



PABLO ALEJANDRO LÓPEZ BEDOYA

**NEOTROPICAL MOUNTAINS AND INSECT DIVERSITY:
ANTHROPOGENIC DRIVERS OF BIODIVERSITY CHANGES
AND CONSERVATION CHALLENGES**

LAVRAS-MG

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Master's Work presented to the Universidade
Federal de Lavras, as part of the requirements of
the Postgraduate Program in Entomology.

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**MONTANHAS NEOTROPICAIS E DIVERSIDADE DE INSETOS: FATORES
ANTROPOGÊNICOS DAS MUDANÇAS NA BIODIVERSIDADE E DESAFIOS DE
CONSERVAÇÃO**

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Approved on 26 February 2025

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DEDICATORY NOTE

“Todos mis logros siempre son dedicados a mi familia, y seguirán siendo dedicados a ellos en el futuro. Por ellos es que trabajo, y por ellos es que he tenido metas y sueños de progreso. Y por ellos también es que deseo construir una familia en el futuro”

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“Sobran las palabras para agradecer a los mayores partícipes de mi vida y progreso, mi familia, que siempre ha estado ahí para mí, con su apoyo y ayuda.

Agradezco también a mi orientador Julio, él me brindó su tiempo, ayuda, y me escucho cuando fue necesario. Yo soy una persona bastante callada, he independiente en el trabajo, pero cuando lo necesité, él estuvo presente. También me abrió las puertas de su hogar junto con su esposa Leticia y nos brindaron esa calidez cuando se es una persona extranjera en un nuevo país.

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ABSTRACT

Neotropical mountain ecosystems are recognized for their high biodiversity and notable species endemism but are increasingly threatened by anthropogenic pressures resulting from historical and ongoing human activities. These pressures, combined with limited ecological knowledge, have hindered the development of effective conservation strategies for these vulnerable biomes. The present research addresses this issue in two chapters. The first chapter addresses a critical challenge, related to the variability in biodiversity responses to anthropogenic impacts reported in localized studies. Insects were selected as the focal group due to their exceptional diversity, critical ecological roles, and increasing vulnerability to environmental changes. I performed a meta-analysis to evaluate insect responses to different types of anthropogenic impacts. I assessed how insect group, type of natural habitat transformed, characteristics of anthropogenic transformation, and geographical variables influenced insect responses. The results show how habitat transformation has negative effects on insect communities in Neotropical mountains. It also shows how ants and dung beetles can be more affected by impacts. Furthermore, these impacts were more severe for agriculture and livestock, in equatorial regions, and at lower altitudes. The second chapter, address how the management characteristics and landscape connectivity, influence the dung beetle response due to natural forest conversion to coffee plantations in the tropical Andes mountains. These results reveal how coffee plantations present lower taxonomic and functional dung beetle diversity. However, shaded system and connectivity to natural forest supports higher taxonomic and functional diversity of dung beetles. The pronounced negative impacts of anthropogenic pressures on Neotropical montane insects highlight the urgent need to prioritize natural habitat protection in future conservation programs. These findings provide valuable insights for structuring effective conservation programs in the Neotropical region, where human development and its associated impacts must be integrated into future sustainable systems aimed at conserving biodiversity.

Keywords: biological conservation; coffee plantations; insect extinction; meta-analysis.

RESUMO

Os ecossistemas das montanhas neotropicais são reconhecidos por sua alta biodiversidade e notável endemismo de espécies, mas estão cada vez mais ameaçados por pressões antrópicas resultantes de atividades humanas históricas e contínuas. Essas pressões, combinadas com o conhecimento ecológico limitado, têm dificultado o desenvolvimento de estratégias de conservação eficazes para esses biomas vulneráveis. A presente pesquisa aborda essa problemática em dois capítulos. O primeiro capítulo aborda um desafio crítico, relacionado à variabilidade das respostas da biodiversidade aos impactos antropogênicos relatados em estudos localizados. Os insetos foram selecionados como grupo focal devido à sua excepcional diversidade, funções ecológicas essenciais e crescente vulnerabilidade às mudanças ambientais. Realizei uma meta-análise para avaliar as respostas dos insetos a diferentes tipos de impactos antropogênicos. Avaliei como o grupo de insetos, o tipo de habitat natural transformado, as características da transformação antropogênica e as variáveis geográficas influenciaram as respostas dos insetos. Os resultados mostram como a transformação do habitat tem efeitos negativos sobre as comunidades de insetos nas montanhas neotropicais. Também mostram como as formigas e os besouros rola-bosta podem ser mais afetados pelos impactos. Além disso, esses impactos foram mais graves para a agricultura e a pecuária, em regiões equatoriais e em altitudes mais baixas. O segundo capítulo aborda como as características de manejo e a conectividade da paisagem influenciam a resposta do besouro rola-bosta devido à conversão da floresta natural em plantações de café nas montanhas tropicais dos Andes. Os resultados revelam como as plantações de café apresentam menor diversidade taxonômica e funcional de besouros rola-bosta. No entanto, o sistema sombreado e a conectividade com a floresta natural sustentam uma maior diversidade taxonômica e funcional de besouros de esterco. Os impactos negativos pronunciados das pressões antrópicas sobre os insetos das montanhas neotropicais destacam a necessidade urgente de priorizar a proteção do habitat natural em futuros programas de conservação. Essas descobertas fornecem percepções valiosas para a estruturação de programas de conservação eficazes na região neotropical, onde o desenvolvimento humano e seus impactos associados devem ser integrados a futuros sistemas sustentáveis que visem à conservação da biodiversidade.

Palavras-chave: conservação biológica; extinção de insetos; meta-análise; plantação de café.

Social, technological, economic and cultural impacts

The research investigates the vulnerability of Neotropical mountains to anthropogenic impacts using various insect groups as bioindicators. Employing meta-analytical strategies, 105 published articles were included, addressing the impact of different anthropogenic pressures on ants, bees, butterflies, and dung beetles. The results demonstrate that habitat transformation has negative effects on insect communities in Neotropical mountains. They also indicate that ants and dung beetles are the most affected by these impacts. Moreover, the effects were more severe in relation to agriculture and livestock activities, particularly in equatorial regions and at lower altitudes. The study also assessed how management characteristics and landscape connectivity influence the response of dung beetles to the conversion of natural forest into coffee plantations in the tropical Andes. The findings reveal that coffee plantations exhibit lower taxonomic and functional diversity of dung beetles. However, shaded coffee systems and connectivity with natural forests support higher taxonomic and functional diversity. These findings provide valuable insights for structuring effective conservation programmes in the Neotropical region, where human development and its associated impacts must be integrated into future sustainable systems aimed at biodiversity conservation. The results have contributed to the development of public policies and sustainable management strategies. The study generates direct environmental impacts by quantifying the effects of anthropogenic pressures, as well as technological and economic impacts, as the data can be used by environmental managers to balance conservation and production goals. The social and cultural impact of the research is reflected in the production of knowledge applicable to local communities and public policy-makers, promoting awareness of the importance of biodiversity. The outreach component of the study is evidenced by its engagement with society beyond UFLA, including the participation of co-supervisors affiliated with other universities, thereby strengthening inter-institutional scientific cooperation. Furthermore, scientific dissemination activities were carried out for non-academic audiences through social media and accessible outreach materials, reaching a wider public, including local communities.

Impactos sociais, tecnológicos, econômicos e culturais

A pesquisa investiga os vulnerabilidade das montanhas Neotropicais pelos impactos antrópicos utilizando diferentes grupos de insetos como bioindicadores. Utilizando estratégias meta-analíticas foram analisados 105 artigos publicados que avaliaram diferentes pressões antropogênicas em abelhas, borboletas, besouros rola bosta ou formigas. Os resultados mostram como a transformação do habitat tem efeitos negativos sobre as comunidades de insetos nas montanhas neotropicais. Também mostram como as formigas e os besouros rola-bosta podem ser mais afetados pelos impactos. Além disso, esses impactos foram mais graves para a agricultura e a pecuária, em regiões equatoriais e em altitudes mais baixas. Além disso também foi avaliado como as características de manejo e a conectividade da paisagem influenciam a resposta do besouro rola-bosta devido à conversão da floresta natural em plantações de café nas montanhas tropicais dos Andes. Os resultados revelam como as plantações de café apresentam menor diversidade taxonômica e funcional de besouros rola-bosta. No entanto, o sistema sombreado e a conectividade com a floresta natural sustentam uma maior diversidade taxonômica e funcional de besouros de esterco. Essas descobertas fornecem percepções valiosas para a estruturação de programas de conservação eficazes na região neotropical, onde o desenvolvimento humano e seus impactos associados devem ser integrados a futuros sistemas sustentáveis que visem à conservação da biodiversidade. Esses resultados ajudaram no fornecimento de políticas públicas e estratégias de manejo sustentável. O estudo gera impactos

ambientais diretos ao quantificar os efeitos dos impactos antrópicos, além de impactos tecnológicos e econômicos, uma vez que os dados podem ser utilizados por gestores ambientais para equilibrar conservação e produção. O impacto social e cultural da pesquisa se manifesta na produção de conhecimento aplicável a comunidades locais e formuladores de políticas públicas, promovendo a conscientização sobre a importância da biodiversidade. O caráter extensionista do estudo é evidenciado pela interação com a sociedade externa à UFLA, incluindo a participação de coorientadores vinculados com outras universidades, ampliando a cooperação científica interinstitucional. Além disso, foram desenvolvidas ações de divulgação científica para o público não acadêmico, por meio de mídias sociais e materiais de divulgação acessíveis, atingindo um público mais amplo, incluindo comunidades locais.

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1. PART I: INTRODUCTION

1.1 Biodiversity conservation and mountain ecosystems

The paradox between biodiversity conservation and human development is becoming increasingly evident in a rapidly changing world. Human population expansion, rising consumption, and growing demands have exerted diverse pressures on natural habitats, primarily through conversion, degradation, and fragmentation (CURTIS et al., 2018). These continuous transformations have resulted in a predominance of anthropogenic habitats over natural ones, particularly in ecosystems such as forests and savannas (FAO, 2025). This trend is expected to worsen, with projections indicating an increase of 30–70% in anthropized areas over the coming decades (HUNTER et al., 2017). Anthropogenic pressures significantly impact biodiversity, as altered habitats often exhibit reduced vegetation complexity and increasingly homogenized microclimates (OLDEN et al., 2006; SENIOR et al., 2017). Consequently, the escalating pressures on natural habitats and biodiversity have heightened conservation concerns, particularly due to their critical role as providers of essential ecosystem services for human well-being (NAEEM et al., 2016).

Traditionally, conservation programs have focused on preserving natural habitats to safeguard biodiversity and maintain ecological structures, often aiming to minimize human activity within protected areas (LE SAOUT et al., 2013). However, a significant proportion of reserves are embedded within landscapes dominated by human activities (McDONALD et al., 2008). This integration has led to the transformation of natural habitats and the biodiversity declines (LAURANCE et al., 2012), as the strict preservation of natural ecosystems is often incompatible with human economic activities and livelihoods (LIU et al., 2007; BENNETT-CURRY et al., 2013). For instance, in many cases, resources derived from natural habitats, such as timber, provide critical economic support for local communities (BENNETT-CURRY et al., 2013). Additionally, natural habitats are frequently converted into other land uses that generate products for human consumption, such as the establishment of coffee plantations in tropical regions (DONALD, 2004; HARVEY et al., 2021).

The conservation of natural habitats and their associated biodiversity must transition to include human development as a central factor to ensure sustainability (LE SAOUT et al., 2013). However, discrepancies persist when evaluating the effects of human pressures on biodiversity. For instance, assessments of habitat fragmentation reveal both positive (FAHRIG et al., 2019) and negative (FLETCHER et al., 2018) outcome, and these inconsistencies can

undermine conservation efforts in landscapes dominated by human activities (WALDRON et al., 2013; ADAMS et al., 2019). To address this issue, it is essential to identify general patterns of biodiversity responses, particularly in regions with high biodiversity levels, while accounting for variations in the effects of different anthropogenic pressures (NEWBOLD et al., 2015). Future conservation strategies must integrate these responses to achieve effective biodiversity conservation while balancing human sustainable intensification (PRETTY et al., 2018).

Mountain ecosystems worldwide are not exempt from the challenges of habitat transformation and biodiversity loss (CHAKRABORTY, 2021). These ecosystems harbour diverse vegetation types and climates, supporting high levels of biodiversity (KÖRNER, 2004; PERRIGO et al., 2020). Additionally, mountain habitats provide crucial ecosystem services, including water production and food provisioning, often mediated by biodiversity (GRÊT-REGAMEY; WEIBEL, 2020). In particular, the mountains of the Neotropical region hold special conservation significance due to their biotic communities, which are characterized by a high proportion of endemic species with restricted distribution ranges (NOGUÉ et al., 2013; QUINTERO; JETZ, 2018). Paradoxically, many countries in the Neotropical region have concentrated major urban centres and economic activities in mountain areas, resulting in a decline in the proportion of preserved natural habitats over time (MYERS et al., 2000; SOH et al., 2018; LÓPEZ-BEDOYA et al., 2024). Therefore, to conserve the unique biodiversity of Neotropical mountains, it is critical to evaluate and understand how natural habitat transformations impact biodiversity.

The present research addresses this issue in two chapters. The first chapter evaluates the response of biodiversity to natural habitat transformation in Neotropical mountains. Specifically, the focus is on insects, a group characterized by high biodiversity, critical ecological roles, and significant conservation concern due to their importance for human well-being (SAMWAYS, 2005; CARDOSO; LEATHER, 2019; WAGNER et al., 2021). The results reveal general effects of natural habitat transformation on biodiversity, as well as specific responses influenced by variables such as the insect group studied, the characteristics of the anthropogenic impact, and the geographical context. The second chapter, address how the management characteristics and landscape connectivity, influence the dung beetle response due to natural forest conversion to coffee plantations in the tropical Andes mountains. I focused on dung beetles due to sensitivity to land-use change, and key ecological role in terrestrial ecosystems (NICHOLS et al. 2007; FUZESSY et al. 2021). The results reveal how coffee plantations present lower taxonomic and functional dung beetle diversity. However, shaded system and connectivity to natural forest supports higher taxonomic and functional diversity of

dung beetles. These findings provide valuable insights for structuring effective conservation programs in the Neotropical region, where human development and its associated impacts must be integrated into future sustainable systems aimed at conserving biodiversity.

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2. PART II: PAPERS

Paper I: López-Bedoya, P.A, Edwards, D.P, Nunes C.A, Louzada, J. Meta-analysis of insect diversity responses to anthropogenic pressures in Neotropical mountains. *Formatted according to: Biological Conservation.*

Paper II: Pablo A. López-Bedoya, Livia Audino, David P. Edwards, Cássio Alencar Nunes, Santiago Rodríguez-García, Julio Louzada. Influence of surrounding natural forest and shaded coffee systems on taxonomic and functional diversity of dung beetles in Andean coffee plantations. *Formatted according to: Agroforestry systems.*

2.1 PAPER I: Meta-analysis of insect diversity responses to anthropogenic pressures in Neotropical mountains

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Meta-analysis of insect diversity responses to anthropogenic pressures in Neotropical mountains

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Abstract

The Neotropical mountains are globally recognized as ecosystems of high biodiversity.

Historical and contemporary human development in these regions has led to significant land-

use change-induced pressures on biodiversity. We addressed the question on how anthropogenic land-use change in Neotropical mountains impacts invertebrate diversity, using four insect groups as indicators (ants, bees, dung beetles, and lepidopterans). We performed a meta-analysis of 105 published papers that reported on insect richness or abundance in anthropogenic systems compared to natural habitats (forest or savanna). We used the Hedges' d metric to quantify the effect size between natural habitats and anthropogenic systems. We assessed how insect group, type of natural habitat transformed, characteristics of anthropogenic transformation (conversion, degradation, fragmentation), and geographical variables (latitude, altitude) influenced insect responses to land-use transformation. Our results show that anthropogenic impacts negatively affect insect richness and abundance in Neotropical mountains, with ants and dung beetles being the most severely impacted. The magnitude of these effects varies depending on the type of natural habitat transformed, with transformations of natural forests showing particularly severe impacts. Additionally, the characteristics of anthropogenic transformation, especially the conversion of natural habitats to agricultural and exotic livestock areas, exhibited the strongest negative effects on insects. Latitude and altitude also influenced insect responses, with the negative effects of natural habitat transformation becoming less severe at higher altitudes and further from the Equator. The pronounced negative impacts of anthropogenic pressures on Neotropical montane insects highlight the urgent need to prioritize natural habitat protection in future conservation programs on these areas.

Keywords: agricultural and livestock areas, elevational and latitudinal gradients, insect conservation, montane tropic, multitaxa approach.

1. Introduction

Neotropical mountains are renowned for their remarkable biodiversity, including a high level of species endemism with restricted geographic distributions (Quintero & Jetz, 2018). However, rapid urbanization and agricultural development have led to significant natural ecosystem transformation, primarily through conversion, degradation or fragmentation of natural habitats (Bax and Francesconi, 2018; Soh et al., 2019). Natural habitat transformation directly affects biodiversity (Newbold et al., 2015), because transformed habitats in most cases present less-structured vegetation and homogeneity compared to natural habitats (López-Bedoya et al., 2021). The constant human pressures on Neotropical mountains have rendered these ecosystems and their biodiversity highly vulnerable to extinction (Myers et al., 2000; Soh et al., 2019; Antonelli, 2022), as the unique niches occupied by mountain biodiversity limit their adaptations to anthropogenic disturbances (Janzen, 1967).

Conservation efforts including totally protected areas, and sustainable agricultural landscapes have been implemented to address the vulnerability of biodiversity in Neotropical mountains (e.g., Harvey et al., 2008; Bax and Francesconi, 2019; Duffus et al., 2023). However, the conservation plans are limited by discrepancies when evaluating the effects of human pressures on biodiversity. For example, assessments of habitat fragmentation reveal both positive (Fahrig et al., 2019) and negative (Fletcher et al., 2018) outcome, and these inconsistencies can undermine conservation efforts. Likewise, the transformation of natural habitats results in both species that suffer reductions in abundance (losers) and that increase in abundance (winners) (Gilroy et al., 2014; Filgueiras et al., 2021).

