perspectivas fisiológicas e ecológicas em diferentes escalas biológicas, como espécies e assembleias permitem uma compreensão em escalas mais gerais e pontuais de processos ecológicos.

Os besouros rola bosta (Coleoptera: Scarabaeinae) são altamente sensíveis tanto a mudanças naturais quanto a intervenções humanas no ambiente (Halffter & Favila, 1993; Nichols et al., 2007; Correa et al., 2020). Esses insetos são capazes de responder rapidamente a alterações nos atributos do habitat em diferentes escalas, desde a nível de espécie até o nível de assembleias (França et al., 2016a; Silva et al., 2019). Além disso, eles estabelecem relações importantes com outros animais, como mamíferos, o que pode modular as assembleias desses besouros. Através de sua resposta rápida e fina a condições bióticas e abióticas, os besouros rola bosta podem servir como aproximações sobre a saúde e a resiliência dos ecossistemas em que habitam (Halffter & Favila, 1993; Gardner et al., 2008). Diversos estudos têm demonstrado que estes besouros são suscetíveis a mudanças nas condições ambientais (e.g. exploração seletiva de madeira, urbanização, expansão agrícola), que afetam a estrutura das suas assembleias e populações (Salomão et al., 2019; Correa et al., 2020; Cultid-Medina et al., 2015; Barreto et al., 2023). No entanto, para uma compreensão mais profunda das implicações das mudanças ambientais na biodiversidade e na saúde dos ecossistemas, estudos sobre a condição fisiológica individual dos besouros rola bosta têm sido cada vez mais reconhecidos a partir da última década. Observou-se que a condição fisiológica desses insetos é negativamente afetada pelas perturbações florestais, fragmentação de habitats e urbanização, refletindo o estresse imposto por essas transformações ambientais

(França et al., 2016b; Salomão et al., 2018, 2020). Medir a condição física desses besouros tornou-se uma ferramenta fundamental para prever como as espécies respondem e se adaptam às mudanças ambientais, ajudando os pesquisadores a entender os impactos dessas transformações no ecossistema em geral (Cooke et al., 2013; França et al., 2016; Salomão et al., 2018, 2020).

A construção de barragens na região Amazônica tem implicações significativas para a biodiversidade e representa um desafio para a dinâmica única desse ecossistema. Essas barragens geram ecossistemas fragmentados e o isolamento de diferentes habitats (Tullos et al., 2014), interrompendo a conectividade de habitats nativos e afetando a distribuição das espécies (Smith et al., 2017), bem como as dinâmicas populacionais (Jellyman et al., 2012; Ngor et al., 2018) e interações ecológicas (Zhu et al., 2021). Entretanto, para o nosso conhecimento não há estudos avaliando as consequencias destas barragens sobre a condição fisiológica das populações que sobrevivem nestas paisagens. O estudo das respostas fisiológicas de espécies e assembleias no contexto das mudanças na composição e estrutura da paisagem pode servir como peça chave para compreender a capacidade adaptativa e a vulnerabilidade dos organismos diante da fragmentação do habitat. Através da análise da fisiologia, os pesquisadores podem obter uma visão mais profunda dos efeitos dessas alterações no ambiente sobre os organismos, como a forma como a energia é alocada e como ocorre a resposta ao estresse em situações de mudanças ambientais (Terborgh et al., 2001). Portanto, as barragens na Amazônia servem como um excelente modelo para estudar as dinâmicas da insularização e os impactos na condição fisiológica das espécies e grupos presentes na região.

OBJETIVOS

Este estudo teve como objetivo investigar os efeitos da insularização na condição fisiológica e no tamanho corporal de besouros rola bosta em um arquipélago florestal na região central da Amazônia. Especificamente, buscamos avaliar o efeito do tamanho, forma, isolamento, proximidade, cobertura florestal e área proporcional de floresta de dossel fechado sobre o tamanho corporal, massa muscular, massa de lipídios e massa seca dos indivíduos. Este estudo foi realizado através de duas escalas biológicas: escala de grupo (assembleia) e escala de espécie. Os processos de insularização geram mudanças na disponibilidade, diversidade e qualidade dos habitats em termos de recursos e grau de perturbação (Welter-Schultes & Williams, 1999; Karanth et al., 2000; Kessler et al., 2005; Crouzeilles et al., 2014; Nyafwono et al., 2015). Com base nesta premissa, ilhas maiores, mais conectadas e com maior cobertura florestal associada devem manter indivíduos com maiores valores de massa seca, a massa muscular e de lipídios, bem como o tamanho corporal. Para a abordagem em escala de espécie, utilizamos as espécies de besouros rola bosta mais amplamente distribuídas na região como organismos-modelo: *Ateuchus murray*, *Canthon triangularis*, *Deltochilum aspericole*, *Dichotomius lucasi* e *Dichotomius boreus*. Até onde sabemos, esta é a primeira avaliação dos efeitos da insularização de uma grande barragem hidrelétrica na condição fisiológica e características corporais de besouros rola bosta em uma paisagem Amazônica.

Capítulo 1

CERQUEIRA, L. V. B. M. P.; TOKMAN, D. G.; CORREA, C. M. A.; STORK-TONON, D.; CUPELLO, M.; SALOMÃO, R. P.

Landscape effects on biodiversity are context dependent – insularization drives physiological condition of Amazonian dung beetles

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Landscape effects on biodiversity are context dependent – insularization drives physiological condition of Amazonian dung beetles

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Abstract

The degradation and fragmentation of natural landscapes pose serious threats to species' population healthy, consequently impairing their survival and maintenance. While most research on habitat fragmentation focuses on terrestrial matrices, the impact on non-terrestrial environments remains poorly understood. Insularization, primarily caused by activities like dam construction, leads to habitat loss and fragmentation, negatively affecting biodiversity.To assess the effects of insularization, we conducted a study on the key aspect of dung beetle physiological condition and body size in the Balbina Hydroelectric Reservoir located in the Central Amazon region. We evaluated this aspect at both individual species and assemblage levels, collecting dung beetles from islands and continuous forest areas while analyzing various landscape variables.The results revealed that landscapes with higher forest cover positivelly affected dung beetle body size. Interestingly, dung beetles response to insularization were species-dependent; larger islands tended to host larger individuals of *Deltochilum aspericole*, while in *Canthon triangulares*, smaller islands showed larger body sizes. However, similar to *Dichotomius lucasi*, individuals from the mainland were larger than those from the islands. Moreover, the proportion of closed-canopy forest in the landscapes also impacted physiological attributes. It negatively affected the body size of *Deltochilum aspericole* and the lipid mass of *Dichotomius boreus*, but positively affected the lipid mass of *Canthon triangulares*. This study sheds light on the impact of insularization on dung beetles' physiological condition and body size. The findings contribute to a better understanding of how habitat fragmentation affects biodiversity. This knowledge is essential in formulating effective conservation strategies for preserving the unique biodiversity of the Amazon region and mitigating the consequences of dam construction.

