Primary forest loss and degradation reduces biodiversity and ecosystem functioning: A global meta-analysis using dung beetles as an indicator taxon

Pablo A. López-Bedoya[1,2], Mauricio Bohada-Murillo[1], María Camila Ángel-Vallejo[1], Livia Dorneles Audino[3], Adrian L. V. Davis[4], Geoff Gurr[5], Jorge Ari Noriega[6]

[1]Grupo de Investigación en Ecosistemas Tropicales, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Manizales, Colombia;
[2]Grupo de Ecología y Diversidad de Anfibios y Reptiles, Facultad de Ciencias Exactas y Naturales, Universidad de Caldas, Manizales, Colombia;
[3]Departamento de Ecologia e Conservação, Universidade Federal de Lavras, Lavras, Brazil;
[4]Invertebrate Systematics and Conservation Group, Department of Zoology and Entomology, University of Pretoria, Hatfield, South Africa;
[5]Graham Centre for Agricultural Innovation, Charles Sturt University, Orange, New South Wales, Australia and
[6] Laboratorio de Zoología y Ecología Acuática – LAZOEA, Universidad de Los Andes, Bogotá, Colombia

*Correspondence: Jorge Ari Noriega. Email: jnorieg@hotmail.com

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: PDJ 150776/2017-9

ABSTRACT

1. Because of continuing degradation or deforestation in areas of undisturbed primary forest, there is a need to study the relative merit of strategies that mitigate their impacts on biodiversity and associated ecological functionality.
2. Here, we provide a global synthesis of forest degradation or deforestation using 48 studies published in peer-reviewed journals that use dung beetles as indicators given their sensitivity to anthropogenic disturbance and their relevance in performing essential ecological functions in terrestrial ecosystems.
3. We evaluated forest cover associated with undisturbed primary forest degradation (i.e. degraded primary forest) and undisturbed primary forest deforestation (i.e. secondary forest, forestry plantations and forestry restoration implementation) on species richness, total abundance, biomass, functional groups' presence and ecological functions provided by dung beetles. Additionally, we determined whether if dung beetle responses to forest disturbances were geographically dependent.
4. We found lower diversity and a decrease in ecological functions associated with all classes of disturbance in primary forest. However, the effects were less severe in the case of forest degradation compared to complete deforestation with natural regeneration of secondary forest, development of forest plantations or active forest restoration by planting indigenous trees. The Neotropical and Oriental regions are particularly vulnerable, given the elevated rates of undisturbed primary forest deforestation and its negative impact on their assemblages' diversity and ecological functions.
5. *Synthesis and applications*. Our results show that efforts for the conservation of remaining undisturbed primary forests need to be prioritized, especially in tropical latitudes. However, in regions where primary forest conservation is not feasible, logging management programs in degraded primary forest may have a potential role in reducing negative impacts for dung beetle diversity and ecological functions. Moreover, we conclude that despite the negative effect of primary forest deforestation and implementation of secondary forest, forestry plantation and forestry restoration,

they can be useful for partial recovery of diversity and ecological functions performed by dung beetles in areas lacking any primary forest (undisturbed or degraded) vegetation cover.

Keywords: anthropogenic disturbance, ecological indicators, ecosystems functions, forest recovery, functional groups, hotspots, Scarabaeidae, vegetation cover loss

1 INTRODUCTION

Undisturbed primary forest conversion (i.e. degradation and deforestation) and associated biodiversity and ecological functions loss are direct effects of increasing anthropogenic activities such as livestock and agricultural production (Fahrig, 2003; Foley et al., 2005; Hooper et al., 2012). Different investigations have considered the current and future impacts of anthropogenic activity increase (Díaz et al., 2006; Newbold et al., 2015; Sala et al., 2000) as well as potential strategies to reduce an impact of undisturbed primary forest conversion for biodiversity (e.g. Chazdon, 2008; Lamb et al., 2005). Undisturbed primary forest affected by logging (selective or conventional) derived in degraded primary forests (Putz & Redford, 2010), whereas undisturbed primary forest deforestation and posterior natural regeneration or direct planting of forest species derived to secondary forests and forestry plantations or forestry restoration respectively (Chazdon, 2008; Lamb et al., 2005).

Over time, the undisturbed primary forest conversion associated with human development could be translated into an increase of the degraded primary forest, secondary forest, forestry plantations and forestry restoration areas. However, the relative merit of these areas for maintaining biodiversity is debatable (Audino et al., 2014; Barlow et al., 2007; Castaño-Villa et al., 2019; Dunn, 2004; Gibson et al., 2011). Both the undisturbed primary forest conversion and the debate on the function of these areas in maintaining biodiversity evince the necessity to evaluate these habitats' role in biodiversity conservation and ecosystem functionality (Brockerhoff et al., 2008; Dunn, 2004; Gibson et al., 2011). Ascertaining the relative merit of these cover areas that favour higher biodiversity levels is important to provide future forest recovery programs. These covers sometimes have environmental characteristics that maintain establishment or influence the re-establishment of groups susceptible to habitat change such as birds or mammals, although their specific responses vary according to management or geographic region (Bohada-Murillo et al., 2020; Castaño-Villa et al., 2019; Gibson et al., 2011). However, the global-scale research is limited considering the effect of undisturbed primary forest conversion on the biodiversity and ecological functions of an invertebrate taxon despite their high diversity, essential roles throughout all ecosystems and endangered status world-wide (Cardoso & Leather, 2019; Wagner et al., 2021).