Three broad factors could explain contrasting biodiversity responses to habitat transformation. First, the taxonomic group assessed (multitaxa assessments) revealing a range of responses (Diaz-Garcia et al., 2020). For example, some biodiversity groups, such as dung

beetles, or birds showed higher negative effects compared to other groups, such as amphibians (Rios-Touma et al., 2023). Second, the transformation characteristics alter responses via landscape complexity (i.e., connectivity, degree of retention of wildlife-friendly features) or microclimate diversity (Jimenez-Carmona et al., 2020). For example, habitat conversion may have more negative effects on biodiversity compared to habitat fragmentation (Gilroy et al., 2014). Third, geographical location (e.g., latitude, altitude) influences the biodiversity response, because communities at lower latitudes or higher elevations show less sensitivity to habitat transformation, and present wider thermal physiological thresholds (Betts et al., 2019; Peters et al., 2019; Mills et al., 2023; Parra-Sanchez and Edwards, 2024). This highlights the need for studies that provide a synthetic understanding of community responses to different habitat transformations across environmental gradients and between taxa to support conservation efforts and planning in Neotropical mountains.

Insects are a key group in terrestrial ecosystems playing essential ecological roles, such as natural pest regulation, organic matter cycling, seed dispersal, and pollination (Noriega et al., 2018; Dangles and Casas, 2019). Paradoxically, despite their ecological importance, insect conservation efforts remain insufficient, with insect populations showing widespread declines globally (Cardoso and Leather, 2019; Cardoso et al., 2020). In Neotropical mountains, local-scale studies comparing the effects of natural habitat transformation on insects display divergent responses, ranging from positive (Horner-Devine et al., 2003; Arellano et al., 2005; Martinez-Sanchez et al., 2020) to negative (Armbrecht and Perfecto, 2003; Tylianakis et al., 2006; Cartagena et al., 2021) when compared to natural habitats. Indeed, insects represent a particularly relevant group for assessing how geographic factors influence responses to habitat transformation (Escobar et al., 2006), as latitudinal and altitudinal gradients exhibit specific communities (Pyrz et al., 2014; Perillo et al., 2021).

Currently, there is a lack of comprehensive synthesis on insect responses to natural habitat transformation. Previous meta-analyses have either focused on specific insect groups (e.g., López-Bedoya et al., 2021, 2022a) or evaluated the effects of natural habitat transformation across broader geographical contexts, including the tropical region (Newbold et al., 2015; Mendez-Rojas et al., 2021). In this sense, identifying insect responses to natural habitat transformation in Neotropical mountains is crucial for informing management recommendations (López-Bedoya et al., 2024).

In this study, we conducted a meta-analysis to evaluate the response of insect diversity to anthropogenic impacts in Neotropical mountains. We examined how insect responses were influenced by the type of natural habitat transformed, the insect group evaluated, and the characteristics and identities of anthropogenic transformations. Additionally, we assessed how geographical attributes, such as latitude and mountain altitude, modulate the effects of anthropogenic impacts. We hypothesize that anthropogenic impacts will: (H1) reduce insect diversity compared to natural habitats; (H2) exhibit differential effects on insect diversity depending on natural habitat type, insect group, and transformation characteristics; and (H3) be influenced by geographic variables.

2. Materials and methods

2.1 Biodiversity groups selection

We selected four insect groups for analysis: (i) ants (Hymenoptera: Formicidae), (ii) bees (Hymenoptera: Apidae), (iii) dung beetles (Coleoptera: Scarabaeidae), and (iv) lepidopterans (both diurnal and nocturnal). These groups were chosen due to their well-established status as bioindicators of anthropogenic disturbance effects (Barlow et al., 2007; Newbold et al., 2015; López-Bedoya et al., 2021). Moreover, these insect groups play critical ecological roles in natural ecosystems and provide essential ecosystem services that are vital

for human well-being such as pollination, soil fertilization, soil bioturbation, seed dispersal, or parasite control (Losey and Vaughan, 2006; Noriega et al., 2018).

2.2 Geographical study area delimitation

To define the geographical scope, we adopted the Neotropical region delineation proposed by Morrone et al. (2022). This approach is particularly suitable for evaluating insect biodiversity, as insects represent one of the most diverse and widely distributed taxonomic groups globally. By utilizing a broader Neotropical region delineation, we aim to minimize potential biases associated with the delimitation of specific regional insect groups (e.g., dung beetles; Davis et al., 2002).

Within the Neotropical region, our focus is on mountain biomes, employing the geographical framework proposed by Karagulle et al. (2017). This approach defines mountain regions in the Neotropical area based on altitude, slope, and landform variables, using satellite imagery with a resolution of 250 m radius (Sayre et al., 2018). Additionally, we adopted the mountain nomenclature proposed by Snethlage et al. (2022) to identify specific mountain ranges within the Neotropical region (e.g., Cordillera de Los Andes, Cordillera Centroamericana, Serra da Mantiqueira).

2.3 Literature research

To assess the impact of anthropogenic pressures on insect biodiversity across the Neotropical mountains, we conducted a meta-analysis. This analytical approach allows for the evaluation of overall effect patterns by synthesizing data from multiple locally published studies. First, we performed a comprehensive literature search using the Scielo, Scopus, and Web of Science (WoS) databases, following the PRISMA methodology (Page et al., 2021) (see Fig. S1). This methodology provides structured recommendations and workflow stages to

ensure the inclusion of high-quality studies in a quantitative synthesis. The search covered the period from January 1900 to December 2023, based on the accessibility of the consulted databases, and included only peer-reviewed journal papers, as these are recognized for their higher quality, rigor, replicability, and methodological transparency compared to grey literature (Nakagawa et al., 2017).

We employed a search equation targeting the title, abstract, and keywords sections of each document. The search terms were designed to identify the relevant taxonomic insect groups, common anthropogenic impacts, and mountain biomes: ("dung beetle*" OR butterfly* OR ant* OR moth* OR bees* OR scarabaei* OR lepidop* OR nymphalid* OR formicid* OR arctiid* OR saturniid* OR sphingid* OR apid*) AND (conversion OR fragment* OR degradat* OR "land use*" OR livestock OR agriculture OR plantat* OR silviculture OR "edge effect*" OR fire) AND/OR (tropic OR tropical OR neotropic* OR mountain*). We used this search equation in English, Spanish, and Portuguese version, to maximize the chance of including a representative number of studies.

2.4 Screening and exclusion criteria

An initial database of 188,310 papers was reduced to 162,438 after eliminating duplicates. We reviewed the title and abstract sections and excluded papers focused on topics unrelated to ecology (*e.g.*, molecular biology, taxonomy, systematics, or computational sciences), as well as other quantitative reviews and meta-analyses to avoid duplication of information.

We accessed the full texts of 97,516 papers, and those without information on the target insect groups or data collected outside the Neotropical mountains limits were excluded. Finally, we filtered the remaining papers based on two criteria. First, the paper had to include a comparison between a control site and a treatment site (see Table S1). Second, the papers

had to provide data on the central tendency of the sample (*e.g.*, mean or median), measures of variability (*e.g.*, standard deviation or interquartile ranges), and sample sizes for observed species richness or individual abundance.

We included two types of natural habitats as control sites: (i) natural forest (as defined by Chazdon et al. 2016) and (ii) natural savanna (as defined by Dinerstein et al., 2017; Jung et al., 2020). Both definitions have been widely used in recent quantitative reviews and meta-analyses focusing on insect taxa (*e.g.*, López-Bedoya et al. 2021; López-Bedoya et al. 2022a; Reis et al., 2024). For treatment sites, we considered three types of natural habitat transformation and specific impacts for each transformation type: (i) conversion (agriculture vs. livestock vs. silviculture); (ii) degradation (fire events vs. restoration); and (iii) fragmentation (edge effect vs. patch size) (*see* Table S1).

For the second criterion, we used observed species richness and individual abundance as proxy metrics, as they are intuitive and easily measurable indicators of biological communities (Magurran and McGill, 2010). Moreover, observed species richness and individual abundance are commonly used in local-scale studies to quantify biodiversity impacts in the Neotropical mountains (López-Bedoya et al., 2024). Based on these criteria, a total of 105 published papers evaluating species richness and/or individual abundance of the target insect groups in Neotropical mountains were included in the meta-analysis (Fig 1; Table S2).

2.5 Missing data account

In many instances, the papers included in the analysis exhibited partially missing data, where: (i) data were available (*e.g.*, in tables and figures) but not readily integrable into the meta-analysis, or (ii) data were not explicitly reported within the paper (*see* Lajeunesse, 2013). To mitigate biases associated with missing data, we extracted mean and standard

deviation values directly from tables, figures, or supplementary materials when available (e.g., Santos-Heredia et al., 2018). Additionally, when results were presented as medians and interquartile ranges (Noriega et al., 2021), we applied the method proposed by Hozo et al. (2005) to estimate means and standard deviations. For data presented solely in graphical form, we utilized GRAPHCLICK 3.0 (Arizona Software, Switzerland) to extract mean and dispersion values. In certain cases, we contacted the original authors to request access to their databases (Gries et al., 2012), enabling us to retrieve the necessary mean and standard deviation values for both control and treatment groups.

2.6 Study cases selection

Each published paper was treated as an independent study case, focusing on the comparison between control and treatment sites. In some instances, multiple study cases were derived from the same paper when independent replicates of control and treatment sites were reported, along with corresponding richness or abundance statistical metrics. For example, studies evaluating multiple conversion types (e.g., agriculture, livestock) within the same paper were treated as separate cases (see Ricketts et al., 2001; Armbrrecht et al., 2006; Tylianakis et al., 2006; Cultid-Medina and Escobar 2016; Allen et al., 2019).

Additionally, when papers employed a multi-taxa approach (e.g., Kambach et al., 2013; Kuchenbecker et al., 2023), comparisons between control and treatment sites were considered independently for each taxonomic group (e.g., ants and dung beetles). This approach ensured that each taxonomic group within a multi-taxa study contributed as a distinct study case, allowing for a more comprehensive evaluation of the effects of anthropogenic impacts on insect biodiversity.

2.7 Effect size estimation

To estimate the effect size for each study case, we employed the Hedge's d statistic (Hedges and Olkin, 1985). Hedge's d is widely used in ecological studies comparing two groups (Gurevitch et al., 2001), as it incorporates the mean and standard deviation to provide results on a continuous distribution scale (Borenstein et al., 2021). Negative effect sizes indicate that the control site exhibits higher diversity values compared to the treatment site, whereas positive effect sizes reflect higher diversity values in the treatment site relative to the control.

2.8 Overall effect model

We estimated the overall effect of anthropogenic impacts in Neotropical mountains using multilevel random-effects models with restricted maximum likelihood estimation (Nakagawa et al., 2023). Multilevel models were implemented to minimize bias in the overall effect size and heterogeneity quantification, while also preventing over-reliance on specific papers when multiple study cases from the same paper were included (Senior et al., 2016). Random factors incorporated into the models included: (i) paper identity and (ii) study case identity. This approach reduces potential confounding factors and enhances the generalizability of the results. The multilevel analysis was conducted using the “`rma.mv`” function in the R package `metafor` (Viechtbauer, 2010). Separate multilevel models were performed for species richness and individual abundance to evaluate their respective responses to anthropogenic impacts.

2.9 Effect of moderating variables

To explain the heterogeneity in overall effect sizes, we incorporated four categorical and two continuous moderator variables as fixed effects in the multilevel random-effects

models (see section 2.8). Four ecological moderator variables were included: (i) insect group evaluated (ants vs. bees vs. dung beetles vs. lepidopterans), (ii) natural habitat transformed (natural forest vs. natural savanna), (iii) transformation type (conversion vs. degradation vs. fragmentation), and (iv) the specific transformation identity (i.e., conversion [agriculture vs. livestock vs. silviculture]; degradation [fire vs. restoration]; fragmentation [edge effect vs. patch size]). Additionally, two geographical moderator variables were included: (i) latitude (expressed as an absolute value, treating north and south as equivalent in terms of latitudinal variation) and (ii) altitude (calculated as the proportion between the local study altitude and the maximum altitude of the mountain range; Karagulle et al., 2017). Latitude and altitude were used as continuous moderators to assess their effects on overall insect species richness and abundance. Furthermore, these variables were analysed concerning natural habitat transformation (e.g., latitude vs. natural forest transformation) and insect taxonomic groups (e.g., latitude vs. dung beetle response).

A single paper could encompass more than one subject category, often evaluating multiple taxonomic groups (e.g., Kuchenbecker et al., 2023) or specific impact types (e.g., Kambach et al., 2013; Filgueiras et al., 2015). When moderator variables were not reported in the included studies, the evaluation of these moderators was restricted to the study cases with available information.

2.10 Statistical analysis

We used multilevel random-effects meta-regressions with a T-test distribution to evaluate heterogeneity across the levels of each moderator variable (Nakagawa et al., 2023). An F-value with $p < 0.05$ indicates significant variation in effects, demonstrating the absence of a unidirectional or common effect among the levels of a given moderator. Conversely, when confidence intervals include zero, the effect is considered neutral. Additionally, due to

potential asymmetries associated with a low number of study cases within certain moderator levels, we excluded moderator levels with fewer than four study cases from the comparative analyses, as they were deemed uninformative. Furthermore, results based on fewer than ten study cases should be interpreted cautiously, as confidence intervals in such cases may be influenced by the limited number of study cases with varying effect sizes. Effect sizes for moderator levels with more than 10 case studies are considered informative and robust.

2.11 Publication bias analysis

Publication bias is a recognized concern in meta-analyses, as it can lead to the exclusion of ecological studies and distort synthesized results (López-Bedoya et al., 2022b). Ecological studies reporting neutral effects are less likely to be published, potentially skewing the overall findings toward significant effects. To address this issue, we applied the Rosenthal test (Rosenthal, 1979) to estimate the number of unpublished studies with neutral effects required to render the overall effects non-significant. The Rosenthal test is considered robust when the confidence number is $\geq 5N + 10$, where N represents the number of study cases. Given the potential imbalance between positive and negative cases in the meta-analyses, we also employed the trim-and-fill method (Duval and Tweedie, 2000). This method evaluates asymmetry in reported study outcomes and recalculates the global average effect size and confidence intervals, providing a more reliable assessment of the results. All statistical analyses were conducted using the R statistical software, version 4.4.2 (R Core Team, 2024).

3. Results

3.1 Overall overview database

We identified 105 studies conducted in Neotropical mountains between 1983 and 2023. These studies were distributed across 12 countries, with Colombia and Brazil being

particularly well-represented, and spanned 15 mountain ranges, including the Cordillera de Los Andes, Cordillera Centroamericana, and the Trans-Mexican Volcanic Belt (Fig. 1; Table S2). From these 105 studies, we extracted 424 case studies, of which 266 reported species richness and 158 reported total abundance (Table S2). Among the total case studies, natural forest was the most commonly used control habitat, accounting for 94.57% of cases, while only 5.42% were conducted in savannas. Dung beetles were the most frequently studied taxonomic group, representing 58.01% of the case studies, followed by ants (20.04%), lepidopterans (11.32%), and bees (10.61%). Regarding habitat transformation, the conversion of natural forests to agriculture accounted for the largest proportion of study cases (33.72%), followed closely by the conversion of natural forests to livestock (31.36%).

3.2 Impact of natural habitat transformation on insect diversity

We found that anthropogenic impacts significantly reduce insect species richness ($d = -1.179$, $CI = -1.641$ to -0.718 , $p < 0.001$; Fig. 2a), and total abundance ($d = -1.059$, $CI = -1.988$ to -0.130 , $p < 0.001$; Fig. 2d) compared to natural habitats in Neotropical mountains. The effects of anthropogenic pressures on natural habitats varied idiosyncratically among taxonomic groups. For species richness, ants and dung beetles exhibited negative effects, whereas bees and lepidopterans showed neutral responses ($F_{4,262} = 8.538$, $p < 0.001$; Fig. 2b). In contrast, for total abundance, only dung beetles displayed negative effects, while ants, bees, and lepidopterans exhibited neutral responses ($F_{4,154} = 4.624$, $p = 0.002$; Fig. 2e).

3.3 Natural habitat, transformation type, and specific impact's identity

We found that the type of natural habitat transformed moderate the effect on insect, with natural forest transformation showing a significant negative effect on species richness ($F_{2,264} = 18.065$, $p < 0.001$; Fig. 2c) and total abundance ($F_{2,156} = 9.276$, $p < 0.001$; Fig. 2f),

whereas savannas showed neutral or positive effects. When evaluating the specific effects of habitat transformation, we observed a negative influence of habitat conversion on insect species richness ($F_{3,263} = 12.145$, $p < 0.001$; Table 1), and a marginal effect on total abundance ($F_{3,155} = 2.151$, $p = 0.096$). In contrast, habitat degradation and fragmentation showed neutral effects on both species' richness and total abundance.

For species richness, the specific transformation identity influenced insect responses. Significant differences were observed for habitat conversion ($F_{3,181} = 19.021$, $p < 0.001$), with agriculture and livestock conversions driving negative effects on species richness, while silviculture showed neutral effects. For habitat degradation, no significant differences were found between degradation types ($F_{2,30} = 3.079$, $p = 0.061$), although the natural habitat degradation and posterior restoration exhibited negative effects compared to the neutral effects of fire events. Habitat fragmentation did not significantly affect species richness ($F_{2,47} = 0.694$, $p = 0.504$), with both patch size and edge effects showing neutral tendencies.

Focusing on insect abundance, we found significant differences in habitat conversion identity ($F_{3,111} = 3.761$, $p = 0.012$), with livestock conversion negatively affecting abundance, while agriculture and silviculture showed neutral effects. However, no significant differences were observed for habitat degradation ($F_{2,8} = 1.721$, $p = 0.239$) or habitat fragmentation ($F_{2,32} = 0.188$, $p = 0.829$) to insect abundance.