Keywords: Habitat fragmentation, Amazon rainforest, landscape ecology, environmental impact, Scarabaeinae.

Introduction

The degradation and division of previously intact landscapes into isolated fragments have detrimental effects on the survival and persistence of species (Thomas, 2000; Chase et al., 2020). While most studies focus on the ecological consequences of habitat fragmentation in plantation, pasture, and urban matrices (e.g. Williams et al., 2006; Didham, 2010; Liu et al., 2016), few studies analyze such dynamics in non-terrestrial matrices (e.g. Benchimol & Peres, 2015). Anthrpogenic-caused insularization, characterized by the loss and fragmentation of habitats, represents a continuous threat for global biodiversity (Krauss et al., 2010). This concerning phenomenon leads to increased habitat isolation, reduced resource availability, and disruption of ecological processes due to the established fragmented landscapes (Didham, 2010). The presence of water as an impassable matrix act as an insurmountable barrier for most terrestrial species (Benchimol & Peres, 2015), exacerbating the challenges they face. Consequently, anthropogenic insularized sites (e.g. hydroelectric dams) comprise a unique fragmented landscape that can be used as a proxy for assessing the loss and fragmentation of natural environments.

By the assessment of ecological processes under different biological scales, novel and wide insights can be drawn (Start et al., 2019). Individual-species scale and the species assemblages scale has been used to present, respectively, finer and coarser understanding of ecological processes (Wellnitz et al., 2001). When analyzing species-scale response, different approaches can be used, as population structure (Laforge et al., 2016; Pecher et al., 2010), behavior (Pinaud et al., 2007; Leu et al., 2016) and physiological condition (Buckley et al., 2011; Cooke et al., 2013). Amongst these approaches, the physiological-condition stands out as essential for comprehending the ecological dynamics associated with habitat changes. Through the study of specific physiological attributes such as lipid mass, muscle mass, and body dry mass, valuable insights can be obtained regarding how individuals, species, and assemblages adapt and respond to altered environmental conditions (França et al., 2016; Salomão et al., 2018, 2020). Moreover, physiological condition has consequences on species behavior and on the ecosystem services provided by them (Adolph, 1990; Amundrud & Srivastava, 2015; Salomão et al., 2021; Servín-Pastor et al., 2021). This integrative approach, combining physiological and ecological perspectives at species and assemblage scale enhances our understanding of the complex relationships between organisms and their transforming habitats, thereby facilitating the development of effective conservation strategies.

Dung beetles (Coleoptera: Scarabaeinae) are excellent indicators of environmental transformation on biodiversity (Halffter & Favila, 1993; Nichols et al., 2007; Correa et al., 2020), responding to changes in biotic and abiotic attributes at both species and assemblage scales (França et al., 2016a; Silva et al., 2019). Studies have demonstrated that dung beetles undergo changes in assemblage attributes (Salomão et al., 2019; Correa et al., 2020) and population structure (Cultid-Medina et al., 2015; Barreto et al., 2023). More recently, individual physiological conditions (e.g. body dry mass, muscle mass, fat mass, see França et al., 2016b; Salomão et al., 2018, 2020) have gained relevance to understand the consequences of environmental changes on biodiversity. Regarding their physiological response towards habitat transformation, it has been observed that dung beetle physiological condition is negatively affected by forest disturbances such as selective logging (França et al., 2016b), fragmentation (Salomão et al., 2018), and urbanization (Salomão et al., 2020). It is important to highlight that some ecological effects on biodiversity may be observed at physiological-condition scale, but not when analyzing broader approaches, as population and assemblage structure (Cooke et al., 2013). Therefore, physical condition measurements can aid to predict how species respond to environmental change (see Cooke et al., 2013; França et al., 2016; Salomão et al., 2020).

The construction of dams in the Amazon region has significant consequences for biodiversity, posing a challenge to its unique and complex ecological dynamics. Dams disrupt and alter continuous rivers and surrounding habitats, leading to the isolation of habitats and the creation of fragmented ecosystems (Tullos et al., 2014). This disruption of natural connectivity has far-reaching impacts on species composition (Smith et al., 2017), population dynamics (Jellyman et al., 2012; Ngor et al., 2018), and ecological interactions (Zhu et al., 2021). Studying the physiological responses of species and assemblages in the context of shifts in landscape composition and structure is crucial for understanding the adaptive capacity and vulnerability of organisms to habitat fragmentation. The Amazonian dams serves as an excellent, but alarming, model for studying the dynamics of insularization and its effects on the physiological condition of species and assemblages (Terborgh et al., 2001). By studying the ecological communities that inhabit forest remnants in Amazonian dams, it is possible to assess how changes in landscape structure and connectivity influence physiological processes, such as energy allocation and stress response. Moreover, effective conservation strategies can be developed to mitigate adverse consequences (Cooke et al., 2013), as those imposed on Amazonian biodiversity due to the establishment of dams.

This study aimed to investigate the effects of insularization on the physiological condition and body size of dung beetles in a forest archipelago in central Amazon. Specifically, we aimed to evaluate the effect of habitat type (island and continous forests), island size, shape, isolation, proximity, forest cover and the proportional area of closed-canopy forest on body size, muscle mass, lipid mass, and body dry mass of individuals. To attain the goal of our study, we analyzed such dynamics under two ecological approaches: assemblage scale and species scale. The insularization processes generate changes in habitat availability, diversity, and quality in terms of resource availability and disturbance degree (Welter-Schultes & Williams, 1999; Crouzeilles et al., 2014; Nyafwono et al., 2015). Thus, we predict that body dry mass, muscle and lipid mass, and body size will be higher in larger, more connected islands with greater associated forest cover. For species-scale approach, we used the most widely distributed dung beetle species in the region as model organisms: *Ateuchus murray*, *Canthon triangularis*, *Deltochilum aspericole*, *Dichotomius lucasi, and Dichotomius boreus.* To our knowledge, this is the first assessment of the insularization effects of a major hydroelectric dam on the physiological condition and body traits of dung beetles.

Material and Methods

Study site

The study was conducted in Balbina Hydroelectric Reservoir, located in the municipality of Presidente Figueiredo, Amazonas state, Brazil (1°52'S, 59°29'W). The reservoir was constructed in 1987, in the Uatumã River (a tributary of the Amazon River). With the closing of the Balbina dam, about 312 thousand hectares of tropical forest were flooded. Due to the topographically hilly characteristic of the area, the higher-altitude regions turned into approximately 3500 islands that vary in size (0.2 ha to 4879 ha), shape, and distance from the nearest continuous forest (ranging from about 0.05 km to about 20 km of distance, Benchimol & Peres, 2015).