Dung beetles have been identified as an appropriate invertebrate taxon to evaluate global patterns associated with the impact of undisturbed primary forest conversion, because their diversity and ecological functions present high sensitivity to anthropogenic perturbations (Bicknell et al., 2014; Fuzessy et al., 2021; López-Bedoya et al., 2021; Nichols et al., 2008; Otavo et al., 2013; Slade et al., 2011; Spector, 2006). Some of the most critical functions involve removing excrement from the surface by burial, nutrient cycling, soil aeration, filtration capacity, secondary seed dispersal, parasite and fly control, and the control of greenhouse gas effects (Nichols et al., 2008; Slade et al., 2016). Knowledge about the response of dung beetle's diversity or ecological functions to undisturbed primary forest conversion has been evaluated by different synthesis (see Fuzessy et al., 2021; López-Bedoya et al., 2021; Nichols et al., 2007, 2008, 2009, 2013). However, these investigations focus a wide range of impacts (e.g. forest area, degradation, edge effect), and not compare the response linked to geographic context or specific impact of these cover areas. Special scenario for the largest dung beetle diversity concentrated in tropical latitudes (Scholtz et al., 2009), linked to the increased undisturbed primary forest conversion (McNeely & Scherr, 2003; Mittermeier et al., 2004; Myers et al., 2000). Moreover, there are zoogeographical regions (e.g. Neotropical and Oriental regions and associated hotspots) that present high dung beetle diversity with elevated rates of undisturbed primary forest conversion (see Davis et al., 2002; Halffter, 1991; Nichols et al., 2013). This scenario could be contributing to the differential response of dung beetles between degraded primary forest, secondary forest, forestry plantations and forestry restoration located in different geographical areas of interest for biodiversity conservation. For example, secondary forest has shown a variety of responses between Neotropical and Oriental regions, from severe reductions to positive responses on species richness, abundance or ecological functions, relative to undisturbed primary forest controls (see Andresen, 2008; Braga et al., 2013; Edwards et al., 2014; Gardner et al., 2008; Noriega et al., 2021).

Accordingly, this work's main objective was to build a global overview of responses to the undisturbed primary forest conversion (both degradation and deforestation) using dung beetles as an indicator tool. We then evaluate if the different assemblages' responses are consistent between tropical and non-tropical latitudes, zoogeographical regions and biodiversity hotspots. Based on bibliographical data, we assessed the extent to which: (a) degraded primary forest, secondary forest, forestry plantation and forestry restoration show reduced diversity and ecological functions compared to undisturbed primary forests, and (b) the effects of these coverages would be more pronounced in the tropical latitudes, especially in regions with high levels of species richness and conservation interest, that is, biodiversity hotspots.

2 MATERIALS AND METHODS

Literature search and inclusion criteria

We performed a literature search following the PRISMA methodology (Moher et al., 2009) and recommendations proposed by Nakagawa et al. (2017), including only indexed articles on the *Scopus* and *Web of Science* databases between January 1950 and December 2020, based on the following directed search equation to the title, abstract and keywords sections of each document: (forest* OR regenerat* OR degradat* OR restorat* OR plantat* OR logged* OR biomass OR dung removal OR "functional group" OR remotion* OR "seed dispersal") AND ("dung beetle" OR scarabaei*). We use these search words based in the common names used for dung beetles and the interest cover types evaluated in this meta-analysis.

We found 1,422 articles in the databases, reduced to 324 articles after removing duplicate results and articles that developed other topics, such as molecular biology or behavioural studies. Full texts of the selected articles were accessed, and only those that met the following criteria were included in our study: (a) they performed a comparison of undisturbed primary forests (control) with degraded primary forest, secondary forest, forestry plantations or forestry restoration (treatments) (we utilized forest definition proposed by Chazdon et al., 2016; and see Table 1 for more details of control and treatments definitions), and (b) they contained data on the descriptive statistics of the sample sizes, mean and their standard deviation (or any other data from which a standard deviation may be calculated) (see Hozo et al., 2005; Wan et al., 2014).