3.4 Overall effect of latitude and altitude

The overall negative effects on insect species richness were significantly influenced by latitude (slope = 0.086, $p = 0.002$; Fig 3), and altitude (slope = 0.033, $p < 0.001$; Fig. 3), indicating that the severity of anthropogenic impacts in Neotropical mountains decreases as latitude increases (toward the poles) and at higher altitudes. However, for insect abundance,

the overall negative effects were independent of latitude (slope = 0.046, $p = 0.471$; Fig. 3) and altitude (slope = 0.026, $p = 0.225$; Fig. 3).

Latitude and altitude also influenced the responses of insect species richness and total abundance when considering natural habitat transformation (e.g., natural forest) and the taxonomic groups assessed (e.g., ants and dung beetles) (Table S3). Specifically, the effects of anthropogenic impacts were less severe further from the equator and at higher altitudes.

3.5 Publication bias

The Rosenthal safety analysis revealed that 19,368 case studies for species richness and 16,096 case studies for individual abundance with neutral effects would be required to produce non-significant results, far exceeding the safety thresholds of 1,360 and 820 cases, respectively. The trim-and-fill procedure indicated that the direction and magnitude of the effects remain consistently negative for both insect species richness and total abundance (see Table S4). These findings suggest that the results are robust and not influenced by potential biases arising from the omission of studies reporting neutral or negative effects.

4. Discussion

We conducted a meta-analysis focusing on insects to evaluate the influence of anthropogenic impacts on species richness and abundance in Neotropical mountains. Our findings supported our research hypotheses, demonstrating that: (i) anthropogenic transformations lead to significant losses in species richness and total abundance, and (ii) the negative effects depend on the insect group, habitat transformation characteristics, and geographical context. The most pronounced negative effects were observed in ants and dung beetles, particularly when natural forests were converted to agriculture or livestock, especially in equatorial latitudes and at lower altitudes. These results highlight the urgent need for

structured conservation programs to minimize the negative impacts of natural habitat transformation. Such programs are essential to preserve insect biodiversity, which provides critical ecological benefits that contribute to human well-being.

4.1 The transformation of natural habitats supports lower insect diversity than conserved natural habitats

Our results demonstrated that anthropogenic pressures have a negative impact on insect species richness and abundance in Neotropical mountains. These findings align with previous local studies on insect diversity in Neotropical mountains which show that natural habitat transformation contributes to biodiversity loss (e.g., Armbrrecht and Perfecto, 2003; Tylianakis et al., 2006; Cartagena et al., 2021; Noriega et al., 2021). This response can be attributed to multiple factors associated with transformed natural habitats, such as changes in habitat structure, microclimates, food resources, and chemical exposure.

For instance, habitat transformations often result in reduced basal area, increased canopy opening (e.g., natural forest transformation; Beiroz et al., 2019), and vegetation homogenization in terms of plant diversity (e.g., natural savanna transformation; McCleery et al., 2018). These changes alter microclimates, leading to reduced soil moisture and increased temperatures (Scheffers et al., 2017; Senior et al., 2017). Additionally, transformations can decrease the availability of food resources such as nectar, dung, or invertebrate prey (Donkersley et al., 2014; Van Huis and Oonincx, 2017; Fuzessy et al., 2021). The frequent use of chemicals in transformed habitats (Tudi et al., 2021) also poses a significant threat to insects, as many of these chemicals are toxic to them (Belsky and Joshi, 2020; Tovar et al., 2023).

These factors help to explain the observed negative effects on insect diversity in response to natural habitat transformation in Neotropical mountains. This is likely due to the

physiological constraints of insects (Chown and Terblanche, 2006; Sheldon et al., 2011) and the reliance of many species on specific microhabitats (e.g., lepidopterans; Kleckova et al., 2014). Ultimately, these transformations disrupt feeding, establishment, and reproduction processes, significantly impacting insect populations (Schowalter, 2012).

4.2 Idiosyncratic response across insect taxa in Neotropical mountains

Our findings revealed an overall negative effect of natural habitat transformation on insect assemblages, highlighting the consequences of habitat alteration across various insect trophic levels (Barlow et al., 2007; Newbold et al., 2015). However, the response to habitat transformation was idiosyncratic among insect groups. Ants and dung beetles exhibited negative effects on species richness and/or abundance, while bees and lepidopterans showed neutral effects for both metrics.

Additional factors may explain the specific responses of different insect groups, such as dispersal capacity and the characteristics of habitat transformation assessed in the studies. In some cases, ants and dung beetles have restricted home range in the landscape (Torres-Contreras and Vasquez, 2004; Cultid-Medina et al., 2015), leading to communities that are highly sensitive to local habitat characteristics (Crist, 2009; López-Bedoya et al., 2021). In contrast, bees and lepidopterans exhibit higher dispersal capacities (Osborne et al., 1999; Dover and Settele, 2009; Jauker et al., 2009), resulting in communities that are less directly influenced by local habitat changes (Collinge et al., 2003; Carré et al., 2009).

Resource availability also plays a critical role. In altered habitats, bees and lepidopterans may exhibit greater plasticity in resource selection and collection compared to ants and dung beetles (Halffter and Arellano, 2002; Dennis et al., 2006; Crist, 2009; Jha and Kremen, 2013; Jachula et al., 2021). This flexibility may allow them to adapt more effectively

to changes in food resources, such as nectar, dung, or prey availability, in transformed landscapes.

Additionally, the type of habitat transformation and its specific characteristics influence the response of insect groups. For instance, the same taxonomic group may respond differently to transformations of natural forests versus natural savannas or to impacts such as habitat conversion versus fragmentation (Diaz-Garcia et al., 2020). Also, despite the neutral effect found for bees and lepidopterans, our meta-analysis does not assess community composition, and the communities between natural and anthropogenic habitats could be different (Allen et al., 2019). These findings underscore the complexity of insect responses to habitat transformation and the importance of considering both local and landscape-level factors when assessing biodiversity impacts.

4.3 Transformation effects across natural forests and natural savannas

Our results revealed an overall negative effect of natural habitat transformation on insect assemblages, with differential effects depending on the type of habitat transformed. Specifically, the transformation of natural forests showed a pronounced negative effect, whereas the transformation of natural savannas exhibited neutral effects. This difference is likely due to the inherent ecological characteristics of these habitats.

Natural savannas generally have lower plant complexity and fewer microhabitats compared to natural forests (Ratnam et al., 2011; Torello-Raventos et al., 2013). When natural savannas are transformed, the altered habitat often retains a similar vegetation structure, soil characteristics, and microclimate to the original savanna (Osborne et al., 2018; Buisson et al., 2019), and in some cases showed more structured habitats (e.g., afforestation; Gries et al., 2012). In contrast, the transformation of natural forests typically results in drastic changes to

vegetation structure, soil properties, and microclimate (Pickett and Rogers, 1997; Beiroz et al., 2019).

Additionally, natural forests tend to harbour a higher proportion of forest specialist insect species, which are more sensitive to habitat changes, compared to generalist species (Diaz-Garcia et al., 2020). In savannas, there is often a more balanced proportion of specialist and generalist species, with generalists being more tolerant of open habitats with lower canopy cover and higher temperatures (Mauda et al., 2018; Neves et al., 2021). This may explain why savanna transformations tend to have neutral or even positive effects on species richness and abundance, while forest transformations lead to local extinctions of forest specialists.

These findings emphasize the importance of considering habitat type when assessing the impacts of natural habitat transformation on biodiversity, as the ecological characteristics of the habitat and the species it supports play a critical role in determining the severity of the effects.

4.4 Transformation type and specific impact's identity

We found that the transformation of natural habitats through degradation and fragmentation had neutral effects on insect species richness and abundance, in contrast to the negative effects observed from habitat conversion. While degradation and fragmentation can alter habitat structure, they often preserve a minimal ecological and vegetation structure of the original habitat (Lonsdale and Braithwaite, 1991; Fahrig et al., 2019). For instance, habitat degradation can maintain consistent vegetation cover in anthropogenic landscapes (e.g., natural forests), reducing the likelihood of soil drying and making its impacts less severe than those of habitat conversion. Similarly, habitat fragmentation can preserve patches of natural

habitat within disturbed landscapes, providing refuges and facilitating the dispersal of insect species (Didham et al., 1996; Hunter, 2002).

However, the specific identity of habitat transformation plays a critical role in determining the responses of insect communities in Neotropical mountains. For example, the conversion of natural habitats to livestock or agricultural lands had a pronounced negative effect compared to silviculture. In our meta-analysis, silviculture included forestry and rubber plantations, which, under certain management practices that allow understory development or the use of native species, can retain structural similarities to natural habitats (e.g., natural forests) and serve as refuges for insect diversity (López-Bedoya et al., 2021). Conversely, agricultural and livestock systems often result in abrupt ecological changes, including the use of chemicals that negatively affect insect populations (Santos-Heredia et al., 2018; Tovar et al., 2023).

Nonetheless, some agricultural systems with specific management practices, such as shade-grown coffee plantations, can support insect diversity (Arellano et al., 2005). These findings underscore the importance of evaluating agricultural management systems that promote insect conservation in Neotropical mountains. We recommend further research to explore the role of such systems in mitigating the negative impacts of habitat transformation on insect biodiversity.

In the case of natural habitat degradation, although we found no differences between the specific impacts, restoration showed a negative impact compared to fire events. This negative effect may be due to the use of multiple native species with slow growth rates, resulting in a longer growth time to reach a vegetation structure that allows the maintenance of insect communities (López-Bedoya et al., 2022a). However, the natural habitat restoration can be a good practice in anthropogenic landscapes for the recovery of biodiversity (Audino et al., 2014). Likewise, although fire events can disrupt natural environments, in some cases,

such as natural savannas, they can regenerate in a short period, facilitating the maintenance of biodiversity (Kuchenbecker et al., 2023).

When we focused on the effects between types of impacts generated by natural habitat fragmentation, we found neutral effects of patch size and edge effect. This might be related to the taxonomic group assessed with some groups such as bees may have a greater ability to disperse between patch fragments (Tonhasca et al., 2002) and could be unaffected by the edge effect (Kambach et al., 2013). However, other groups, such as ants or dung beetles, may be directly affected by patch size and edge effect (Caitano et al., 2020; Fuzessy et al., 2021). A recommendation is to assess how characteristics of the anthropized matrix associated with natural habitat affect insect response, because there may be differences between adjacent matrix types (e.g., agriculture, livestock, roads) (Magura et al., 2017).

4.5 Latitude and altitude effects in Neotropical mountains

Latitude and altitude also influenced insect responses, with the negative effects of natural habitat transformation becoming less severe at higher altitudes and further from the Equator. The observed patterns may be linked to the loss of specialist species at lower altitudes, where these species are more sensitive to changes in natural cover (Hodkinson, 2005). In contrast, at higher altitudes, generalist species, which are more tolerant of habitat changes and physiological stress, may dominate (Chown et al., 2002; Escobar et al., 2006; Espinoza & Noriega, 2018). This dominance of generalists could explain the lack of significant effects on abundance at higher altitudes, as the loss of specialist species is compensated by the higher abundance of generalist species that thrive in these high mountain ecosystems. Similarly, the response of species richness and abundance to latitude may reflect the greater presence of specialist species in equatorial regions compared to higher latitudes

closer to the poles (Brown, 2014), where generalist species are more prevalent and better adapted to environmental changes (Gilchrist, 1995; Hodkinson, 2005).

Another factor influencing these patterns could be the differences in responses among taxonomic groups. For instance, ants and dung beetles appear to be less impacted at higher altitudes, possibly due to their lower species diversity in these regions (Longino and Colwell, 2011; Noriega and Realpe, 2018). The few species that do occur in equatorial regions and at higher altitudes (ants and dung beetles) may be more tolerant of environmental changes and exhibit higher dominance in abundance (winners and losers), which could buffer the overall impact of habitat transformation (Frank et al., 2018; Alvarado et al., 2020). These findings highlight the complex interplay between species traits, such as specialization and dispersal capacity, and environmental gradients, emphasizing the need to consider both taxonomic and ecological factors when assessing the effects of habitat transformation on insect diversity.

5. Conclusions

Our findings showed a significant loss in insect species richness and abundance by anthropogenic transformations. The most pronounced negative effects were observed in ants and dung beetles, particularly when natural forests were converted to agriculture or livestock, especially in equatorial latitudes and at lower altitudes. These findings highlight the urgent need for structured conservation programs in the Neotropical region (Duffus et al., 2023) to minimize the negative impacts of natural habitat transformation. These initiatives should be associated with assessing and implementing management systems that minimize the impacts generated, especially by agriculture and livestock. For example, the case of shade cropping systems in the Neotropical mountains may be a pathway for biodiversity conservation, which should be investigated in different taxonomic groups against any impact on yield. The pronounced negative impacts of anthropogenic pressures on Neotropical montane insects

highlight the urgent need to prioritize natural habitat protection in future conservation programs.

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7. Conflict of interest

All the authors declare that there is no conflict of interest.

8. Data availability statement

Additional supporting information can be found online in the supporting information tab for this article.

9. References

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10. Tables and figures

Table 1. Effects of anthropogenic pressures on insect diversity in Neotropical mountains, detailing the transformation type, and the specific impact type for species richness and total abundance.

Fig. 1 Distribution of the included papers in the current meta-analysis. The 105 papers were distributed among 12 countries and 15 mountain ranges. Some points include more than one paper with field surveys conducted in different years. Multitaxa = papers that evaluate more than one taxonomic group.

Fig. 2 Effects attributed to anthropogenic pressures on insect diversity in Neotropical mountains. The average and 95% confidence intervals are shown for: overall effect, taxonomic group, and natural habitat transformed. (a-c) Richness represented by circle symbol, and (d-f) total abundance represented by triangle symbol. The number of case studies per level of the moderator is given in parenthesis. Confidence intervals of the effect for each moderator level that move away from zero indicate that there is a significant effect ($p < 0.05$). Asterisks denote confidence intervals that are significantly different from zero. Significance levels were determined as: $NSp \geq 0.05$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Fig. 3 Relationship between latitude (a, c) and altitude (b, d) with insect species richness (a, b) and abundance (c, d) in relation with anthropogenic pressures on Neotropical mountains.

Table 1. Effects of anthropogenic pressures on insect diversity in Neotropical mountains, detailing the transformation type, and the specific impact type for species richness and total abundance.

Moderator	Study cases number	Hedges d value	Standard error	P-value
Species richness				
Transformation				
Conversion	185	-1.499	0.250	< 0.001
Degradation	32	-0.737	0.475	0.122
Fragmentation	49	-0.245	0.416	0.556
Conversion type				
Agriculture	87	-1.176	0.309	< 0.001
Livestock	86	-2.246	0.305	< 0.001
Silviculture	12	-1.004	0.684	0.143
Degradation type				
Fire	15	1.290	0.954	0.186
Restoration	17	-2.309	1.109	0.046
Fragmentation type				
Edge effect	17	-0.170	0.580	0.770
Patch size	32	-0.611	0.530	0.254
Total abundance				
Transformation				
Conversion	114	-1.267	0.524	0.015
Degradation	10	-1.412	1.203	0.242
Fragmentation	34	-0.309	0.787	0.694
Conversion type				
Agriculture	56	-0.657	0.652	0.308
Livestock	47	-1.952	0.644	0.003
Silviculture	11	-2.850	1.580	0.074
Degradation type				
Fire	6	2.225	2.680	0.430
Restoration	4	-5.724	3.450	0.135
Fragmentation type				
Edge effect	13	-0.522	0.931	0.578
Patch size	21	-0.210	0.809	0.789

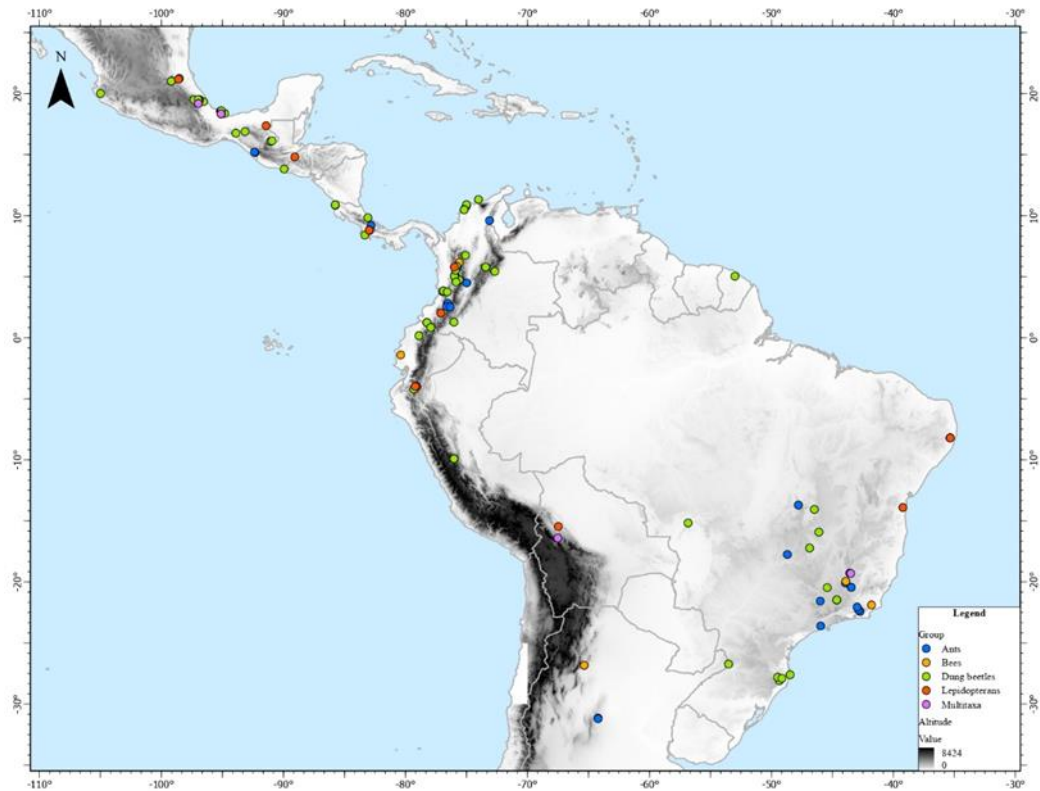


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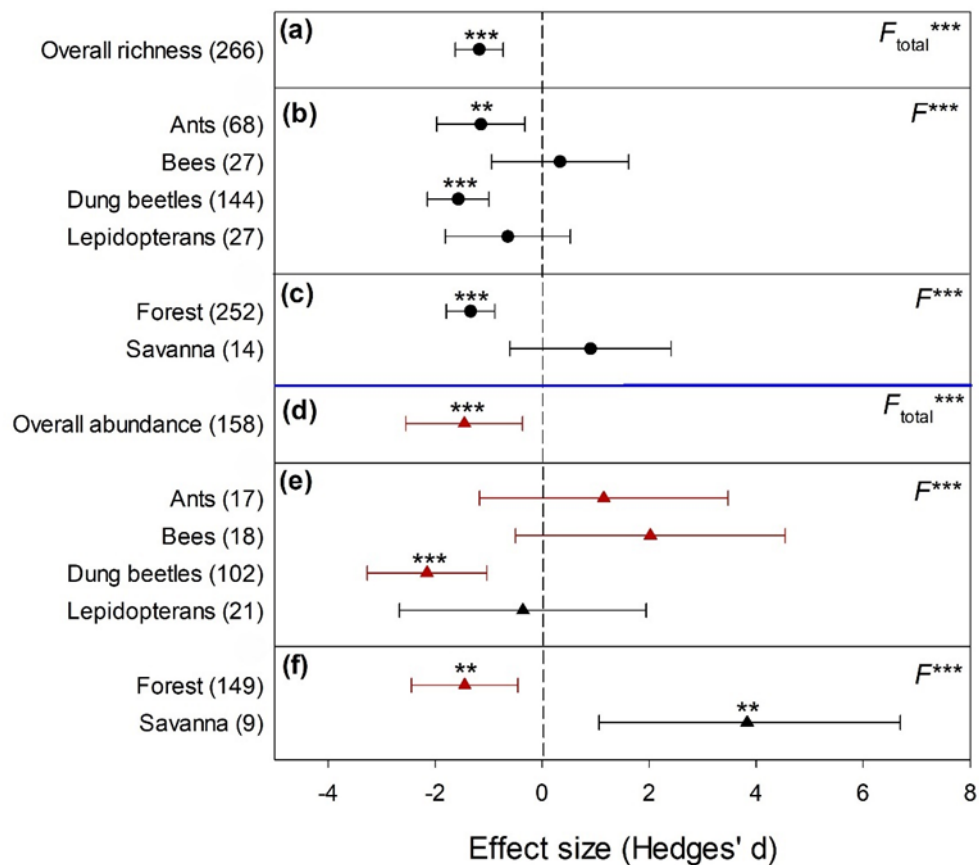