According to Walker et al. (1999), the flooded vegetation was predominantly primary rainforest with an average tree height of 30-35 meters. Currently, the group of islands forms a diverse landscape, with some islands retaining their original vegetation, while others have been affected by fires and wind (Aurélio-Silva et al., 2016). It is possible to observe islands under forest regeneration process, with a predominance of ruderal herbaceous vegetation, and others with a mosaic of secondary and primary forest (Aurélio-Silva et al., 2016; Benchimol & Peres, 2015). The forests adjacent to the hydroelectric lake are classified as primary rainforests. The climate of the region is defined as hot, humid, and rainy tropical (Am according to Köppen classification), presenting an average annual rainfall of 2376 mm, with a rainy season occurring from November to April (Peel et al., 2007; Walker et al., 1999). The average annual temperature varies around 28°C, and the average relative humidity remains around 97.2% throughout the year.

Experimental design

Sampling was carried out between April and May (end of the rainy season) in 2022. The study was conducted on 20 islands within the reservoir and two adjacent continuous forest areas, each study site spacing at least 1 km from each other. The islands were selected to form a gradient of size, degree of isolation from the nearest continuous forest, and forest coverage.

In each study site, pitfall traps were used to collect dung beetles. Pitfall traps consisted of a cylindrical plastic container of 500 mL with a smaller bait-container plastic cup (50 mL) installed ca. 3 cm above the larger plastic container. A suspended plastic lid was installed over the trap to prevent the entry of leaves, branches, and rainwater. To preserve the collected material for physiological measurements, 70% ethanol was placed inside the container. Ten traps were installed in each island and in each continuous forest area, baited with approximately 25 g of fresh human feces. To maximize and standardize the sampling effort, each trap was placed at least 20 m apart from each other (adapted from Salomão et al., 2021). In addition, to avoid external influences on the sampling, the traps were placed at a minimum distance of 20 m from the forests edges (adapted from Salomão et al., 2021). All traps were active in field for 48 hours. The collected individuals were taken to National Institute of Amazonian Research (INPA) laboratories, where morphological traits and physiological condition were obtained.

Landscape variables

The landscape variables were obtained from Storck-Tonon et al. (2020). Therefore, using a seamless RapidEye mosaic (5 m pixel resolution) of georeferenced satellite imagery we obtained the island area (ha); island forest cover (%); the proportional area (%) of closed-canopy forest and island shape. Island shape was calculated using an index that comprises the ratio of the perimeter to the area of each. In addition, we also obtained a proximity index (proximity among islands within the 250, 500 and 1000 m) buffer and isolation index (isolation distance (m) from the nearest mainland site). The landscape variables were calculated using circular landscapes (buffers) of 250, 500 and 1000 m radius. These different scales will be used since the responses of tropical dung beetles vary according to the analyzed scale (e.g., Salomão et al., 2019, 2020). For more information on our landscape variables, see (Storck-Tonon et al. 2020).

Physiological condition and body size

Three indicators of physiological condition were used: body dry mass, lipid mass, and muscle mass. Body dry mass directly reflects individuals' fitness (Briffa & Sneddon, 2007; Córdoba-Aguilar et al., 2016); lipid mass represents the amount of energy reserves of individuals (Schulte-Hostedde et al., 2005); muscle mass is directly related to reproduction (Marden & Cobb, 2004) since it approximates courtship vigor and testicular mass (Droney & Hock, 1998). Following the procedures of Lee, Raubenheimer & Simpson (2004), to estimate body dry mass (i.e., dry weight), beetles were dried in a 50°C oven for 48 hours. Then, each individual was weighed using a

Mettler Toledo AB265-S precision balance with a resolution of 0.0001 g. Next, lipids were extracted by placing the individual dried beetles in containers containing 2 mL of chloroform for 24 hours, twice in a row. After this period, the beetles were dried (at the same time and temperature used previously) and weighed again. The difference between dry weight and the weight of the beetle after lipid extraction was considered as lipid mass. For muscle mass measurements, the procedures of Marden (1989) and Baines et al. (2015) were adjusted. After lipid mass was determined, beetles were placed in 2 mL of 0.8M KOH for 48 hours, rinsed, dried, and weighed again. The difference between the weight without lipid mass and this new weight was considered muscle mass. Body size was estimated from the widest linear distance of the pronotum margins (horizontal line in relation to the longitudinal axis of the individual) (Salomão et al., 2018). Body size was measured using digital images taken through an AxioCam ICc 3 camera attached to a ZEISS SteREO Discovery.V12 stereomicroscope.

Data analyses

To identify the spatial scale at which each landscape variable best explains our response variables, we used the area-landscape approach proposed by Fahrig (2013). Linear regressions were performed between landscape variables (island isolation index, proximity index, island size, percentage of closed-canopy forest) at different scales (250, 500, and 1000 m of radius) and each response variable. From these regressions, we used the coefficient of determination (R^2) as an estimator of the goodness of fit of each model. For our analyses, we only used the scale of landscapes with highest R^2 values (Fahrig, 2013).

We used linear mixed models (LMM) and generalized linear models (GLM) to analyze the effects related to insularization on the physiological condition and body size of dung beetles. As predictor variables, we used the landscape variables and the type of habitat (island or mainland). As response variable, we used individuals' body dry mass, lipid mass, muscle mass, and body size. For the variables body dry mass, lipid mass, and muscle mass, the values were relativized by the individuals' body size (i.e., individual body masses were divided by body size). In order to observe the magnitude of the effects of insularization on the physiological condition and body size of the beetles, we analyzed all species simultaneously (assemblage scale) and for each one separately (species scale). At the species scale, GLMs were performed with

Gaussian distribution and at assemblage scale, LMMs were performed with the species identity being considered as a random variable. At species scale, only the species that we collected more than 10 individuals and in more than 7 sites were selected. Therefore, for the species-scale analyses we used *Ateuchus murrayi, Canthon triangularis, Deltochilum aspericole, Dichotomius boreus, Dichotomius lucasi*. *Ateuchus* dung beetles from Amazonia have challenging taxonomic issues (Lopera-Toro et al., 2020), and thus we had logistical limitations to identify such dung beetles. Since physiological experiments need to be quickly conducted after collecting beetles, we were unable to make physiological experiments with *Ateuchus* species. Therefore, for *Ateuchus murrayi* beetles it was only possible to analyze the effects related to insularization on body size and body dry mass. Residual normality, homoscedasticity and presence of outliers were checked using the DHARMa package (Hartig, 2022). When variances were heterogeneous, different variance structures were tested. In order to use the predictor variables that best explained the distribution of dung beetles' physiological condition and body size, we performed model selection (Johnson & Omland, 2004). The best-supported model was selected based on the Akaike Information Criterion (AIC) value (Zuur et al., 2009), by the stepAIC function of the MASS package (Venables & Ripley, 2002). We used conditional graphs, via the visreg package (Breheny & Burchett, 2017), to visualize the fit of the regression model, which show the variation in the response variable (partial residual) in relation to the predictor variables alone (Breheny & Burchett, 2017). All analyses were performed using R software version 4.2.1 (R Core Development Team, 2020).

Results

A total of 321 individuals belonging to 20 species were collected (see Supplementary Material). The island with the highest abundance (Jabuti) comprised 37 individuals from six species. On the other hand, the three least abundant islands (Bacaba, Fuzarca and Pé Torto) had only one individual each, belonging to *D. subaenaeus*, *D. lucasi*, and *C. triangularis*, respectively (Supplementary Material). The most abundant species in island habitats were also the most widely distributed species (*C. triangularis* – n = 66, being recorded in six islands; *A. murrayi* – n = 51, recorded in seven islands). Interestingly, all 71 individuals of *Ateuchus simplex* were collected only from the mainland. Therefore, *A. simplex* was not included in the species-level analyses of insularization effects on individuals' physiological condition and body size. The rarest species, *Uroxys sp.* and *Deltochilum submetallicum* (Castelnau, 1840), were each represented by only one individual.

The largest and heaviest (i.e. highest body dry mass) species were *D. boreus* (15.16 ± 1.55 mm; 6.70 ± 2.20*10^{-1} g) and *D. subaenaeus* (9.64 ± 1.12 mm; 2.20 ± 0.80*10^{-1} g) (Table 1) and the smallest and lightest specie were *Uroxys sp*. (1.59 mm; 0.01*10^{-1} g) (Table 1). Among the species used to analyze insularization effects at the species-scale approach, *D. boreus* was the largest and heaviest and *A. murrayi* (2.69 ± 0.19 mm; 0.01 ± 0.02 g*10^{-1} g) was the smallest and lightest (Table 1). Also, according to the species used in the species-scale approach, *D. boreus* was the one with highest relative fat mass (6.04 ± 3.82*10^{-3} g), while *Deltochilum aspericole* was the one with lowest fat mass (0.45 ± 0.38*10^{-3}g, Table 1). *Deltochilum submetallicum* was the one with highest relative muscle mass (9.09*10^{-3} g), and *D. boreus* was the one with lowest relative muscle mass (1.53 ± 2.80 *10^{-3} g, Table 1).

The landscape scale that best explained the distribution of response variables in the following result sections are included in the Supplementary Material. Statistical effects of insularization, both at assemblage scale and species scale, are shown in Table 2. The variables not presented in the following statistical results were not included in the best model following the AIC criteria (see 'variables not selected by the best-supported model' in Table 2).

Assemblage-scale effects of insularization

The forest cover affected body size of dung beetle assemblages. Landscapes with higher forest cover encompassed dung beetles with larger body sizes (Fig. 2A). Regarding habitat type (island and mainland), individuals from the mainland have larger body size than those from the islands (Fig. 2B). However, habitat type did not affect dung beetles' body masses. Similarly, island shape, proximity, the proportion of closed canopy forest, island area and isolation did not affect individuals' body size and body masses.

Species-scale effects of insularization

Insularization effects on the studied dung beetle species are summarized in Table 2. Larger islands encompasses individuals with higher body dry mass in *D.*

aspericolle (Fig. 3A), but also encompassed individuals with lower body dry mass (Fig. 3B) and body size in *C. triangularis* (Fig. 3C). Moreover, larger islands were positively related with the amount of lipid mass in *D. aspericolle* (Fig. 3D). When comparing habitat types, mainland individuals of *D. lucasi* and *C. triangularis*, were statistically larger than those conspecifics recorded in islands (Figs. 3E and F, respectively). Landscapes with higher percentage of closed-canopy forest dwelled smaller-bodied populations of *D. aspericolle* (Fig. 3G), and lower lipid mass in the largest species, *D. boreus* (Fig. 3H). Nonetheless, the percentage of closed-canopy forests had a positive relationship with lipid mass in *C. triangularis* individuals (Fig. 3I). Islands with higher perimeter-to-area ratio present individuals with higher muscle mass in *D. boreus* individuals (Fig. 3J). Landscapes with higher island proximity dwelled larger individuals of *D. aspericolle* (Fig. 3K).

Discussion

In this study, we explored how insularization in the Amazonian forest has affected the body size and physiological condition of dung beetles 36 years after the creation of this human-made insular scenario caused by flooding in the Amazonian region. We analyzed these fitness-related traits of dung beetles under a landscape and habitat type perspective. At the species scale, island area and the proportional amount of closed-canopy forests emerged as the most determinant variables for body size and physiological condition of dung beetles. At the assemblage scale, habitat type and forest cover featured the most influential variables. Species of dung beetles responded differently to landscape metrics, emphasizing the importance of considering species-specific responses in when assessing ecological dynamics. By focusing on the physiological condition and body traits of dung beetles, our study offers a reliable proxy of how isolation and landscapes within islands impact the health and fitness of individual organisms in one of the most diverse regions in the world. Our results indicated that body size and physiological condition of the dung beetles vary between the islands and mainland. Such findings provided novel insights into landscape ecology, demonstrating the complex interplay between landscape metrics and assemblage-species-scale traits in shaping the body size and physiological condition of dung beetles.

Island area were important landscape-scale drivers of dung beetles' physiology and *body size*

The amount of habitats can affect the availability of food resources, microclimatic conditions, and habitat structure in tropical rainforests (Karanth et al., 2000; Nyafwono et al., 2015; Kessler et al.; 2005), which are known to influence dung beetles' metabolism, energy balance, and body traits (Feer, 2013; Batilani-Filho, 2017; Kerley et al., 2018, Salomão et al., 2018). Our study found that island area had a positive relationship with the body dry mass and lipid mass of *D. aspericolle*, but had a negative relationship with the body dry mass and body size of *C. triangularis*. Studies have shown that larger islands dwell higher mammal species richness and abundance (Palmeirim et al., 2018; Neto et al., 2022), which are the main providers of food resources for dung beetles (Nichols et al., 2008). Our results partially support the idea that larger islands offer more resources and more stable habitats, since *D. aspericolle* (but not *C. triangularis*) presented proxies of such trend. Under conditions of low food availability, such as on small islands, dung beetles may face trade-offs between allocating energy to processes such as reproduction and growth or investing energy on vital physiological functions such as maintenance and repair (Kooijman, 1986; Stearns, 1989). Competition for resources is another factor that can significantly impact animal fitness, particularly in habitats where resources are scarce or where species are abundant (Hanski, 1991; Rodenhouse et al., 2003; Sillet et al., 2004). Competition among individuals for access to those resources can lead to changes in the physiological and morphological characteristics of animals over time (Yund, 1991; Svanbäck et al., 2005; Svanbäck & Bolnick, 2007). Although competition and energetical availability are key factors in determining individual physiological condition, it is still uncertain what mechanisms could have driven the opposite patterns observed in *C. triangularis* and *D. aspericolle* beetles. Natural history and species traits (e.g., dial activity flight, perching and nesting behavior) may give us future cues of how each species uses and is affected by landscape parameters in disturbed forests.