Fig. 2 Effects attributed to anthropogenic pressures on insect diversity in Neotropical mountains. The average and 95% confidence intervals are shown for: overall effect, taxonomic group, and natural habitat transformed. (a-c) Richness represented by circle symbol, and (d-f) total abundance represented by triangle symbol. The number of case studies per level of the moderator is given in parenthesis. Confidence intervals of the effect for each moderator level that move away from zero indicate that there is a significant effect ($p < 0.05$). Asterisks denote confidence intervals that are significantly different from zero. Significance levels were determined as: NS $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

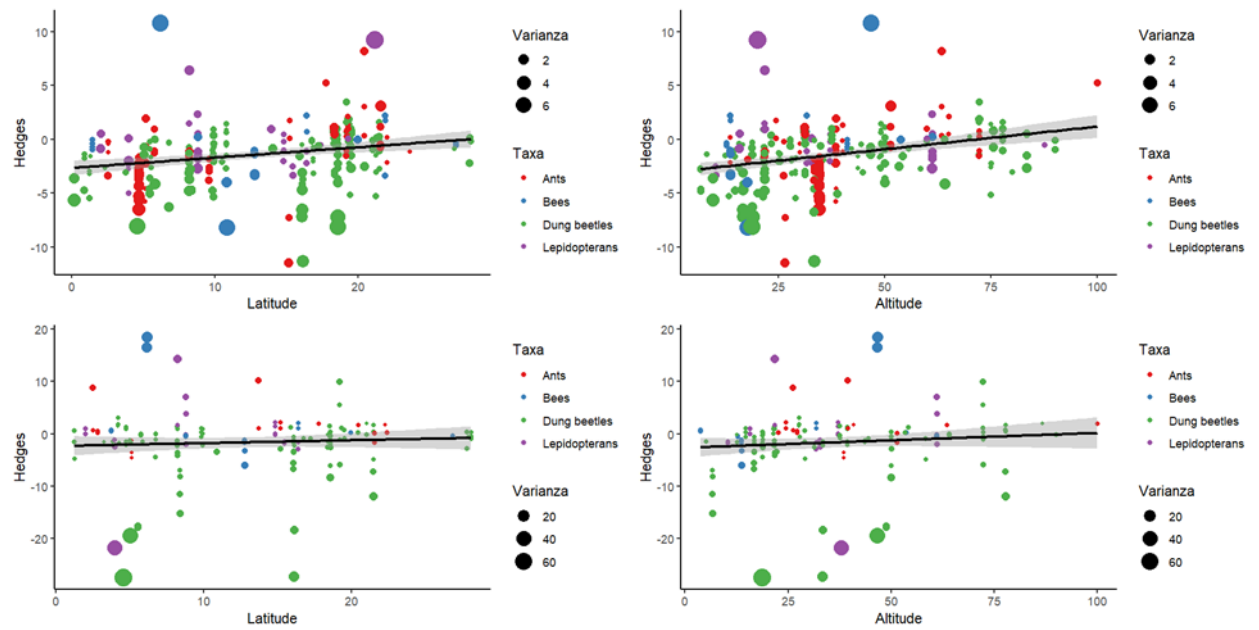


Fig. 3 Relationship between latitude (a, c) and altitude (b, d) with insect species richness (a, b) and abundance (c, d) in relation to anthropogenic pressures on Neotropical mountains.

11. Supplementary material

Meta-analysis of insect diversity responses to anthropogenic pressures in Neotropical mountains

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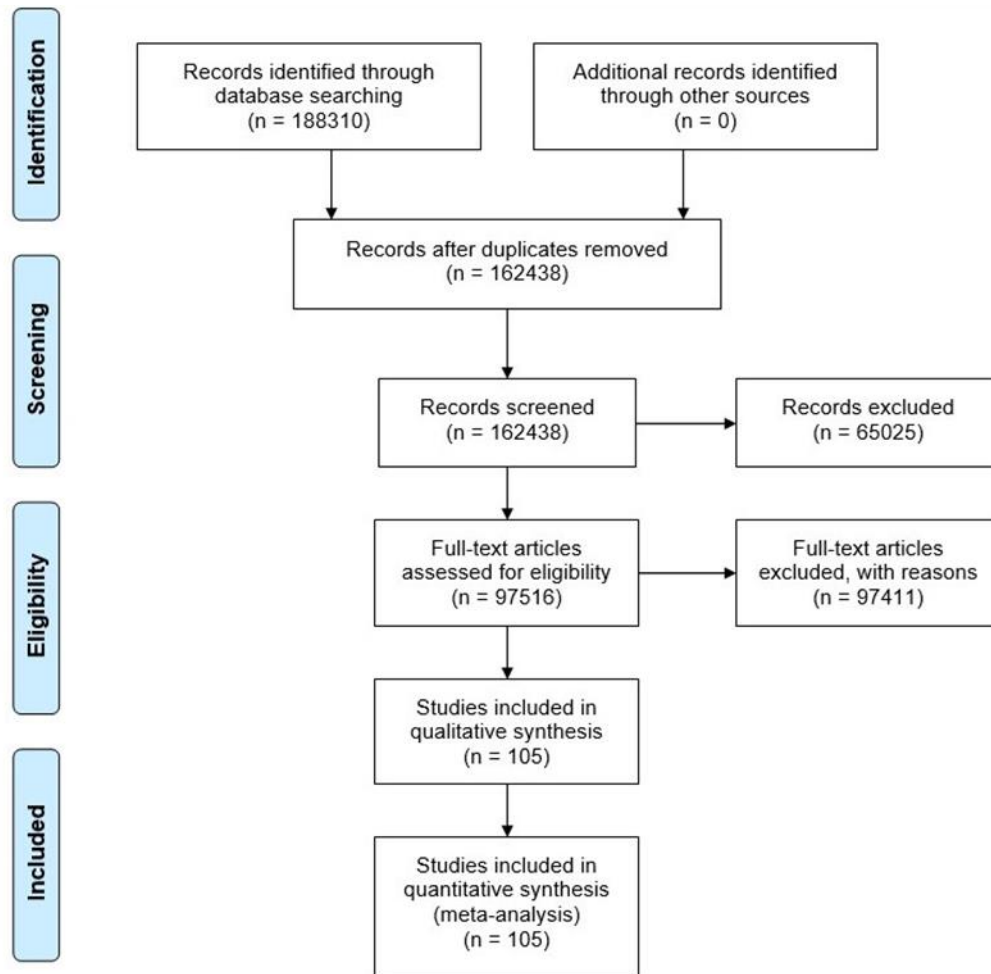


Fig S1. PRISMA flow diagram methodology (Preferred Reporting Items for Systematic Reviews and Meta-analysis) utilized in this study.

Table S1. Transformation types included in this meta-analysis, which describes the control and treatment sites description.

Transformation type	Control site	Treatment site	References
Fragmentation			
Patch size	Natural forest or savannas remnants with an area of 600 ha or more. In cases where the minimum area for a control site is not met, we include the published paper if the control site is at least 10 times larger than the smallest fragment	Fragments with an area of 200 ha or less will serve as treatment sites.	Global reference definition (Markl et al. 2012; Fontúrbel et al. 2015); study case examples in this meta-analysis (Tonhasca et al. 2002; Filgueiras et al. 2015)
Edge effect	The most interior natural forest or savanna. Generally, 100 m inside of natural habitat	The abrupt transitions between native forest or savanna and anthropogenic matrix	Global reference definition (Magura et al. 2017); study case examples in this meta-analysis (Kambach et al. 2013; Villada-Bedoya et al. 2017)

Degradation

Fire event	Unburned natural forest or savanna	Burned natural forest or savanna	Global reference definition (He et al. 2019); study case examples in this meta-analysis (Kambach et al. 2013; Kuchenbecker et al. 2023)
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Restoration	Natural forest or savanna	Land areas with restoration process	Global reference definition (Lamb et al. 2005; Bechara et al. 2016;); study case examples in this meta-analysis (Herrera-Rangel et al. 2015; Díaz-García et al. 2020)
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Conversion

Agriculture	Natural forest or savanna	Covers related to agricultural development how annual crops, coffee, cocoa, potato, sugar cane.	Global reference definition (Curtis et al. 2018); study case examples in this meta-analysis (Horner-Devine et al. 2003; Allen et al. 2019)
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Livestock	Natural forest or savanna	Land areas implemented with exotic pastures to livestock production	Global reference definition (Curtis et al. 2018); study case examples in this meta-analysis (Kambach et al. 2013; Jimenez-Carmona et al. 2020)
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Silviculture	Natural forest or savanna	Forestry plantations established to wood biomass production (e.g., timber and other wood products as paper pulp)	Global reference definition (Curtis et al. 2018; FRA 2020); study case examples in this meta-analysis (Medina et al. 2002; Gries et al. 2012)
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Table S2. Summary of the case studies for insect species richness and abundance used in the meta-analysis, detailing taxa, natural habitat transformed (natural forest, natural savanna), transformation type, impact type, and mountain range location. Some references provided more than one case study, referred to different sampling locations or different sampling time, which were considered as independent cases. Hedges' d and variance values (Var) are reported.

Richness							
Paper ID	Taxa	Habitat	Transformation	Impact type	Mountain	Hedges	Var
Aizen & Feinsinger 1994	Bees	Forest	Fragmentation	Patch size	Sierras Pampeanas	-0.293	0.168
Aizen & Feinsinger 1994	Bees	Forest	Fragmentation	Patch size	Sierras Pampeanas	-0.588	0.174
Aizen & Feinsinger 1994	Bees	Forest	Fragmentation	Patch size	Sierras Pampeanas	-0.527	0.172
Estrada et al. 1998	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-0.462	0.684
Estrada et al. 1998	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-0.785	0.718
Estrada et al. 1998	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-7.169	4.949
Estrada et al. 1998	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-1.398	0.829
Estrada et al. 1998	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-8.116	6.156
Estrada et al. 1999	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-3.650	0.502
Estrada et al. 1999	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-3.974	1.487
Estrada et al. 1999	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-2.227	0.937
Escobar & Chacon de Ulloa 2000	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-2.964	0.131
Ricketts et al. 2001	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	-1.480	0.933
Ricketts et al. 2001	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	-1.767	1.010
Ricketts et al. 2001	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	-2.690	1.904
Ricketts et al. 2001	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	-1.111	0.853
Estrada & Coates-Estrada 2002	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-0.717	0.043
Medina et al. 2002	Dung beetles	Forest	Conversion	Silviculture	Cordillera de los Andes	-1.892	0.289
Tonhasca et al. 2002	Bees	Forest	Fragmentation	Patch size	Serra do Mar	2.189	0.267
Tonhasca et al. 2002	Bees	Forest	Fragmentation	Patch size	Serra do Mar	-3.394	0.407
Tonhasca et al. 2002	Bees	Forest	Fragmentation	Patch size	Serra do Mar	1.774	0.232

Tonhasca et al. 2002	Bees	Forest	Fragmentation	Patch size	Serra do Mar	2.230	0.270
Arellano & Halffter 2003	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-0.034	0.417
Arellano & Halffter 2003	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-0.630	0.691
Arellano & Halffter 2003	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	0.527	0.861
Arellano & Halffter 2003	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-2.667	1.545
Arellano & Halffter 2003	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-1.489	1.055
Armbrecht & Perfecto 2003	Ants	Forest	Conversion	Agriculture	Cordillera Centroamericana	-7.237	0.511
Armbrecht & Perfecto 2003	Ants	Forest	Conversion	Agriculture	Cordillera Centroamericana	-11.452	1.168
Horner-Devine et al. 2003	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	0.535	0.516
Horner-Devine et al. 2003	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	2.321	0.799
Armbrecht et al. 2004	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	0.972	0.559
Armbrecht et al. 2004	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.249	0.598
Armbrecht et al. 2004	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.062	0.571
Escobar 2004	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-3.185	0.142
Escobar 2004	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-5.444	0.294
Arellano et al. 2005	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	0.762	1.073
Arellano et al. 2005	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-0.767	1.074
Hilt & Fiedler 2005	Lepidopterans	Forest	Conversion	Livestock	Cordillera de los Andes	0.126	0.835
Hilt & Fiedler 2005	Lepidopterans	Forest	Conversion	Livestock	Cordillera de los Andes	-1.971	1.485
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-0.381	0.508
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	0.355	0.677
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-2.054	0.734
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-0.301	0.253
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	0.434	0.423
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.355	0.301
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-0.456	0.342
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	0.350	0.507
Horgan 2005	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-2.053	0.509
Pineda et al. 2005	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	1.869	0.958
Rivera & Armbrecht 2005	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-2.201	1.071
Rivera & Armbrecht 2005	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-0.709	0.709
Rivera & Armbrecht 2005	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	1.942	0.981
Armbrecht et al. 2006	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-4.556	0.060
Armbrecht et al. 2006	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.545	0.022
Armbrecht et al. 2006	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-5.758	0.086
Harvey et al. 2006	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	-0.994	0.164
Harvey et al. 2006	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	-1.573	0.350
Harvey et al. 2006	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	-4.710	0.943
Horgan 2006	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.720	0.457
Tylianakis et al. 2006	Bees	Forest	Conversion	Agriculture	Cordillera de la Costa	-0.019	0.167
Tylianakis et al. 2006	Bees	Forest	Conversion	Agriculture	Cordillera de la Costa	-0.653	0.176
Tylianakis et al. 2006	Bees	Forest	Conversion	Agriculture	Cordillera de la Costa	-0.921	0.184
Tylianakis et al. 2006	Bees	Forest	Conversion	Agriculture	Cordillera de la Costa	-0.346	0.169
Deloya et al. 2007	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	0.961	0.744
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-1.204	0.182
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	1.177	0.180
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-2.222	0.249
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-1.376	0.206
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-4.756	0.638

Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-1.723	0.228
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-3.581	0.521
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-4.979	0.820
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-0.194	0.201
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-4.600	0.729
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-5.060	0.840
Escobar et al. 2007	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-0.860	0.218
Halffter et al. 2007	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	1.404	0.096
Halffter et al. 2007	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-2.574	0.141
Halffter et al. 2007	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-5.147	0.332
Brosi et al. 2008	Bees	Forest	Fragmentation	Patch size	Cordillera Centroamericana	0.263	0.569
Brosi et al. 2008	Bees	Forest	Fragmentation	Patch size	Cordillera Centroamericana	0.258	0.840
Feer 2008	Dung beetles	Forest	Fragmentation	Edge effect	Tumucumaque Uplands	-1.502	0.256
Navarrete & Halffter 2008	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-0.510	0.147
Navarrete & Halffter 2008	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-6.375	1.066
Navarrete & Halffter 2008	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-4.139	0.555
Horgan 2009	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	0.927	0.345
Horgan 2009	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-0.691	0.250
Horgan 2009	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-5.315	0.698
Pacheco et al. 2009	Ants	Forest	Conversion	Silviculture	Serra do Mar	-1.087	0.046
Milder et al. 2010	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	0.502	0.206
Milder et al. 2010	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.171	0.201
Milder et al. 2010	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.982	0.224
Milder et al. 2010	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	-2.033	0.303
Némesio & Silveira 2010	Bees	Forest	Fragmentation	Patch size	Serra do Espinhaço	0.000	1.000
Almeida et al. 2011	Dung beetles	Savanna	Conversion	Livestock	Mantiqueira mountains	-2.689	0.222
Filgueiras et al. 2011	Dung beetles	Forest	Fragmentation	Patch size	Northeastern Highland	-0.723	0.417
Filgueiras et al. 2011	Dung beetles	Forest	Fragmentation	Patch size	Northeastern Highland	-3.684	1.553
Filgueiras et al. 2011	Dung beetles	Forest	Fragmentation	Patch size	Northeastern Highland	-1.472	0.635
Achury et al. 2012	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-1.840	0.569
Frizzo et al. 2012	Ants	Savanna	Degradation	Fire	Central Highland	5.286	0.449
Gries et al. 2012	Dung beetles	Forest	Conversion	Silviculture	Mantiqueira mountains	0.241	0.646
Gries et al. 2012	Dung beetles	Forest	Conversion	Silviculture	Mantiqueira mountains	-1.046	0.661
Gries et al. 2012	Dung beetles	Savanna	Conversion	Silviculture	Mantiqueira mountains	1.591	0.407
Gries et al. 2012	Dung beetles	Savanna	Conversion	Silviculture	Mantiqueira mountains	-0.136	0.278
Leal et al. 2012	Ants	Forest	Fragmentation	Patch size	Northeastern Highland	-1.592	0.603
Leal et al. 2012	Ants	Forest	Fragmentation	Patch size	Northeastern Highland	-1.115	0.958
Leal et al. 2012	Ants	Forest	Fragmentation	Patch size	Northeastern Highland	-1.379	0.652
Noriega et al. 2012	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-0.090	0.222
Arellano et al. 2013	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-2.049	0.122
Arellano et al. 2013	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-3.150	0.175
Arellano et al. 2013	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.764	0.089
Arellano et al. 2013	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-1.797	0.113
De la Mora et al. 2013	Ants	Forest	Conversion	Agriculture	Cordillera Centroamericana	1.802	0.232
De la Mora et al. 2013	Ants	Forest	Conversion	Agriculture	Cordillera Centroamericana	0.115	0.167
Kambach et al. 2013	Bees	Forest	Fragmentation	Edge effect	Cordillera de los Andes	0.723	0.266
Kambach et al. 2013	Bees	Forest	Degradation	Fire	Cordillera de los Andes	2.199	0.401
Kambach et al. 2013	Lepidopterans	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-1.128	0.290
Kambach et al. 2013	Lepidopterans	Forest	Degradation	Fire	Cordillera de los Andes	-2.217	0.404
Barragán et al. 2014	Dung beetles	Forest	Conversion	Livestock	Sierra Madre Oriental	-5.290	0.360

Barragán et al. 2014	Dung beetles	Forest	Conversion	Livestock	Sierra Madre Oriental	-1.462	0.101
Barragán et al. 2014	Dung beetles	Forest	Conversion	Livestock	Sierra Madre Oriental	-3.017	0.171
Barragán et al. 2014	Dung beetles	Forest	Conversion	Livestock	Sierra Madre Oriental	0.255	0.081
Adams & Fiedler 2015	Lepidopterans	Forest	Conversion	Silviculture	Cordillera de los Andes	-2.437	0.087
Adams & Fiedler 2015	Lepidopterans	Forest	Conversion	Livestock	Cordillera de los Andes	-4.961	0.204
Adams & Fiedler 2015	Lepidopterans	Forest	Degradation	Fire	Cordillera de los Andes	-2.798	0.099
Anjos et al. 2015	Ants	Savanna	Degradation	Fire	Serra do Espinhaço	0.344	0.169
Filgueiras et al. 2015	Dung beetles	Forest	Fragmentation	Edge effect	Northeastern Highland	-1.306	0.607
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Agriculture	Northeastern Highland	-3.678	1.346
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Livestock	Northeastern Highland	-4.814	1.948
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Agriculture	Northeastern Highland	-2.172	0.795
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Livestock	Northeastern Highland	-3.136	1.114
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Agriculture	Northeastern Highland	-2.748	0.972
Herrera-Rangel et al. 2015	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-1.691	0.905
Herrera-Rangel et al. 2015	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-2.211	1.074
Herrera-Rangel et al. 2015	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-3.333	1.593
Herrera-Rangel et al. 2015	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-3.120	1.478
Herrera-Rangel et al. 2015	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-2.412	0.999
Herrera-Rangel et al. 2015	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-6.500	3.601
Herrera-Rangel et al. 2015	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-3.715	1.217
Herrera-Rangel et al. 2015	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-4.350	1.935
Herrera-Rangel et al. 2015	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-5.303	2.592
Herrera-Rangel et al. 2015	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-5.521	2.143
Herrera-Rangel et al. 2015	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-2.920	1.192
Herrera-Rangel et al. 2015	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-5.309	2.597
Herrera-Rangel et al. 2015	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-5.627	2.209
Cultid-Medina & Escobar 2016	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.530	0.048
Cultid-Medina & Escobar 2016	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-2.649	0.070
González-Valdivia et al. 2016	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.484	0.172
Montoya-Molina et al. 2016	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-3.074	0.308
Morón & Arce-Perez 2016	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	0.351	0.677
Morón & Arce-Perez 2016	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	0.000	0.667
Morón & Arce-Perez 2016	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	0.991	0.748
Neves et al. 2016	Ants	Savanna	Degradation	Fire	Serra do Espinhaço	1.340	0.163
Neves et al. 2016	Ants	Savanna	Degradation	Fire	Serra do Espinhaço	0.501	0.138
Neves et al. 2016	Ants	Savanna	Degradation	Fire	Serra do Espinhaço	-0.111	0.134
Neves et al. 2016	Ants	Savanna	Degradation	Fire	Serra do Espinhaço	2.150	0.210
Rangel-Acosta et al. 2016	Dung beetles	Forest	Fragmentation	Edge effect	Serrania del Piojó	1.467	0.254
Rangel-Acosta et al. 2016	Dung beetles	Forest	Fragmentation	Edge effect	Serrania del Piojó	-1.503	0.256
Rangel-Acosta et al. 2016	Dung beetles	Forest	Conversion	Agriculture	Serrania del Piojó	0.642	0.210
Rangel-Acosta et al. 2016	Dung beetles	Forest	Conversion	Livestock	Serrania del Piojó	-0.307	0.202
Rangel-Acosta et al. 2016	Dung beetles	Forest	Conversion	Agriculture	Serrania del Piojó	-0.461	0.205
Rangel-Acosta et al. 2016	Dung beetles	Forest	Conversion	Livestock	Serrania del Piojó	-2.679	0.379

Sánchez-de-Jesús et al. 2016	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-6.525	3.195
Sánchez-de-Jesús et al. 2016	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-7.172	2.588
Sánchez-de-Jesús et al. 2016	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-4.652	2.129
Sánchez-de-Jesús et al. 2016	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-3.096	1.465
Anjos et al. 2017	Ants	Savanna	Degradation	Fire	Serra do Espinhaço	8.234	0.948
Anjos et al. 2017	Ants	Savanna	Degradation	Fire	Serra do Espinhaço	3.063	0.217
Cambui et al. 2017	Lepidopterans	Forest	Conversion	Silviculture	Geraizinhos Highlands	0.996	0.933
Rangel-Acosta & Martínez-Hernandez 2017	Dung beetles	Forest	Conversion	Agriculture	Serrania del Piojó	-0.551	0.069
Rangel-Acosta & Martínez-Hernandez 2017	Dung beetles	Forest	Conversion	Livestock	Serrania del Piojó	0.887	0.073
Sepulveda-Cano et al. 2017	Bees	Forest	Fragmentation	Edge effect	Cordillera de los Andes	10.880	6.319
Sepulveda-Cano et al. 2017	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	10.803	6.236
Villada-Bedoya et al. 2017	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-0.743	1.069
Villada-Bedoya et al. 2017	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.403	1.246
Assis et al. 2018	Ants	Forest	Conversion	Agriculture	Mantiqueira Mountains	-0.736	0.712
Assis et al. 2018	Ants	Forest	Conversion	Agriculture	Mantiqueira Mountains	3.097	2.199
Assis et al. 2018	Ants	Forest	Fragmentation	Edge effect	Mantiqueira Mountains	1.141	0.775
Assis et al. 2018	Ants	Forest	Fragmentation	Edge effect	Mantiqueira Mountains	-0.482	0.686
García-Cardenas et al. 2018	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-0.373	0.057
García-Cardenas et al. 2018	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.187	0.065
Gonzalez-Tokman et al. 2018	Dung beetles	Forest	Degradation	Restoration	Trans-Mexican Volcanic Belt	-0.345	0.169
Gonzalez-Tokman et al. 2018	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-2.642	0.468
Martínez-Falcon et al. 2018	Dung beetles	Forest	Fragmentation	Edge effect	Sierra Madre Oriental	-0.087	0.500
Martínez-Falcon et al. 2018	Dung beetles	Forest	Conversion	Livestock	Sierra Madre Oriental	-0.938	0.555
Santos-Heredia et al. 2018	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	-3.700	0.452
Santos-Heredia et al. 2018	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	-6.769	1.121
Santos-Heredia et al. 2018	Dung beetles	Forest	Conversion	Silviculture	Cordillera Centroamericana	-11.295	2.825
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.044	0.758
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.257	0.798
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.183	0.783
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.376	0.824
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-3.325	1.588
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-3.220	1.531
Apolinario et al. 2019	Ants	Forest	Conversion	Silviculture	Serra do Mar	0.165	0.084
Apolinario et al. 2019	Ants	Forest	Conversion	Livestock	Serra do Mar	-2.126	0.130
Arenas-Clavijo & Armbrrecht 2019	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-3.379	0.607
Arenas-Clavijo & Armbrrecht 2019	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-0.169	0.251
Filgueiras et al. 2019	Lepidopterans	Forest	Fragmentation	Edge effect	Northeastern Highland	1.494	0.320
Filgueiras et al. 2019	Lepidopterans	Forest	Fragmentation	Patch size	Northeastern Highland	6.437	1.545
Gallego-López & Gallego-Roperó 2019	Lepidopterans	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-0.886	1.098
Gallego-López & Gallego-Roperó 2019	Lepidopterans	Forest	Conversion	Agriculture	Cordillera de los Andes	0.552	1.038
Montes-Rodríguez et al. 2019	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-0.262	0.252
Montes-Rodríguez et al. 2019	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-0.325	0.253

Montes-Rodriguez et al. 2019	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-0.257	0.252
Montes-Rodriguez et al. 2019	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-6.256	1.473
Rocha-Ortega & Coronel-Arellano 2019	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	0.114	0.751
Rocha-Ortega & Coronel-Arellano 2019	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-0.344	1.015
Rocha-Ortega & Coronel-Arellano 2019	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	0.754	1.071
Rocha-Ortega & Coronel-Arellano 2019	Ants	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	0.722	0.793
Rocha-Ortega & Coronel-Arellano 2019	Ants	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	1.088	1.148
Rocha-Ortega & Coronel-Arellano 2019	Ants	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	0.500	1.031
Alvarado et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-0.424	0.227
Alves et al. 2020	Dung beetles	Forest	Conversion	Agriculture	Serra do Mar	-0.843	0.145
Davies et al. 2020	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-1.673	0.126
Davies et al. 2020	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-2.604	0.214
Diaz-García et al. 2020	Dung beetles	Forest	Degradation	Restoration	Trans-Mexican Volcanic Belt	1.574	0.291
Diaz-García et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	3.491	0.561
Diaz-García et al. 2020	Dung beetles	Forest	Degradation	Restoration	Trans-Mexican Volcanic Belt	-1.398	0.276
Diaz-García et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	0.676	0.235
Diaz-García et al. 2020	Ants	Forest	Degradation	Restoration	Trans-Mexican Volcanic Belt	-1.059	0.253
Diaz-García et al. 2020	Ants	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-1.520	0.286
Diaz-García et al. 2020	Ants	Forest	Degradation	Restoration	Trans-Mexican Volcanic Belt	0.775	0.239
Diaz-García et al. 2020	Ants	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	0.279	0.224
Jimenez-Carmona et al. 2020	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-2.684	1.098
Jimenez-Carmona et al. 2020	Ants	Forest	Degradation	Restoration	Cordillera de los Andes	-2.731	1.116
Jimenez-Carmona et al. 2020	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-4.156	1.409
Martinez-Sanchez et al. 2020	Lepidopterans	Forest	Conversion	Livestock	Sierra Madre Oriental	9.247	7.793
Rangel-Acosta et al. 2020	Dung beetles	Forest	Conversion	Livestock	Serrania del Piojó	-2.077	0.308
Rivera et al. 2020	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.073	0.343
Rivera et al. 2020	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.192	0.326
Salomão et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-2.943	0.512
Salomão et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-3.274	0.498
Bravo et al. 2021	Bees	Forest	Conversion	Livestock	Cordillera Centroamericana	-8.162	6.218
Bravo et al. 2021	Bees	Forest	Conversion	Livestock	Cordillera Centroamericana	-4.020	2.013
Cartagena et al. 2021	Lepidopterans	Forest	Conversion	Agriculture	Cordillera de los Andes	-2.531	0.360
Cartagena et al. 2021	Lepidopterans	Forest	Conversion	Agriculture	Cordillera de los Andes	-3.351	0.481
Sarmiento-Garcés & Hernandez 2021	Dung beetles	Forest	Conversion	Silviculture	Serra do Mar	0.176	0.586
Sarmiento-Garcés & Hernandez 2021	Dung beetles	Forest	Conversion	Livestock	Serra do Mar	-2.240	0.814
Whitworth et al. 2021	Dung beetles	Forest	Degradation	Restoration	Cordillera Centroamericana	-4.821	0.558
Whitworth et al. 2021	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-2.840	0.287
Whitworth et al. 2021	Dung beetles	Forest	Degradation	Restoration	Cordillera Centroamericana	-4.614	0.523
Whitworth et al. 2021	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-2.722	0.275
Arias-Alvarez et al. 2022	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-8.076	6.101
da Silva et al. 2022	Dung beetles	Forest	Conversion	Livestock	Central Highland	-0.888	1.098
Simões-Clivatti & Hernandez 2022	Dung beetles	Forest	Conversion	Silviculture	Serra do Mar	-0.200	0.335
Kuchenbecker et al. 2023	Dung beetles	Forest	Degradation	Fire	Serra do Espinhaço	-0.199	0.293
Kuchenbecker et al. 2023	Ants	Forest	Degradation	Fire	Serra do Espinhaço	0.986	0.326
Kuchenbecker et al. 2023	Bees	Forest	Degradation	Fire	Serra do Espinhaço	0.038	0.292

Kuchenbecker et al. 2023	Lepidopterans	Forest	Degradation	Fire	Serra do Espinhaço	0.070	0.292
Maciel et al. 2023	Dung beetles	Savanna	Conversion	Livestock	Central Highland	-1.551	0.867
Maciel et al. 2023	Dung beetles	Savanna	Conversion	Livestock	Serra da Canastra	-2.533	1.201
Maciel et al. 2023	Dung beetles	Savanna	Conversion	Livestock	Central Highland	-0.605	0.697
Marquez-Peña & Domínguez-Haydar 2023	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-2.960	0.524
Marquez-Peña & Domínguez-Haydar 2023	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-2.567	0.456
Marquez-Peña & Domínguez-Haydar 2023	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-2.641	0.468
Marquez-Peña & Domínguez-Haydar 2023	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-3.830	0.708
Marquez-Peña & Domínguez-Haydar 2023	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.850	0.357
Marquez-Peña & Domínguez-Haydar 2023	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.843	0.356
Marquez-Peña & Domínguez-Haydar 2023	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-1.817	0.353
Marquez-Peña & Domínguez-Haydar 2023	Ants	Forest	Conversion	Livestock	Cordillera de los Andes	-2.930	0.518
Rios-Touma et al. 2023	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-3.640	1.771
Rios-Touma et al. 2023	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-5.623	3.301
Salomão et al. 2023	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	0.000	0.667
Salomão et al. 2023	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-4.131	2.089

Abundance							
Paper_ID	Taxa	Habitat	Transformation	Impact	Mountain	Hedges	Var
Janzen 1983	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-3.416	2.459
Aizen & Feinsinger 1994	Bees	Forest	Fragmentation	Patch size	Sierras Pampeanas	-0.315	0.169
Aizen & Feinsinger 1994	Bees	Forest	Fragmentation	Patch size	Sierras Pampeanas	-0.515	0.172
Aizen & Feinsinger 1994	Bees	Forest	Fragmentation	Patch size	Sierras Pampeanas	-0.483	0.172
Medina & Kattan 1996	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.449	0.252
Estrada et al. 1998	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	0.269	0.673
Estrada et al. 1998	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-2.222	1.078
Estrada et al. 1998	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-1.773	0.929
Estrada et al. 1998	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-2.528	1.199
Estrada et al. 1998	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-0.287	0.674
Estrada et al. 1999	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-6.184	0.904
Estrada et al. 1999	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-0.577	0.521
Estrada et al. 1999	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-8.380	5.600
Escobar & Chacon de Ulloa 2000	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-4.766	0.240
Ricketts et al. 2001	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	-0.205	0.754
Ricketts et al. 2001	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	-1.922	1.058
Ricketts et al. 2001	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	-1.908	1.455
Ricketts et al. 2001	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.178	0.753
Estrada & Coates-Estrada 2002	Dung beetles	Forest	Fragmentation	Patch size	Trans-Mexican Volcanic Belt	-1.116	0.046
Medina et al. 2002	Dung beetles	Forest	Conversion	Silviculture	Cordillera de los Andes	-2.127	0.313
Medina et al. 2002	Dung beetles	Forest	Conversion	Silviculture	Cordillera de los Andes	-1.411	0.250
Medina et al. 2002	Dung beetles	Forest	Conversion	Silviculture	Cordillera de los Andes	0.977	0.224
Medina et al. 2002	Dung beetles	Forest	Conversion	Silviculture	Cordillera de los Andes	1.373	0.247
Horner-Devine et al. 2003	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	3.842	1.320
Horner-Devine et al. 2003	Lepidopterans	Forest	Conversion	Agriculture	Cordillera Centroamericana	6.991	3.215
Otero & Sandino 2003	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	0.662	0.703
Otero & Sandino 2003	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	0.438	0.683
Escobar 2004	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	0.525	0.517