Habitat Type Effects

We found that individuals from the mainland were larger than those from islands, but physiological condition was not affected by habitat type. Body size is determined during larval development, while physiological condition is sensitive to current conditions (Moczek, 1998; Karino et al., 2004; Baines et al., 2015). Thus, our results indicate that the insularization effects are not similar during larval development and adult stage. Indeed, insects larvae that feeds on high amount of good-quality resources emerge as large adults (Moczek, 1998; Karino et al., 2004), which may indicate, in a first moment, that resource availability/quality for larval development is different between mainland and islands. Body size is determinant for animal fitness, with large-bodied individuals tending to present higher mating success than smaller ones (Nosil, 2002; Arnott & Elwood, 2009; Chamorro-Florescano et al., 2011). In addition, larger beetles could have advantages in food competition, obtaining food more successfully, and therefore could choose the most valuable resource (i.e. the most nutritious one or the best resource for breeding) (Salomão et al. 2019). Thus, we may expect that intra- and interspecific competition dynamics within dung beetle assemblages could differ between mainland and the islands of the current ecosystem. Curiously, physiological condition trends were scale-dependent, with clear relationships between landscape metrics and physiological condition, but the absence of the effect of habitat type. The absence of habitat effect on physiological condition may indicate that the different island properties (e.g. landscape metrics, plant and animal diversity, vegetation structure) could blurry the potential consequences of insularization. Such trend is observed in ecological studies in tropical ecosystems (Douda, 2010; Lomba et al., 2011; Hernández et al., 2011), thus highlighting the importance to locate the best scale to explain ecological processes. An alternative hypothesis is that the smaller-bodied populations that dwells in islands could need present lower energetical needs, therefore buffering physiological consequences of insularized landscapes on individual physiological condition.

Special Topic 1: Forest Cover did not affect dung beetles' physiological condition

While the crucial role of forest cover in determining biodiversity in tropical ecosystems has been widely recognized (Arroyo-Rodríguez et al., 2016; Alvarado et al., 2018; Galán-Acedo et al., 2019; Watling et al., 2020), our study sheds light on the context-dependent nature of its influence. Specifically, our investigation of the Amazonian archipelago reveals that the impact of forest cover on biodiversity may differ in this unique ecological setting compared to others landscapes. When compared to other fragmented rainforest landscapes (e.g. Atlantic Forest), the Amazonian archipelago have different characteristics and ecological dynamics that set it apart. Possibly, one of the main differences is the water matrix, comprising a physical barrier for most animals and plants. The presence of islands, as well as factors like island area and proportion of closed-canopy forest, introduces additional complexities to the relationship between forest cover and biodiversity. Considering that matrix type is a determinant factor for forest fragmentation dynamics (Jules & Shahani, 2003; Prevedello & Vieira, 2010), we believe that the water-matrix fragmented landscape that we studied herein may play a key role for ecological dynamics. This hypothesis is reinforced by the previous study with dung beetle assemblages in the same Amazonian archipelago (Storck-Tonnon et al. 2020). Compared to rainforest patches in plantation or pastureland matrices (e.g. Quintero & Roslin, 2005; Filgueiras et al., 2015), the forest fragments in a water matrix maintain astonishingly poor species richness and abundance of dung beetles (Storck-Tonnon et al. 2020). Interestingly, our findings suggest that landscape metrics other than forest cover exert a stronger influence on the physiology and body size of dung beetles. Consequently, in the Amazonian archipelago, the relative importance of forest cover in determining dung beetles' physiology may be overshadowed by the effects of the water-matrix scenario. These factors likely play a more dominant role in shaping the ecological dynamics and characteristics of dung beetle assemblages in this specific context.

It is important to recognize that our findings do not diminish the overall importance of forest cover for biodiversity conservation in tropical ecosystems. Forest cover remains a fundamental factor for the maintenance of ecosystem stability, as it provides habitat, resources, and ecosystem services to a wide range of species (Lee et al., 2007; Solomon et al., 2019; Zellweger et al., 2020). However, in the case of the Amazonian archipelago, other environmental factors related to island dynamics and microclimatic conditions, such as island area and the proportion of closed-canopy forest, may exert a stronger influence on dung beetles' physiology. To gain a comprehensive understanding of the complex relationships between forest cover, environmental factors, and biodiversity in the Amazonian archipelago, further research is needed. Future studies could explore the specific mechanisms through which island characteristics and microclimatic conditions interact with forest cover to shape dung beetle health and fitness.

Special Topic 2: Species-Specific contrasting physiological response to insularization

One of the key results of this study comes from the specific and contrasting responses presented by each dung beetle species. Species-specific physiological responses may be related to ecological requirements (e.g. temperature conditions and landscape configuration) and life history strategies of each species (Salomão et al. 2018; Williamson et al. 2022). Our study reveals that the impact of the proportion of closed-canopy forests on dung beetle species is complex, with contrasting effects on the studied species. Specifically, we found a negative relationship between the proportion of closed canopy and the lipid mass of *D. boreus* individuals, but a positive relationship with the lipid mass of *C. triangularis* individuals. It is possible that each species has developed different ecological strategies in response to light, temperature, and humidity, which are influenced by closed canopy coverage. For example, *D. boreus* may gain a competitive advantage in open environments, benefiting from its adaptability as a nocturnal species. Interestingly, a study by Barretto et al. (2021) showed that a species of the genus *Dichotomius* exhibited reduced activity within forested areas and displayed higher mobility in non-forest areas. Conversely, *C. triangularis* may thrive in areas with closed canopy coverage, utilizing the canopy as a resource to find food due to its diurnal behavior. Our findings underscore the importance of understanding species-specific responses when assessing the impact of environmental changes on biodiversity and emphasize the need for further research on the physiological implications of habitat transformation.

Conclusion

Insularization effects on animal physiology remain largely untested and deserve further attention in organisms that play key roles in maintaining ecosystem functioning, such as dung beetles. Our results indicate that islands are more restrictive habitats for dung beetles than continuum forests. This study highlights the importance of categorizing systems to obtain a more comprehensive understanding of how environmental transformations affect species and community responses. It is worth noting that forest cover, isolation, island area and the amount of closed canopy forests plays a crucial role in determining biodiversity in tropical insular ecosystems. Nonetheless, our results were contrasting and species-dependent, providing a complex set of cause and consequences between landscape variables and assemblage and species physiological condition.

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Supplementary Material. Landscape variables of each studied island (A); distribution of dung beetles collected in each studied island (B); Spatial scale that bes explained the distribution of response variables (C).

Figure captions

Figure 1. Map of Brazil (A) highlighting the region of the Amazonas state that encompasses the reservoir of the Balbina Hydroelectric Power Plant, with the studied islands (red dots), and the mainland sites (green dots) (B).

Figure 2. Statistical models showing the assemblage-scale effects of forest cover (buffer 500m) (A) and habitat type (B) on body size.

Figure 3. Statistical models showing the effects of island area on body dry mass (A) of *Deltochilum aspericolle*; island area on body dry mass (B) of *Canthon triangularis*; island area on body size (C) of *Canthon triangularis*; island area on lipid mass (D) of *Deltochilum aspericolle*; habitat type on body size (E) of *Dichotomius lucasi*; and habitat type on body size (F) of *Canthon triangularis*; closed-canopy forest (buffer 250m) (G) on body size of *Deltochilum aspericolle*; closed-canopy forest (buffer 250m) on lipid mass (H) of *Dichotomius boreus*; closed-canopy forest on lipid mass (I) of *Canthon triangularis*; island shape on muscle mass (J) of *Dichotomius boreus*; island proximity (K) on body size of *Deltochilum aspericolle.*

Figure 1.

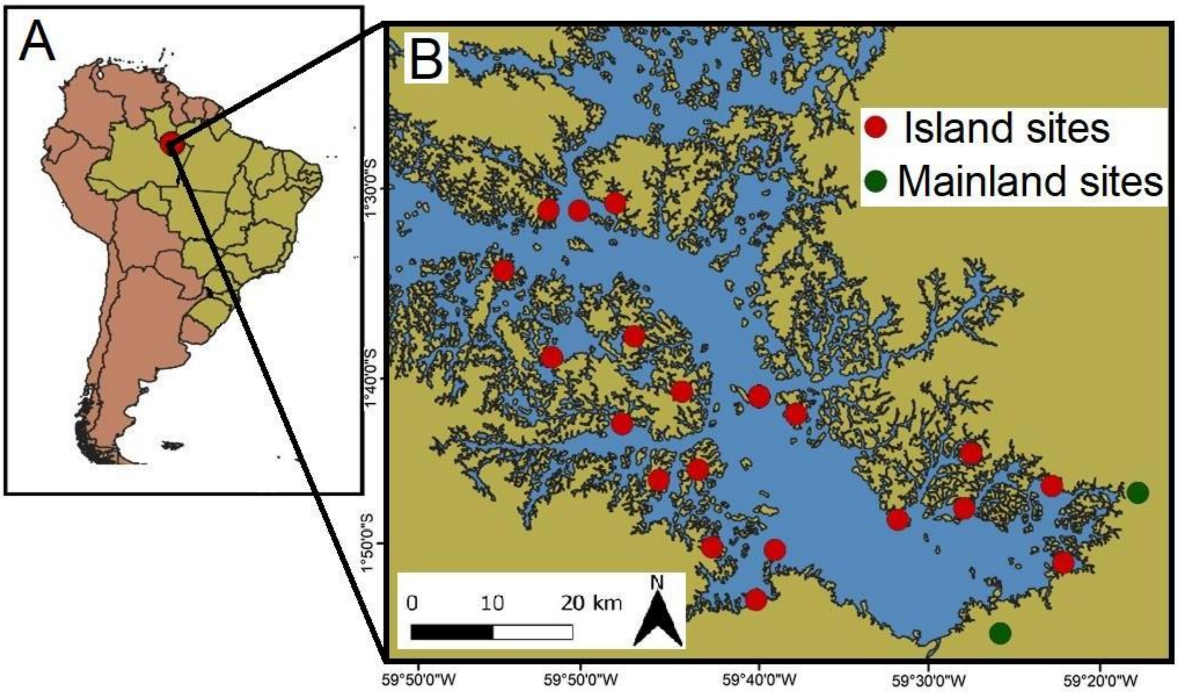

Figure 2.

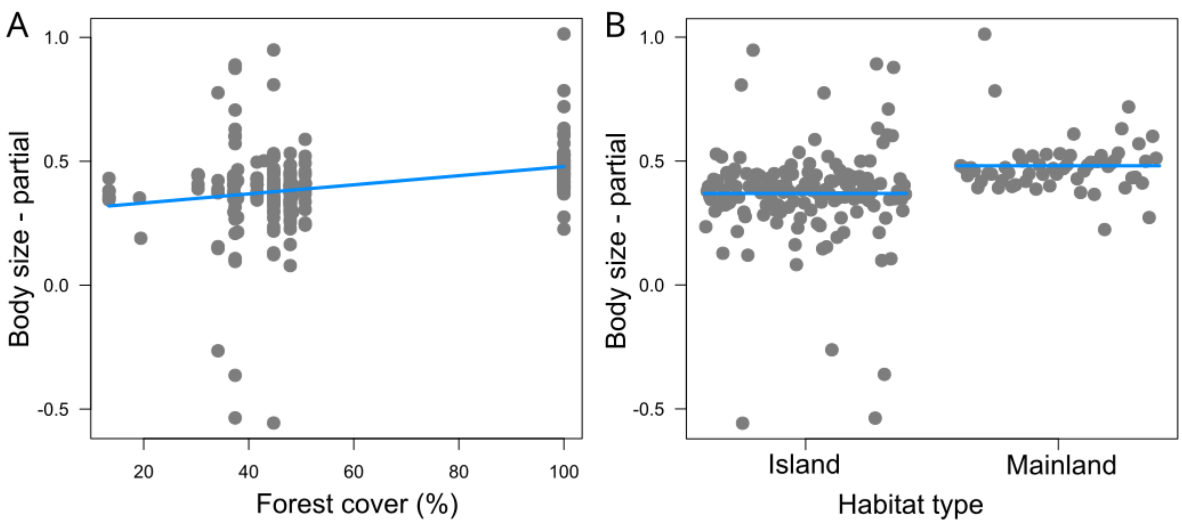

Figure 3.