Escobar 2004	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-1.514	0.643
Hilt & Fiedler 2005	Lepidopterans	Forest	Conversion	Livestock	Cordillera de los Andes	-1.190	0.684
Hilt & Fiedler 2005	Lepidopterans	Forest	Conversion	Livestock	Cordillera de los Andes	-2.406	1.232
Pineda et al. 2005	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	1.041	0.757
Armbrecht et al. 2006	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-3.584	0.043
Armbrecht et al. 2006	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.327	0.020
Armbrecht et al. 2006	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	-4.576	0.060
Harvey et al. 2006	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	-0.593	0.157
Harvey et al. 2006	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	0.291	0.271
Harvey et al. 2006	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	1.039	0.284
Deloya et al. 2007	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	0.736	0.712
Brosi et al. 2008	Bees	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-0.349	0.570
Brosi et al. 2008	Bees	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-0.526	0.861
Feer 2008	Dung beetles	Forest	Fragmentation	Edge effect	Tumucumaque Uplands	-1.532	0.259
Navarrete & Halffter 2008	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-0.616	0.150
Navarrete & Halffter 2008	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-1.658	0.242
Navarrete & Halffter 2008	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-1.254	0.217
Horgan 2009	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	0.050	0.321
Horgan 2009	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	0.943	0.260
Horgan 2009	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-2.242	0.251
Milder et al. 2010	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	1.414	0.250
Milder et al. 2010	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	2.219	0.323
Milder et al. 2010	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.195	0.201
Milder et al. 2010	Lepidopterans	Forest	Conversion	Livestock	Cordillera Centroamericana	0.044	0.200
Némesio & Silveira 2010	Bees	Forest	Fragmentation	Patch size	Serra do Espinhaço	0.182	0.837
Almeida et al. 2011	Dung beetles	Savanna	Conversion	Livestock	Mantiqueira mountains	-4.917	0.464
Filgueiras et al. 2011	Dung beetles	Forest	Fragmentation	Patch size	Northeastern Highland	0.889	0.429
Filgueiras et al. 2011	Dung beetles	Forest	Fragmentation	Patch size	Northeastern Highland	-1.393	0.722
Filgueiras et al. 2011	Dung beetles	Forest	Fragmentation	Patch size	Northeastern Highland	1.297	0.605
Frizzo et al. 2012	Ants	Savanna	Degradation	Fire	Central Highland	1.996	0.150
Gries et al. 2012	Dung beetles	Forest	Conversion	Silviculture	Mantiqueira mountains	-11.908	8.520
Gries et al. 2012	Dung beetles	Forest	Conversion	Silviculture	Mantiqueira mountains	-7.308	3.039
Gries et al. 2012	Dung beetles	Savanna	Conversion	Silviculture	Mantiqueira mountains	1.667	0.416
Gries et al. 2012	Dung beetles	Savanna	Conversion	Silviculture	Mantiqueira mountains	0.393	0.283
Noriega et al. 2012	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.439	0.280
De la Mora et al. 2013	Ants	Forest	Conversion	Agriculture	Cordillera Centroamericana	2.245	0.267
De la Mora et al. 2013	Ants	Forest	Conversion	Agriculture	Cordillera Centroamericana	1.051	0.189
Elizalde & Queiroz 2013	Ants	Forest	Fragmentation	Patch size	Serra do Mar	0.165	0.578
Kambach et al. 2013	Bees	Forest	Fragmentation	Edge effect	Cordillera de los Andes	1.133	0.290
Kambach et al. 2013	Bees	Forest	Degradation	Fire	Cordillera de los Andes	2.094	0.387
Kambach et al. 2013	Lepidopterans	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-1.577	0.328
Kambach et al. 2013	Lepidopterans	Forest	Degradation	Fire	Cordillera de los Andes	-2.923	0.517
Anjos et al. 2015	Ants	Savanna	Degradation	Fire	Serra do Espinhaço	1.658	0.224
Cultid-Medina et al. 2015	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.169	0.098
Filgueiras et al. 2015	Dung beetles	Forest	Fragmentation	Edge effect	Northeastern Highland	-1.339	0.612
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Agriculture	Northeastern Highland	-2.239	0.813
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Livestock	Northeastern Highland	-2.344	0.843
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Agriculture	Northeastern Highland	-3.542	1.284
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Livestock	Northeastern Highland	-4.073	1.537
Filgueiras et al. 2015	Dung beetles	Forest	Conversion	Agriculture	Northeastern Highland	-2.240	0.814

Bourg et al. 2016	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-0.188	0.025
Bourg et al. 2016	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-1.630	0.033
Cultid-Medina & Escobar 2016	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.564	0.048
Cultid-Medina & Escobar 2016	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-1.742	0.051
Morón & Arce-Perez 2016	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-0.388	0.679
Morón & Arce-Perez 2016	Dung beetles	Forest	Conversion	Agriculture	Trans-Mexican Volcanic Belt	-0.294	0.674
Morón & Arce-Perez 2016	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	1.450	0.842
Ortega-Martinez et al. 2016	Dung beetles	Forest	Conversion	Livestock	Sierra Madre Oriental	1.939	0.082
Sánchez-de-Jesús et al. 2016	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-5.619	2.507
Sánchez-de-Jesús et al. 2016	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-6.760	2.349
Sánchez-de-Jesús et al. 2016	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-3.457	1.437
Sánchez-de-Jesús et al. 2016	Dung beetles	Forest	Fragmentation	Patch size	Cordillera Centroamericana	-3.372	1.614
Camara et al. 2017	Ants	Forest	Fragmentation	Patch size	Serra do Mar	1.678	0.090
Sepulveda-Cano et al. 2017	Bees	Forest	Fragmentation	Edge effect	Cordillera de los Andes	16.427	13.893
Sepulveda-Cano et al. 2017	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	18.485	17.484
Villada-Bedoya et al. 2017	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-19.480	48.434
Villada-Bedoya et al. 2017	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	-19.492	48.493
Arenas-Clavijo & Armbrrecht 2018	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	0.196	0.251
Arenas-Clavijo & Armbrrecht 2018	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	0.554	0.260
Assis et al. 2018	Ants	Forest	Conversion	Agriculture	Mantiqueira mountains	-1.743	0.920
Assis et al. 2018	Ants	Forest	Conversion	Agriculture	Mantiqueira mountains	0.067	1.001
Martinez-Falcon et al. 2018	Dung beetles	Forest	Fragmentation	Edge effect	Sierra Madre Oriental	-0.201	0.503
Martinez-Falcon et al. 2018	Dung beetles	Forest	Conversion	Livestock	Sierra Madre Oriental	-0.228	0.503
Santos-Heredia et al. 2018	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	-2.207	0.268
Santos-Heredia et al. 2018	Dung beetles	Forest	Conversion	Agriculture	Cordillera Centroamericana	-18.362	7.191
Santos-Heredia et al. 2018	Dung beetles	Forest	Conversion	Silviculture	Cordillera Centroamericana	-27.322	15.719
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.327	0.813
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.157	0.778
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.668	0.898
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.350	0.819
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-5.952	3.619
Allen et al. 2019	Bees	Forest	Conversion	Agriculture	Cordillera de los Andes	-3.212	1.526
Arenas-Clavijo & Armbrrecht 2019	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	8.806	2.673
Arenas-Clavijo & Armbrrecht 2019	Ants	Forest	Conversion	Agriculture	Cordillera de los Andes	0.674	0.264
da Silva et al. 2019	Dung beetles	Forest	Conversion	Livestock	Serra do Mar	-0.973	0.447
da Silva et al. 2019	Dung beetles	Forest	Conversion	Livestock	Serra do Mar	-0.380	0.407
da Silva et al. 2019	Dung beetles	Forest	Conversion	Livestock	Serra do Mar	-0.693	0.424
da Silva et al. 2019	Dung beetles	Forest	Conversion	Livestock	Serra do Mar	0.323	0.405
Filgueiras et al. 2019	Lepidopterans	Forest	Fragmentation	Edge effect	Northeastern Highland	1.684	0.339
Filgueiras et al. 2019	Lepidopterans	Forest	Fragmentation	Patch size	Northeastern Highland	14.312	6.651
Gallego-López & Gallego-Roperio 2019	Lepidopterans	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-0.115	1.002
Gallego-López & Gallego-Roperio 2019	Lepidopterans	Forest	Conversion	Agriculture	Cordillera de los Andes	0.895	1.100

Montes-Rodriguez et al. 2019	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-1.124	0.289
Montes-Rodriguez et al. 2019	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-0.111	0.250
Montes-Rodriguez et al. 2019	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	0.092	0.250
Montes-Rodriguez et al. 2019	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-4.505	0.884
Alvarado et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-0.846	0.242
Davies et al. 2020	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-17.578	3.686
Davies et al. 2020	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-17.818	4.652
Diaz-García et al. 2020	Dung beetles	Forest	Degradation	Restoration	Trans-Mexican Volcanic Belt	-5.835	1.168
Diaz-García et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-1.016	0.251
Diaz-García et al. 2020	Dung beetles	Forest	Degradation	Restoration	Trans-Mexican Volcanic Belt	5.494	1.061
Diaz-García et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	9.904	2.947
Rivera et al. 2020	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.802	0.370
Rivera et al. 2020	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-0.809	0.350
Salomão et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-2.467	0.376
Salomão et al. 2020	Dung beetles	Forest	Conversion	Livestock	Trans-Mexican Volcanic Belt	-2.603	0.394
Carrión-Paladines et al. 2021	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	1.480	0.106
Carrión-Paladines et al. 2021	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	3.125	0.185
Carrión-Paladines et al. 2021	Dung beetles	Forest	Conversion	Agriculture	Cordillera de los Andes	1.597	0.110
Carrión-Paladines et al. 2021	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	1.806	0.117
Cartagena et al. 2021	Lepidopterans	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.878	0.288
Cartagena et al. 2021	Lepidopterans	Forest	Conversion	Agriculture	Cordillera de los Andes	-1.412	0.250
Gaona et al. 2021	Lepidopterans	Forest	Conversion	Livestock	Cordillera de los Andes	-21.827	40.369
Sarmiento-Garcés & Hernandez 2021	Dung beetles	Forest	Conversion	Silviculture	Serra do Mar	0.330	0.591
Sarmiento-Garcés & Hernandez 2021	Dung beetles	Forest	Conversion	Livestock	Serra do Mar	-2.851	1.008
Whitworth et al. 2021	Dung beetles	Forest	Degradation	Restoration	Cordillera Centroamericana	-15.179	4.257
Whitworth et al. 2021	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-11.499	2.504
Whitworth et al. 2021	Dung beetles	Forest	Degradation	Restoration	Cordillera Centroamericana	-8.111	1.318
Whitworth et al. 2021	Dung beetles	Forest	Conversion	Livestock	Cordillera Centroamericana	-6.971	1.011
Arias-Alvarez et al. 2022	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-27.470	63.552
Costa et al. 2022	Ants	Forest	Degradation	Fire	Central Highland	1.049	0.228
Costa et al. 2022	Ants	Savanna	Degradation	Fire	Central Highland	10.182	2.792
da Silva et al. 2022	Dung beetles	Forest	Conversion	Livestock	Central Highland	-2.792	1.975
Simões-Clivatti & Hernandez 2022	Dung beetles	Forest	Conversion	Silviculture	Serra do Mar	-0.620	0.349
Maciel et al. 2023	Dung beetles	Savanna	Conversion	Livestock	Central Highland	1.220	0.791
Maciel et al. 2023	Dung beetles	Savanna	Conversion	Livestock	Serra da Canastra	0.204	0.670
Maciel et al. 2023	Dung beetles	Savanna	Conversion	Livestock	Central Highland	-0.958	0.743
Salomão et al. 2023	Dung beetles	Forest	Fragmentation	Edge effect	Cordillera de los Andes	-0.068	0.667
Salomão et al. 2023	Dung beetles	Forest	Conversion	Livestock	Cordillera de los Andes	-0.366	0.678

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Table S3. Relationships between geographical variables with habitat transformed and insect group for insect species richness, and total abundance on Neotropical mountains.

Moderator	Study cases number	Slope	P-value
Species richness			
Latitude			
Habitat type			
Natural forest	252	0.072	0.008
Natural savanna	14	-0.327	0.48
Insect group			
Ants	68	0.163	0.038
Bees	27	-0.083	0.602
Dung beetles	144	0.087	0.002
Lepidopterans	27	0.09	0.428
Altitude			
Habitat type			
Natural forest	252	0.026	0.002
Natural savanna	14	0.051	0.252
Insect group			
Ants	68	0.077	0.001
Bees	27	0.063	0.295
Dung beetles	144	0.033	0.001
Lepidopterans	27	-0.007	0.801
Total abundance			
Latitude			
Habitat type			
Natural forest	149	0.035	0.596
Natural savanna	9	-0.74	0.078
Insect group			
Ants	17	0.017	0.884
Bees	18	-0.282	0.359
Dung beetles	102	0.109	0.157
Lepidopterans	21	0.034	0.889

Altitude			
Habitat type			
Natural forest	149	0.016	0.507
Natural savanna	9	-0.099	0.353
Insect group			
Ants	17	0.001	0.979
Bees	18	0.079	0.487
Dung beetles	102	0.031	0.23
Lepidopterans	21	0.031	0.641

Table S4. Observed and adjusted overall effect size values after trim and fill procedure.

Richness				
	Studies trimmed	Effect estimate	Lower limit	Upper limit
Observed values		-1.179	-1.641	-0.718
Adjusted values	0	-1.179	-1.641	-0.718
Abundance				
Observed values		-1.059	-1.988	-0.130
Adjusted values	0	-1.059	-1.988	-0.130

2.2 PAPER II: Influence of surrounding natural forest and shaded coffee systems on taxonomic and functional diversity of dung beetles in Andean coffee plantations

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Running headline: Dung beetles and Andean coffee plantations

Influence of surrounding natural forest and shaded coffee systems on taxonomic and functional diversity of dung beetles in Andean coffee plantations

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Abstract

The global expansion of agriculture, particularly in tropical biomes, has led to significant natural forest loss, resulting in declines in biodiversity and ecosystem functions. Coffee plantations (*Coffea arabica*), one of the most rapidly expanding crops, have raised concerns about their capacity to support biodiversity. Focusing on the Colombian Andes as one of the global epicentres of coffee production, this study evaluates the response of dung beetles (Coleoptera: Scarabaeidae) in natural forests and coffee plantations. We examined how coffee management practices (shaded vs. sun-grown) and landscape connectivity (connected vs. isolated plantations to natural forest) influence dung beetle species richness, abundance, biomass, and functional diversity. Our findings show that dung beetle taxonomic and functional diversity were consistently lower in coffee plantations than in natural forests. However, shaded and connected plantations mitigated some negative effects compared to sun-grown and isolated systems. In the Andean region, where coffee expansion is driven by economic growth, promoting shaded coffee practices and enhancing landscape connectivity and forest protection may help reduce biodiversity loss. These strategies offer promising approaches to conserving dung beetle diversity and the ecosystem services they provide in tropical agricultural landscapes.

Keywords: forest conversion, friendly habitats, land-sharing, Scarabaeidae, tropical mountains.

1. Introduction

Agricultural expansion is a leading driver of natural forest loss worldwide (Curtis et al. 2018), altering biodiversity through habitat simplification and microclimatic homogenization (Newbold et al. 2015). Over the past decades, this expansion has been particularly intense in tropical biomes, with an estimated 170 million ha deforested (Gibbs et al. 2010; Keenan et al. 2015). The tropical Andes, a region of exceptional biodiversity (Myers et al. 2000), has been significantly impacted by this trend (Etter and Wyngaarden 2000). Among the agricultural crops expanding in this region, coffee plantations (*Coffea arabica* L., Rubiaceae) play a central role, driven by their economic importance for regional development (Jha et al. 2014). However, the increasing shift toward intensified management systems, such as sun-grown coffee, contrasts with traditional shaded coffee systems (Valkila 2009). Additionally, there has been a transition from small, forest-adjacent plantations to larger, more isolated plantations (Philpott et al. 2008; Mendez-Rojas et al. 2022). Given projections of further intensification to meet global demands (e.g., Sala et al. 2000), it is critical to evaluate how coffee plantations and their management characteristics affect biodiversity.

In the tropical Andes, biodiversity responses to coffee plantations are varied, with both positive and negative outcomes reported (e.g., Noriega et al. 2012; Guzmán et al. 2016; Villada-Bedoya et al. 2017; Roach et al. 2020; Bohada-Murillo et al. 2020). These contrasting effects may be influenced by plantation characteristics, such as management practices and landscape configuration, or the metrics used to measure biodiversity (Cultid-Medina and Escobar 2016; Medeiros et al. 2019; Manson et al. 2024). For instance, more structurally complex coffee systems have been associated with less severe impacts on biodiversity (Mendez-Rojas et al. 2021). While traditional metrics like species richness and abundance remain commonly used (Mora-Aguilar et al. 2023; López-Bedoya et al. 2024a), they may not fully capture biodiversity responses, as they are often influenced by generalist and abundant

species (Ferrante et al. 2017; Arenas-Clavijo and Armbrrecht 2019). Alternative metrics, such as biomass and functional diversity, which incorporate life-history traits, provide a more comprehensive understanding of biodiversity and ecosystem functioning (Mouillot et al. 2013; Audino et al. 2014; Edwards et al. 2014). These approaches complement traditional metrics and offer deeper insights into the ecological impacts of natural forest conversion (Wood et al. 2013; Edwards et al. 2014; Davies et al. 2021).

In this context, it is essential to conduct studies that incorporate a variety of coffee plantation characteristics, focus on sensitive groups, and use complementary biodiversity metrics. Such research can provide a more nuanced understanding of the impacts of coffee plantations and inform management strategies aimed at balancing agricultural productivity with biodiversity conservation.

Dung beetles (Coleoptera: Scarabaeidae) are widely recognized as a key invertebrate group for assessing the impacts of anthropogenic disturbances (Nichols et al. 2007; Fuzessy et al. 2021; López-Bedoya et al. 2021, 2022). They perform essential ecological functions, including dung removal, soil aeration, and secondary seed dispersal, which are critical for maintaining ecosystem processes (Nichols et al. 2008). These characteristics make dung beetles an effective model for evaluating the ecological impacts of coffee plantation expansion and managements. In this study, we assess the taxonomic and functional responses of dung beetles to coffee plantations in the tropical Andes. Specifically, we examine how landscape configuration (connected vs. isolated plantations) and management practices (shaded vs. sun-grown coffee) influence dung beetle diversity and functional traits.

Coffee plantations simplify habitat composition and structure, which can negatively affect species closely associated with the stable conditions of natural forests (Mason et al. 2024).

Based on this, we hypothesize that (H1) coffee plantations will support lower taxonomic and functional diversity compared to natural forests, and (H2) shaded and/or connected coffee

plantations will have less severe impacts on dung beetle diversity and functionality than sun-grown or isolated plantations. By addressing these hypotheses, this study aims to provide insights into the ecological consequences of coffee plantation characteristics and inform strategies to mitigate biodiversity loss in tropical agricultural landscapes.

2. Materials and methods

2.1 Study area description

The study was conducted on the western slope of the Central Andes of Colombia, in the municipality of Salamina, Caldas (5°22'37"N, 75°27'22"W; Fig. 1). The landscape in this region consists of a mosaic of land uses, including degraded patches of primary forest, secondary forests, and various agroecosystems. These agroecosystems are primarily composed of cattle pastures, coffee plantations (*C. arabica*), avocado orchards (*Persea americana* Mill., Lauraceae), and sugarcane fields (*Saccharum officinarum* L., Poaceae) (POT de Salamina 2001; López-Bedoya et al. 2024b). The area experiences a seasonal rainfall regime, characterized by two distinct rainy seasons occurring from March to June and from October to December (POT de Salamina 2001).

2.2 Study design

We evaluated four habitat types representing the characteristic coffee plantation systems and natural forest conditions in the landscape: (i) degraded primary forest, (ii) connected shaded coffee plantation, (iii) isolated shaded coffee plantation, and (iv) sun-grown coffee plantation (Fig. 1). The elevation of these habitats ranged from 1900 to 2200 m a.s.l. Based on previous studies in the tropical Andes (Escobar et al. 2007), we assumed that this elevation range (≤ 300 m difference) would not have a significant effect on dung beetle assemblages. The degraded primary forest covered an area of approximately 20 ha and had

experienced historical selective logging by local farmers. However, during the last 20 years before sampling, the degraded forest did not show any impact. Shaded coffee plantations were characterized by the presence of shade trees from various commercial species, such as *Musa paradisiaca* L. (Musaceae), *Cordia alliodora* (Ruiz & Pav.) (Boraginaceae), and *Inga edulis* Mart. (Fabaceae). In contrast, sun-grown coffee plantations were monocultures without shade trees. Both shaded and sun-grown coffee plantations were ~4 years old, each covering an area of approximately 5 ha. Agrochemical use, including herbicides and insecticides, was reported in both shaded and sun-grown systems.

To determine whether shaded coffee plantations were connected to forests, we applied the landscape definition proposed by Driscoll et al. (2013), considering the limited mobility of dung beetles in anthropogenic Andean landscapes (Cultid-Medina et al. 2015). A coffee plantation was classified as connected if it was located within 500 m or less (measured from the plantation edge) of a natural forest patch (da Silva and Hernández 2015).

2.3 Dung beetle collection

Data collection was conducted in October 2017, during the rainy season, when dung beetles are most active in that time of the year (Noriega et al. 2021). Sampling was carried out using a single 200 m linear transect in each habitat. Along each transect, five baited pitfall traps were installed, spaced 50 m apart (Larsen and Forsyth 2005). Each trap was baited with 50 g of fresh, homogenized human dung, following the recommendations of Noriega and Fagua (2009). The traps were left in the field for 48 hours to capture dung beetles. After this period, all dung beetle specimens were collected and preserved in 95% ethanol. Identification of dung beetles to the species level was performed using various taxonomic keys (Genier 1996; Edmonds 2000; Edmonds and Zidek 2004; Camero 2010; Vaz-de-Mello et al. 2011).

2.4 Dung beetle traits

Species were characterized based on five functional traits following the standardized framework proposed by deCastro-Arrazola et al. (2023): food relocation behavior (rollers, tunnellers, or dwellers), diet (coprophages or copro-necrophages), diel activity (nocturnal or diurnal), biomass, and body size. Information on food relocation behavior, diet, and diel activity was obtained from the literature and expert consultation.

Dung beetle biomass was calculated as the product of the mean dry weight of each species and its abundance per trap following the protocol of Cultid-Medina and Escobar (2016). To determine biomass, all collected individuals were dried at 40 ± 5 °C for 48 hours, after which each specimen was weighed using a precision digital balance (accuracy: 0.0001 g). Body size was measured as the total length of each individual, from the external border of the clypeus to the external border of the pygidium, using an electronic digital caliper (Powerfix–Z22855, accuracy: ± 0.01 mm). These measurements provided detailed insights into the functional traits of the dung beetle assemblages.

2.5 Data analysis

To calculate functional diversity, we used five dung beetle traits that are particularly important for ecosystem functioning: food relocation behavior, diet, diel activity, biomass, and body size (Audino et al. 2014; deCastro-Arrazola et al. 2023). Four functional diversity indices were calculated for each study area: functional richness (FRic), related to functional space occupied by the species in a community independent of their abundances; functional evenness (FEve) referring to homogeneity in the distribution of abundances of the species of a community in a functional space; functional divergence (FDiv) related to functional similarity between the dominant species in the community; and functional dispersion (FDis) referring to

variation in the specialization between different species in a community (Villéger et al. 2010). These measures are indicative of the potentially exploited niches in a community and their vulnerability to impacts related to underexploited niches and higher specialization (Mason et al. 2013). These indices were computed using the dbFD function from the FD package in R (Laliberté and Shipley 2012).

To test whether habitat types (forest, connected shaded coffee, isolated shaded coffee, and sun-grown coffee plantations) differed in terms of species richness, abundance, biomass, and functional diversity indices, we applied generalized linear mixed models (GLMMs). Traps were treated as the sampling unit, habitat type was used as the explanatory variable, and pitfall trap identity were included as a random factor. For count data (species richness and abundance), we used Poisson errors, correcting for overdispersion with quasi-Poisson models when necessary (O'Hara and Kotze 2010). Overdispersion was addressed by fitting GLMMs with multivariate normal random effects using Penalized Quasi-Likelihood. For other response variables, Gaussian errors were applied. Residual analyses were performed to ensure the adequacy of model fit and residual distribution.

To identify significant differences between habitat types, we conducted a Tukey contrast analysis using the multcomp package (Hothorn et al. 2017). All statistical analyses were performed in R version 4.4.2 (R Core Team 2024), utilizing the lme4 and MASS packages for model implementation.

3. Results

3.1 General patterns

A total of 695 dung beetle individuals, representing 20 species, were collected across the evaluated habitats (Table 1). The most abundant species were *Canthon politus* Harold, 1868 and *Uroxys* sp. 2, accounting for 29.5% and 23.9% of the total abundance, respectively.

Among the habitats, two species, *Dichotomius quinquelobatus* (Felsche, 1901) and *C. politus*, were common to all four habitat types. Additionally, five species were exclusive to a single habitat: *Canthon* sp. 1 and *Eurysternus plebejus* Harold, 1880 were found only in degraded forest, while *Ataenius gr. complicatus* sp. 1, *Ateuchus* sp. 1, and *Ateuchus* sp. 2 were restricted to shaded coffee plantations (Table 1).

3.2 Taxonomic diversity and biomass

Mean species richness ($F = 123.58$; $p < 0.001$; Fig. 2) varied significantly across habitat types. Forests exhibited the highest mean species richness, followed by connected shaded coffee plantations, isolated shaded coffee plantations, and sun-grown coffee plantations. The number of species recorded in forests was 3.5 times greater than in sun-grown coffee plantations. Similarly, we found differences in the number of individuals ($\chi^2 = 375.46$; $p < 0.001$; Fig. 2), and biomass ($F = 40.28$; $p < 0.001$; Fig. 2) between habitat types. The number of individuals and biomass were highest in forests, followed by connected shaded coffee plantations, and isolated shaded coffee and sun-grown coffee plantations showed the lowest values for both abundance and biomass. The abundance and biomass observed in forests were substantially higher compared to isolated shaded coffee and sun-grown coffee plantations. Specifically, the number of individuals in forests was 5.3 times greater than in isolated shaded coffee plantations and nearly 8 times greater than in sun-grown coffee plantations. Biomass in forests was almost 4 times higher than in these two habitat types.

3.3 Functional diversity

All functional diversity indices varied significantly among habitat types. For instance, functional richness ($F = 15.32$, $p < 0.001$; Fig. 3) was highest in forests and both types of shaded coffee plantations (connected and isolated), with no statistical differences observed

between these habitats. The lowest functional richness was recorded in sun-grown coffee plantations. Functional evenness ($F = 23.19$, $p < 0.001$; Fig. 3), exhibited the highest mean values in isolated shaded coffee plantations, while forests showed the lowest. Intermediate values were observed in connected shaded coffee and sun-grown coffee plantations. The functional divergence ($F = 3.65$, $p = 0.04$; Fig. 3), was greatest in sun-grown coffee plantations and lowest in forests, with shaded coffee plantations (both connected and isolated) presenting intermediate values. Finally, focusing on functional dispersion ($F = 10.38$, $p = 0.001$; Fig. 3), the highest was found in connected and isolated shaded coffee plantations, which were statistically similar. The lowest functional dispersion values were found in forests and sun-grown coffee plantations, which were also statistically comparable.

4. Discussion

Coffee is one of the major land-uses in the montane tropics. Our study aligns with our initial hypothesis and predictions. Coffee plantations exhibit lower taxonomic and functional diversity compared to natural forests. However, coffee plantations that incorporate shade systems and/or maintain connectivity with natural forests mitigate the negative impacts on dung beetle diversity. These findings emphasize the critical role of natural forest conservation in preserving dung beetle diversity.

In the tropical Andes, where agricultural expansion driven by emerging economies is reducing the availability of land for conservation (Bax and Francesconi 2019), promoting shade-grown coffee systems and implementing landscape connectivity strategies could serve as effective measures to minimize biodiversity loss. Such approaches may balance agricultural productivity with biodiversity conservation, offering a practical pathway to reduce the ecological impacts of coffee production.

4.1 Forest conversion on coffee plantations reduced dung beetle taxonomic and functional diversity

We observed lower species richness, abundance, and biomass of dung beetles in coffee plantations compared to natural forests. These findings align with previous studies finding biodiversity loss in coffee plantations (Philpott et al. 2008; Noriega et al. 2012; Costa et al. 2017). The conversion of natural forests into agricultural systems is associated with reduced vegetation structure, altered microhabitat conditions, and limited resource availability for biodiversity (Newbold et al. 2015; Scheffers et al. 2017). Dung beetles, in particular, are highly dependent on environmental conditions and resource availability to sustain their physiological functions, feeding, reproduction, and establishment (Hanski and Cambefort 2014; Holley and Andrew 2019).

Coffee plantations often exhibit reduced vegetation structural complexity, leading to increased soil exposure to sunlight, elevated soil temperatures, and reduced soil moisture (DaMatta 2004). Additionally, these systems typically support lower vertebrate diversity, resulting in decreased dung resource availability (Caudill et al. 2014; Mertens et al. 2020). These habitat modifications between natural forests and coffee plantations significantly influence dung beetle richness, abundance, and biomass due to altered microclimatic conditions and limited resources, which intensify intra- and interspecific competition (Raine et al. 2018).

Beyond reductions in taxonomic diversity and biomass, functional diversity also declined between natural forests and coffee plantations, particularly in sun-grown coffee systems. Our results are consistent with studies documenting reduced functional diversity in disturbed habitats (Audino et al. 2014; Edwards et al. 2014; Gomez-Cifuentes et al. 2017). This reduction may be explained by the higher levels of disturbance in sun-grown coffee plantations, where only a limited subset of species with specific traits are able to tolerate the

altered conditions in these anthropogenic environments (Vandewalle et al. 2010; Mouillot et al. 2013). Also, higher values for functional evenness and functional divergence may be associated with community characteristics and species abundance (Villéger et al. 2008).

For instance, higher functional evenness and divergence values found in coffee plantations may indicate that dung beetle species with different functional attributes have similar abundances; conversely, the lower functional evenness and divergence values in natural forest showed how abundant and dominant dung beetle species present similar functional traits adapted to forest habitat. These findings highlight the importance of incorporating functional diversity assessments to better understand how habitat transformation impacts biodiversity and ecological processes.

4.2 Management and connectivity in coffee plantations

Our findings indicate that shaded management and connectivity to natural forests mitigate the negative impacts of coffee plantations on dung beetle species richness, abundance, and biomass. Specifically, shaded coffee plantations and those connected to natural forests exhibited similar or even higher functional diversity compared to natural forests. Shaded systems enhance habitat structure and understory complexity, creating microclimates favourable for invertebrates (Perfecto et al. 1996; Méndez-Rojas et al. 2021). In contrast, sun-grown coffee plantations, characterized by higher levels of habitat transformation, reduce the availability of microhabitats (Cultid-Medina and Escobar 2016; Villada-Bedoya et al. 2017). Consequently, shaded systems appear to lessen the negative effects on species richness, abundance, and biomass at local scale. Additionally, the more structured environments in shaded plantations may reduce disturbance levels, allowing species with functional traits similar to those in forests to persist (Sarmiento-Garcés and Hernández 2021).

Previous studies on dung beetles in coffee plantations have also demonstrated that shaded systems can support species richness and abundance levels comparable to those in natural forests (Arellano et al. 2005; Pineda et al. 2005). However, shade systems vary widely, ranging from plantations under natural forest cover to those shaded by commercially planted species (Harvey et al. 2021). These differences in shade type may influence biodiversity responses, as observed in other beetle families in tropical Andean coffee plantations (Méndez-Rojas et al. 2021). Therefore, it is essential to evaluate how different shade types affect both taxonomic and functional diversity, and may affect ecosystem services.

Dung beetle assemblages are also influenced by the distance of coffee plantations from natural forests within anthropogenic landscapes. Limited movement ranges, constrained by physiological and morphological factors, reduce their ability to traverse fragmented landscapes (Cultid-Medina et al. 2015; Franco et al. 2023). Proximity to natural forests can facilitate the arrival of vertebrates, potentially increasing the availability of dung resources (Caudill et al. 2014). Furthermore, landscape connectivity with natural forests may enhance the flow of species with specific functional traits, thereby improving the functional structure of agricultural systems (Schirmel et al. 2016; Davies et al. 2021). These findings underscore the importance of integrating shaded systems and connectivity strategies to support biodiversity and ecosystem functioning, with a scale perspective of coffee-producing landscapes.

Finally, it's important to mention that the impacts on the reference habitat may have an effect on the results found (Edwards et al. 2014). The degraded forest evaluated in this study is characterised by the presence of selective logging in the past, which could influence a lower diversity in this natural habitat, resulting in similar diversity values compared to coffee plantations in some cases. However, we consider that the absence of impacts in the degraded

forest during the last 20 years prior to the study, minimises the effect generated in our results by the disturbance that the natural forest may have had.

5. Concluding remarks

We observed lower taxonomic and functional diversity of dung beetles in coffee plantations compared to natural forests in the tropical Andes of Colombia. However, specific management practices and the connectivity of coffee plantations to natural forests appear to reduce these negative effects. Shaded coffee systems, in particular, create more structured habitats, supporting higher taxonomic and functional diversity compared to sun-grown coffee systems.

Future research should explore how different shade types and strata structures may influence dung beetle responses, as suggested by prior studies (e.g., Méndez-Rojas et al. 2021). For instance, some studies showed how biodiversity responds differentially between commercial-shaded or natural forest-shaded systems (Manson et al. 2024). Also, it is common in Andean landscapes to find matrices where coffee crops may be embedded in other predominant matrices such as pastures (Cultid-Medina and Escobar 2016). For this reason, understanding how the predominant matrix can influence the role of coffee plantations in supporting biodiversity is needed for biodiversity managements. Moreover, studies in agroecosystems should incorporate the evaluation of ecological functions performed by dung beetles, such as dung removal, soil bioturbation, and seed dispersal (e.g., Santos-Heredia et al. 2018). Assessing these functions would provide valuable insights for making informed decisions about forest management and conservation in highly altered landscapes like those found in the tropical Andes. Such approaches could help balance agricultural productivity with biodiversity conservation in these fragile ecosystems.

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7. Conflict of interest

All the authors declare that there is no conflict of interest.

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9. Tables and figures

Table. 1 Dung beetle species found in the four habitats: degraded primary forest (DPF), connected shade coffee plantation (SC-C), isolated shade coffee plantation (SC-I), and sun-grown coffee plantation (SGC).

Fig. 1 Geographic location of the sampling site (black dot) in the Colombian tropical Andes.

Fig. 2 Mean $\pm$ standard deviation of species richness (A), number of individuals (B) and biomass (C) among habitat types (forest, connected shaded coffee – “shaded_coffee_C”, isolated shaded coffee – “shaded_coffee_I”, and sun growth coffee). Different letters indicate statistical differences among habitat types ($p < 0.05$). In the boxplot graphs, continuous lines are the median values of each habitat type and dashed lines are the average values. Forest is the positive control, being represented by dark grey boxes and sun growth coffee is the negative control, being represented by white boxes.

Fig. 3 Mean $\pm$ standard deviation of functional richness (A), functional evenness (B), functional divergence (C) and functional dispersion (D) among habitat types (forest, connected shaded coffee – “shaded_coffee_C”, isolated shaded coffee – “shaded_coffee_I”, and sun growth coffee). Different letters indicate statistical differences among habitat types ($p < 0.05$). In the boxplot graphs, continuous lines are the median values of each habitat type and dashed lines are the average values. Forest is the positive control, being represented by dark grey boxes and sun growth coffee is the negative control, being represented by white boxes.