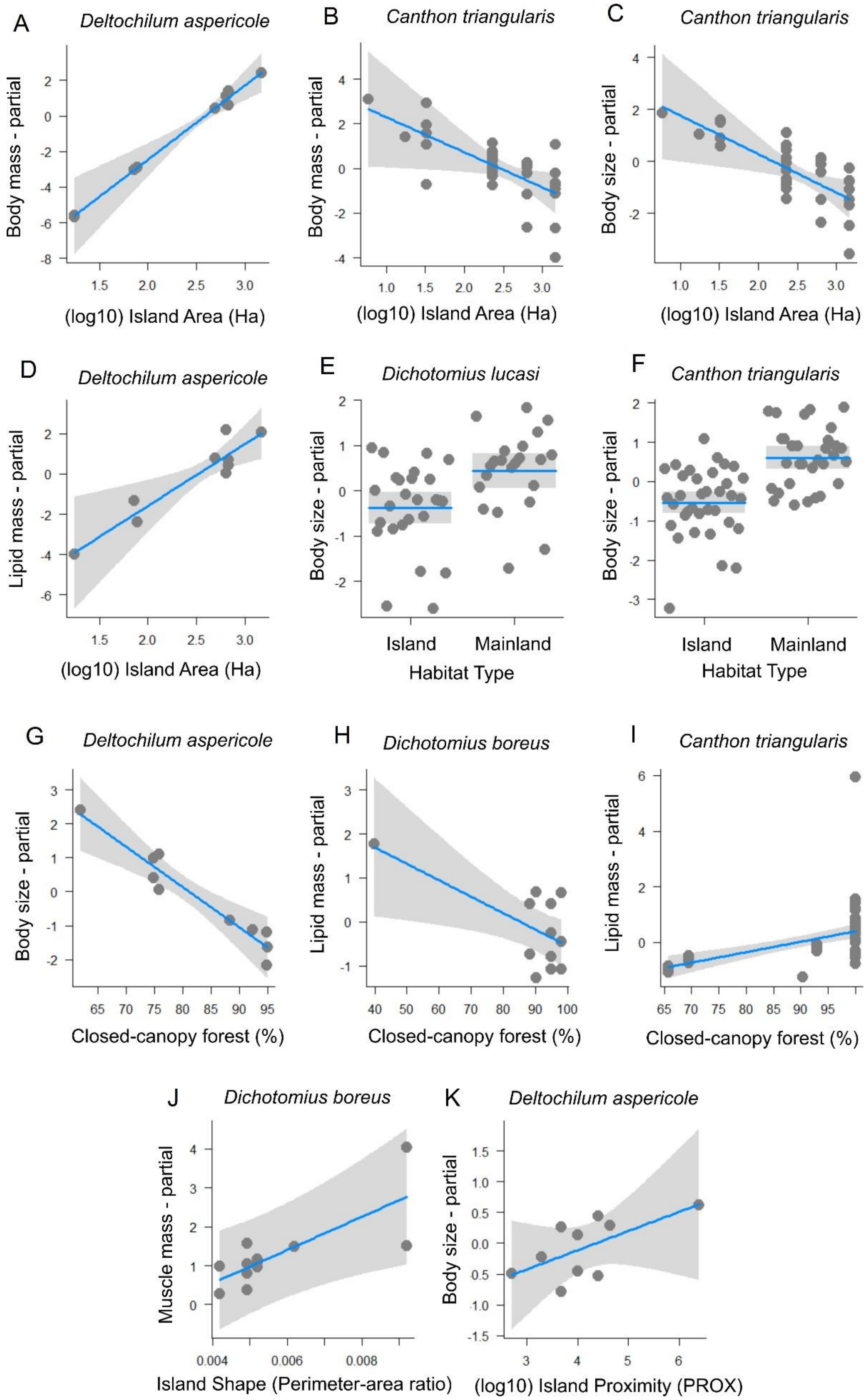
A
Deltochilum aspericole
Body mass - partial
(log10) Island Area (Ha)
B
Canthon triangularis
Body mass - partial
(log10) Island Area (Ha)
C
Canthon triangularis
Body size - partial
(log10) Island Area (Ha)
D
Deltochilum aspericole
Lipid mass - partial
(log10) Island Area (Ha)
E
Dichotomius lucasi
Body size - partial
Island
Mainland
Habitat Type
F
Canthon triangularis
Body size - partial
Island
Mainland
Habitat Type
G
Deltochilum aspericole
Body size - partial
Closed-canopy forest (%)
H
Dichotomius boreus
Lipid mass - partial
Closed-canopy forest (%)
I
Canthon triangularis
Lipid mass - partial
Closed-canopy forest (%)
J
Dichotomius boreus
Muscle mass - partial
Island Shape (Perimeter-area ratio)
K
Deltochilum aspericole
Body size - partial
(log10) Island Proximity (PROX)

Table 1. Abundance, body size, body dry mass, relative lipid mass, and relative muscle mass of the species collected.

Species	Body size (mean ±SD mm)	Body dry mass (mean ±SD g*10)	Relative lipid mass (mean±SD g/mm*10³)	Relative muscle mass (mean±SD g/mm*10³)
Ateuchus cereus (n = 11)	2.01 ± 0.17	0.03 ± 0.01	NA	NA
Ateuchus globulus (n = 4)	2.27 ± 0.07	0.04 ± 0.01	NA	NA
Ateuchus murrayi (n = 51)	2.69 ± 0.19	0.01 ± 0.02	NA	NA
Ateuchus simplex (n = 71)	3.88 ± 0.16	0.20 ± 0.04	NA	NA
Ateuchus sp (n = 1)	NA	NA	NA	NA
Canthidium deyrollei (n = 1)	NA	NA	NA	NA
Canthon sordidus (n = 5)	4.24 ± 0.80	0.20 ± 0.04	NA	NA
Canthon triangularis (n = 66)	5.57 ± 0.20	0.40 ± 0.10	0.65 ± 0.53	3.57 ± 1.31
Coprophanaeus jasius (n = 3)	NA	NA	NA	NA
Coprophanaeus lancifer (n = 1)	NA	NA	NA	NA
Deltochilum aspericole (n = 11)	5.42 ± 0.17	0.40 ± 0.10	0.45 ± 0.38	2.30 ± 1.49
Deltochilum icarus (n = 1)	NA	NA	NA	NA
Deltochilum submetallicum (n = 1)	7.19 ± 0.00	1.70 ± 0.00	2.77 ± 0.00	9.09 ± 0.00
Dichotomius boreus (n = 15)	15.16 ± 1.55	6.70 ± 2.20	6.04 ± 3.82	1.53 ± 2.80
Dichotomius lucasi (n = 48)	7.56 ± 0.37	1.00 ± 0.40	2.10 ± 2.07	2.53 ± 1.64
Dichotomius subaenaeus (n = 20)	9.64 ± 1.12	2.20 ± 0.80	3.94 ± 3.76	4.24 ± 2.88
Eurysternus atrosericus (n = 5)	NA	NA	NA	NA
Eurysternus caribaeus (n = 4)	NA	NA	NA	NA
Ontherus sp (n = 1)	NA	NA	NA	NA
Uroxys sp (n = 1)	1.59 ± 0.00	0.01 ± 0.00	NA	NA

Table 2. Results of the statistical models that analyzed the influence of predictive variables on the physiological condition and body size of dung beetles at both the species and assemblage levels. Variables that were statistically significant are shown in bold. NS = variables not selected by the best-supported model; NA = Variables not applied in the model.