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Subfamily	Specie	Habitat			
		DPF	SC-C	SC-I	SGC
Aphodiinae	<i>Trichaphodiellus</i> cf. <i>brasiliensis</i> (Castelnau, 1840)	2	2	3	0
	<i>Ataenius</i> gr. <i>complicatus</i> sp. 1	0	1	0	0
	<i>Ateuchus</i> sp. 1	0	0	1	0
	<i>Ateuchus</i> sp. 2	0	0	2	0
	<i>Uroxys</i> sp. 1	5	2	6	1
	<i>Uroxys</i> sp. 2	168	2	0	0
	<i>Uroxys</i> sp. 3	12	20	2	7
	<i>Ontherus lunicollis</i> Génier, 1996	5	6	0	3
	<i>Canthidium</i> sp. 1	1	3	6	0
	<i>Canthidium</i> sp. 2	11	5	0	0
Scarabaeinae	<i>Canthidium</i> sp. 3	12	3	6	0
	<i>Canthidium</i> sp. 4	6	2	1	0
	<i>Dichotomius quinquelobatus</i> (Felsche, 1901)	44	26	15	9
	<i>Canthon politus</i> Harold, 1868	107	38	26	28
	<i>Canthon</i> sp. 1	2	0	0	0
	<i>Deltochilum</i> gr. <i>parile</i> sp. 1	7	4	0	0
	<i>Eurysternus marmoreus</i> Castelnau, 1840	9	4	0	0
	<i>Eurysternus plebejus</i> Harold, 1880	5	0	0	0
	<i>Onthophagus</i> gr. <i>clypeatus</i> sp. 1	12	29	10	2
	<i>Oxysternon conspicillatum</i> (Weber, 1801)	6	4	0	2
	Species richness	17	16	11	7
	Total abundance	414	151	78	52

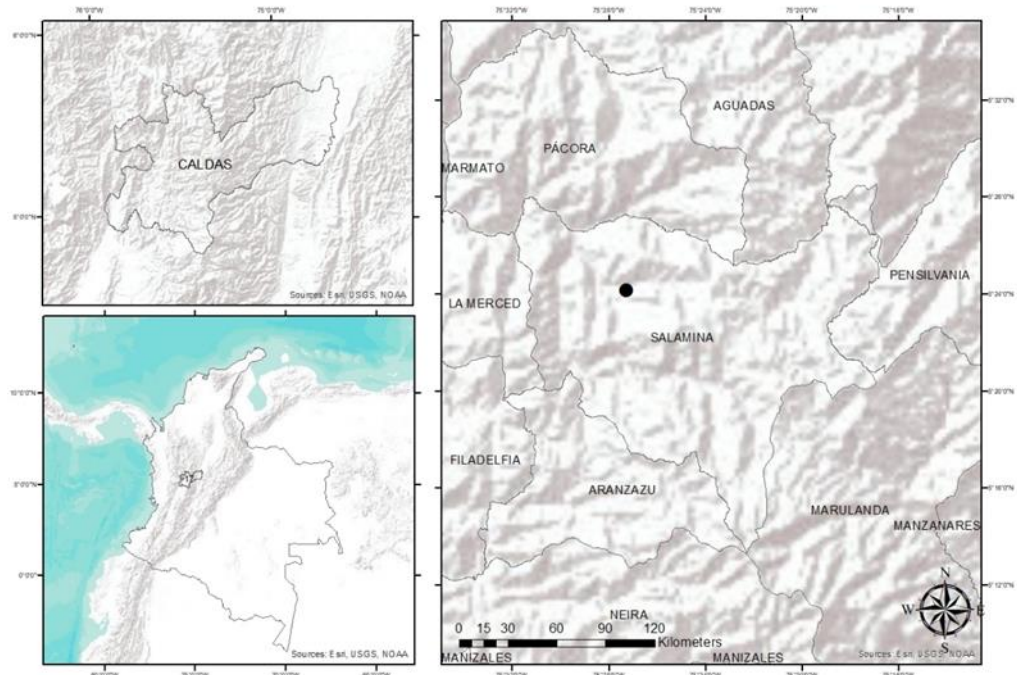


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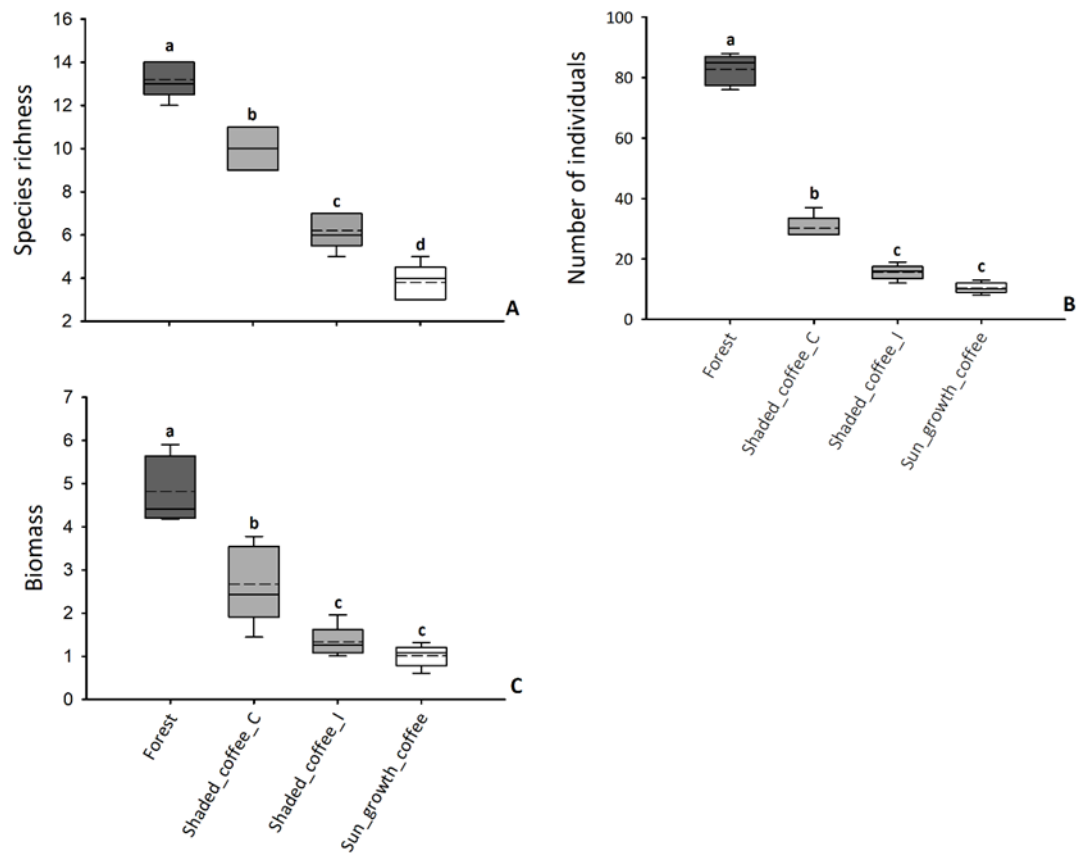


Fig. 2 Species richness (A), number of individuals (B) and biomass (C) among habitat types (forest, connected shaded coffee – “shaded_coffee_C”, isolated shaded coffee – “shaded_coffee_I”, and sun growth coffee). Different letters indicate statistical differences among habitat types ($p < 0.05$). In the boxplot graphs, continuous lines are the median values of each habitat type and dashed lines are the average values. Forest is the positive control, being represented by dark grey boxes and sun growth coffee is the negative control, being represented by white boxes.

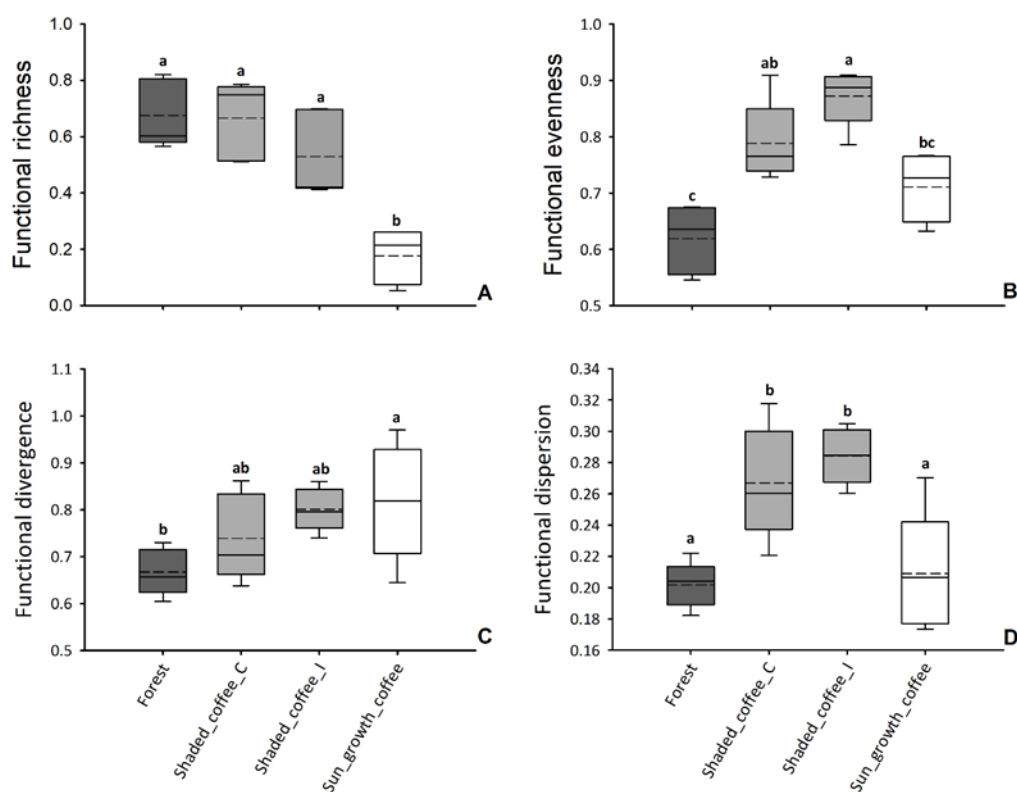


Fig. 3 Mean $\pm$ standard deviation of functional richness (A), functional evenness (B), functional divergence (C) and functional dispersion (D) among habitat types (forest, connected shaded coffee – “shaded_coffee_C”, isolated shaded coffee – “shaded_coffee_I”, and sun growth coffee). Different letters indicate statistical differences among habitat types ($p < 0.05$). In the boxplot graphs, continuous lines are the median values of each habitat type and

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3. PART III: SCIENTIFIC DISSEMINATION

As part of the outcomes to scientific dissemination, the results of this master dissertation have been partially presented at scientific meetings of the Universidade Federal de Lavras, local communities, and using new information technologies.

1.1 “XXXIII Congresso da Pós-Graduação da UFLA”

I presented part of the results of my master's thesis at the postgraduate congress of the Federal University of Lavras. The congress took place in November 2024. I participated in this congress with an oral presentation (Fig. 1). The presentation focused on the response of dung beetles to anthropogenic impacts in Neotropical mountains (see abstract submitted to congress below).

Efeito dos impactos antrópicos nos rola-bosta (Coleóptera: Scarabaeinae) nas montanhas Neotropicais

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Palavras-chave: Conservação, Degradação, Fragmentação.

Area do trabalho: Entomologia, Programa de Pós-graduação em entomologia.

As montanhas neotropicais são reconhecidas globalmente como biomas de alta biodiversidade, caracterizados por um notável endemismo de espécies. No entanto, o desenvolvimento humano histórico nessas regiões resultou em pressões antrópicas significativas sobre a biodiversidade. Nesse contexto, nosso objetivo foi apresentar uma meta-análise dos impactos antrópicos nos biomas das montanhas neotropicais, utilizando besouros rola-bosta (Coleóptera: Scarabaeinae) como indicadores. Nos bancos de dados Scopus e WoS foram selecionados estudos que informaram sobre a riqueza ou abundância de rola-bostas em sistemas antrópicos em comparação com florestas naturais, e foi utilizada a métrica Hedges' d para avaliar o efeito entre a floresta e o sistema antrópico. Além disso, avaliamos como diferentes tipos de impacto antrópico como fragmentação, degradação e conversão afetaram a riqueza e a abundância de rola-bostas. Nossos resultados indicaram que os impactos antrópicos têm efeitos negativos sobre a riqueza e a abundância de rola-bostas nas montanhas neotropicais, com a magnitude desse efeito variando conforme o tipo de impacto. Em particular, a conversão de florestas naturais para agricultura, silvicultura ou áreas de pastagem apresentou os efeitos mais adversos sobre a riqueza e a abundância de rola-bostas, em comparação com a fragmentação ou degradação das florestas. Destacamos que, nas montanhas neotropicais, as pressões antrópicas impactam negativamente a diversidade de rola-bostas, ressaltando a necessidade de priorizar a preservação das florestas naturais. No entanto, quando a conservação das florestas naturais não é viável, é essencial implementar programas de manejo sustentável que minimizem os efeitos dos impactos antrópicos nas florestas e, consequentemente, nos rola-bostas.

Agradecimentos

Os autores agradecem o apoio financeiro da agência FAPEMIG.



Fig. 1 Presentation of dung beetles and anthropogenic impacts in the “XXXIII Congresso da Pós-Graduação da UFLA”.

1.2 Information dissemination to local communities

The results have been disseminated to the local community, especially to children. In these meetings, information has been disseminated about the importance of insects, their role in society and why we should conserve them (Fig. 2a, b). The meetings took place in the Departamento de Ecologia in the Universidade Federal de Lavras.



Fig. 2a, b Science communication days with children at the Universidade Federal de Lavras campus.

1.3 Dissemination using new technologies

The world is changing and advancing, and with this change comes new ways of sharing science. Instagram is becoming a widely used platform that allows results to be shown to a wide cross-section of society. I construct post with information related to insects and Neotropical mountains to be shared within the “Instagram” profile ‘LECIN (Laboratório de Ecologia e Conservação de Invertebrados)’ (see below). These posts share general information, as well as specific information from my master's work on how insects are threatened by anthropogenic impacts, and some strategies to reduce these threats. The posts were published between January and February 2025, with a number of ‘likes’ over 80.

 Você gostou de “**Animais Fantásticos e Onde Habitam**” ou de mundos de fantasia?

Vamos conhecer do fantástico mundo dos **insetos e onde eles habitam...**



 Primeiro, onde você pode encontrar **insetos**?



Em todo o mundo!!
Embora tem lugares que podem ter uma diversidade de **insetos maior**



 **E quais seriam esses lugares?**



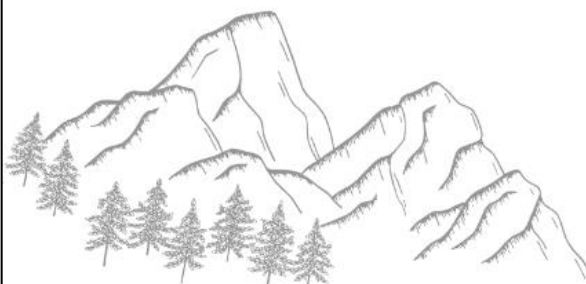
As regiões de montanha têm climas e habitats diferentes que abrigam muitos **insetos**

Você pode encontrar besouros, formigas, abelhas ou borboletas.



 **Você já conheceu algum lugar **montanhoso**?**

Se você mora em um país da América do Sul, não precisa ir muito longe...



 **Por exemplo, o Brasil que tem montanhas e muitos insetos**



Curioso?
Vamos lá meu amigo, saia de casa e conheça alguns insetos de montanha que vão te surpreender!



 **Gostou?**



Compartilha, ou Deixa um comentário se você já visitou um lugar com montanhas....





Montanhas Neotropicais & *INSETOS*

As atividades humanas podem
ter consequências?



Existe um dilema entre a
conservação dos insetos e o
desenvolvimento humano...



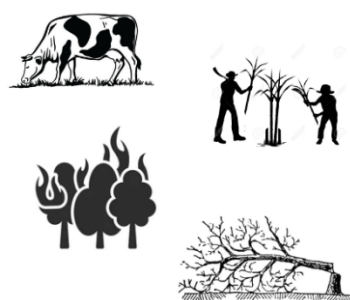
É possível **conservar** quando as
pessoas precisam sobreviver?



Infelizmente, a realidade mostra que muitos habitats naturais são transformados...



As montanhas e os insetos são afetados por esse problema



Os habitats naturais podem ser afetados pela agricultura, fogo, criação de gado, ou silvicultura



A questão é...

Quais grupos de insetos e quais impactos têm os efeitos mais negativos?



Precisamos dessas informações para saber como concentrar esforços para conservar



Em um nosso **estudo** nas **montanhas neotropicais**, quisemos responder a estas perguntas



Usando novas **ferramentas meta-analíticas**, procuramos identificar respostas gerais associadas a esse problema



O que fizemos?

Procuramos estudos que comparassem **habitats naturais** com locais que sofreram **impactos pelo homem**



Para cada estudo, comparamos a **riqueza** ou a **abundância** de **insetos**



Utilizamos **4 grupos** de insetos, **abelhas**, **besouros rola-bosta**, **borboletas**, e **formigas**



Depois de **analisar** muitos artigos, encontramos que os **insetos** são afetados negativamente nas **montanhas neotropicais...**



Especialmente os **besouros rola-bosta** e **formigas**. Em alguns casos, **abelhas** e **borboletas** têm respostas **neutras**.



A **agricultura** e a **criação de gado** tiveram um **impacto negativo maior**



Então, por que precisamos **conservar** esses grupos de **insetos**?



Estes **insetos** ajudam na **polinização**, **dispersão de sementes**, ou **fixação de nutrientes no solo**, e podem controlar **outros insetos pragas...** mas eles precisam de **habitats mais amigáveis** para viver



Gostou?



Agora precisamos
identificar como
minimizar esses impactos
e ser mais **sustentáveis...**



De onde veio esta pesquisa?

Ola, este conteúdo é
baseado em minha
dissertação trabalhando
com meta-analise com
insetos em montanhas. Sou
Pablo A. López, estudante de
mestrado do programa de
pós-graduação em
Entomologia da
Universidade Federal de
Lavras