	Habitat type	Forest Cover	Closed-Canopy Forest	Shape Index (Per/Area)	Proximity	Island area	Isolation
Species-scale effects:							
Deltochilum aspericolle							
Body Size	F_2 = 0.38, P = 0.55	NS	**F_1 = 15.77, P = 0.01**	F_1 = 4.85, P = 0.08	**F_1 = 10.54, P = 0.02**	NS	F_1 = 1.44, P = 0.28
Body dry mass	F_2 = 1.74, P = 0.22	F_1 = 7.09, P = 0.80	F_1 = 8.85, P = 0.06	F_1 = 2.08, P = 0.25	F_1 = 2.85, P = 0.19	**F_1 = 43.53, P = 0.01**	F_1 = 0.80, P = 0.44
Lipid Mass	F_2 = 0.87, P = 0.38	NS	NS	F_1 = 2.19, P = 0.18	NS	**F_1 = 8.78, P = 0.02**	NS
Muscle Mass	F_2 = 1.81, P = 0.21	F_1 = 1.44, P = 0.30	NS	F_1 = 0.01, P = 0.92	F_1 = 5.40, P = 0.08	F_1 = 6.00, P = 0.07	F_1 = 2.36, P = 0.20
Dichotomius boreus							
Body Size	F_2 = 3.67, P = 0.08	NS	NS	F_1 = 3.73, P = 0.08	NS	NS	NS
Body dry mass	F_2 = 0.85, P = 0.37	NS	F_1 = 0.33, P = 0.58	NS	NS	NS	NS
Lipid Mass	F_2 = 0.02, P = 0.91	NS	**F_1 = 6.08, P = 0.04**	F_1 = 4.08, P = 0.07	NS	NS	NS
Muscle Mass	F_2 = 0.37, P = 0.56	F_1 = 0.20, P = 0.67	F_1 = 3.29, P = 0.11	**F_1 = 8.77, P = 0.02**	F_1 = 0.59, P = 0.47	NS	NS

	Habitat type	Forest Cover	Closed-Canopy Forest	Shape Index (Per/Area)	Proximity	Island area	Isolation
Dichotomius lucasi							
Body Size	**$F_2 = 9.37, P < 0.01$**	NA	NA	NA	NA	NA	NA
Body dry mass	$F_2 = 0.37, P = 0.55$	NA	NA	NA	NA	NA	NA
Lipid Mass	$F_2 = 1.08, P = 0.30$	NA	NA	NA	NA	NA	NA
Muscle Mass	$F_2 = 0.88, P = 0.35$	NA	NA	NA	NA	NA	NA
Canthon triangularis							
Body Size	**$F_2 = 31.17, P < 0.01$**	NS	NS	$F_1 = 0.96, P = 0.33$	NS	**$F_1 = 6.78, P = 0.01$**	NS
Body dry mass	$F_2 = 2.55, P = 0.12$	NS	NS	$F_1 < 0.01, P = 0.95$	NS	**$F_1 = 4.72, P = 0.04$**	NS
Lipid Mass	$F_2 = 0.77, P = 0.39$	NS	**$F_1 = 25.5, P < 0.01$**	NS	NS	NS	NS
Muscle Mass	$F_2 = 0.16, P = 0.69$	NS	NS	NS	NS	NS	NS
Ateuchus murrayi							
Body Size	NA	NS	$F_1 = 3.14, P = 0.08$	NS	NS	NS	NS
Body dry mass	NA	NS	$F_1 = 3.19, P = 0.08$	NS	NS	NS	NS

	Habitat type	Forest Cover	Closed-Canopy Forest	Shape Index (Per/Area)	Proximity	Island area	Isolation
Assemblage-scale effects:							
Body Size	**t = 3.68, P < 0.01**	**t = 3.63, P < 0.01**	NS	NS	NS	NS	NS
Body dry mass	t = 0.78, P = 0.44	NS	t = 0.35, P = 0.73	NS	t = -0.19, P = 0.85	NS	NS
Lipid Mass	t = -0.68, P = 0.50	NS	NS	NS	t = -0.58, P = 0.56	NS	NS
Muscle Mass	t = 0.46, P = 0.65	NS	NS	t = 0.81, P = 0.42	t = -1.5, P = 0.14	t = 0.89, P = 0.38	NS

Competing Interests Statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contributions section

Leonardo Vilas-Bôas M.P. de Cerqueira: Conceptualization (equal); formal analysis (lead); investigation (equal); writing – original draft (lead); writing – review and editing (equal); data curation (equal); methodology (equal). **Daniel González Tokman**: Writing – review and editing (equal); supervision (equal); methodology(equal). **César M. A. Correa:** Writing – review and editing (equal). **Danielle Stork-Tonon:** Resources (equal); investigation (equal). **Mario Cupello:** Data curation (equal). **Renato Portela Salomão:** Conceptualization (equal); investigation (equal); writing – original draft (equal); writing – review and editing (lead); funding acquisition (lead); project administration (lead); data curation (equal); methodology(equal).

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CONCLUSÕES

Isolamento, área das ilhas e de floresta de dossel fechado foram os principais preditores do tamanho corporal e da condição fisiológica dos besouros rola bosta em um arquipélago amazônico. Essas métricas indicam que algumas espécies persistiram nas ilhas, apesar de estarem altamente limitadas em recursos durante as fases larvais ou adultas, à medida que o isolamento e a perda de floresta primária aumentaram. Os efeitos da insularização na fisiologia dos animais ainda são amplamente desconhecidos e merecem maior atenção em organismos que desempenham papéis-chave na manutenção do funcionamento dos ecossistemas, como os besouros rola bosta. Vale ressaltar que a cobertura florestal desempenha um papel crucial na determinação da biodiversidade nos ecossistemas tropicais, como já demonstrado anteriormente. No entanto, nosso estudo sugere que a cobertura florestal teve poder explicativo limitado no arquipélago amazônico analisado aqui. Além disso, este estudo destaca a importância de categorizar sistemas para obter uma compreensão mais abrangente de como as transformações ambientais afetam as respostas de espécies e comunidades.

CONCLUSIONS

Isolation, island area and closed canopy forest were the most important predictors of dung beetle body size and physiological condition in an Amazonian archipelago. These metrics indicate that some species have persisted in islands despite being highly resource-limited during larval or adult stages as isolation and primary forest loss have increased. Insularization effects on animal physiology remain largely untested and deserve further attention in organisms that play key roles in maintaining ecosystem functioning, such as dung beetles. It is worth noting that forest cover plays a crucial role in determining biodiversity in tropical ecosystems, as previously demonstrated. Nonetheless, our study suggests that forest cover had limited explaining power in the Amazonian archipelago analyzed herein. Moreover, this study highlights the importance of categorizing systems to obtain a more comprehensive understanding of how environmental transformations affect species and community responses.