TABLE 1. Coverage definitions of the different types of forests included in the meta-analysis with their reference and examples used

Coverage forest type definition	Global area	References
Primary forest is defined as natural forests that have never undergone selective logging events or total clear-cutting	1,110 million ha	Global reference definition (Wilcove et al., 2013); global area (FAO, 2020); study case examples in this meta-analysis (Audino et al., 2014; Slade et al., 2011)
Degraded native forests are defined as natural forests with selective logging but always with a constant natural forest cover	480 million ha	Global reference definition (Putz & Redford, 2010); global area (FAO, 2020; Poudyal et al., 2018); study case examples in this meta-analysis (Edwards et al., 2017; Slade et al., 2011)
Secondary forest is defined as natural forest derived from natural regrowth after total clearance of primary forest	2,160 million ha	Global reference definition (FAO, 2020; Poorter et al., 2016); global area (FAO, 2020); study case examples in this meta-analysis (Andresen, 2008; Gardner et al., 2008)
Forestry plantations were established by seeding or planting to achieve primarily economic objectives related explicitly to wood biomass production (e.g. timber and other wood products as paper pulp)	150 million ha	Global reference definition (FAO, 2020; Stephens & Wagner, 2007); global area (FAO, 2020); study case examples in this meta-analysis (Beiroz et al., 2016; Gardner et al., 2008)
Forestry restoration was established by multiple seeding or planting forest species to achieve conservation and rehabilitation of degraded areas primarily	140 million ha	Global reference definition (Bechara et al., 2016; Lamb et al., 2005); global area (FAO, 2020; Masiero et al., 2015); study case examples in this meta-analysis (Audino et al., 2014; Derhé et al., 2016)

On these criteria, 48 articles were included in the analysis that evaluated one or more metrics for dung beetles (Figure S1). The included articles sampled dung beetle's species richness or abundance using pitfall traps, generally utilizing excrement of human, pig or cow in the baits for pitfall traps or functional functions measurements. Moreover, we considered that the study design utilized in many of these investigations utilized sufficiently interspersed unit samples guaranteeing the independence between sampling units, with distances more than 250 m between sampling points when the sampling unit was the patch, and 50 m or more when the sampling unit was the pitfall trap (e.g. Audino et al., 2014; Beiroz et al., 2016; Slade et al., 2011). In articles that evaluated different vegetation covers, locations or sampling sites in the same study, we considered each case independently (see Fontúrbel et al., 2015). Also, in studies with measures over different periods, for example, 2 or more years, rainy or dry seasons, we considered these different sampling events as independent (e.g. Borenstein et al., 2009; Mengersen et al., 2013) since there was no *a priori* rule based on randomness to choose a time unit for the analyses. A list of data sources used in the study is provided in the supplementary material.

Modelling effect and magnitude

We estimated each case study's effect using the Hedges *d* statistic, which uses weighted standardized deviations (Hedges & Olkin, 1985). This measure is used to determine the magnitude of a treatment variable's effect concerning a control group (Borenstein et al., 2009; Gurevitch et al., 2001). We used random effects models based on the inclusion of degraded primary forest with different logging intensity, and secondary forest, forestry plantations or forestry restoration with different ages or patch size area. This type of model reduces the bias generated when comparing research with different habitat attributes (Konstantopoulos & Hedges, 2010).

Dung beetle and environmental variables influence moderators

The global effect on dung beetles of undisturbed primary forest conversion was estimated taking into account: (a) species richness, (b) total abundance, (c) biomass, (d) percentage of dung removal, (e) amount of excavated soil and (f) percentage of seed dispersal. For species richness and total abundance, four influential environmental variables were defined: (a) cover type (degraded primary forest, secondary forest, forestry plantation and forestry restoration), (b) latitudinal biome (tropical between 23°N and 23°S, or non-tropical), (c) zoogeographical region (see Davis et al., 2002) and (d) overlap with biodiversity hotspots (see Mittermeier et al., 2004; Myers et al., 2000).

According to variations in functional group structure measured by species richness and abundance, each group plays different and complementary functional roles in the ecosystem (Milotic et al., 2018; Slade et al., 2007, 2019); in addition, the genus of dung beetle can influence the response that has the abundance (Nichols et al., 2013). For this reason, we have defined four functional variables for dung beetle abundance: (a) abundance per genus, (b) relocation type (tunnellers or rollers), (c) beetle size (large or small) and (d) functional group (large tunnellers, small tunnellers, large rollers or small rollers). For these moderators, we utilized articles that provided abundance mean and statistic metrics for genus or functional group (see Braga et al., 2013; Davis & Philips, 2005; Edwards et al., 2017; Escobar & Chacón de Ulloa, 2000; Neita & Escobar, 2012; Shahabuddin, 2010; Shahabuddin et al., 2005; Slade et al., 2011).

The classification of beetle size was done for each database independently. This procedure avoids the bias caused by potential differences in size of the beetles (large vs. small species) compared between studies. All the articles included performed functional classification based on small dung beetles (between 0 and <10 mm) and large dung beetles (10 mm or more). For articles that did not evaluate abundance by functional group, but presented abundance values per species, we classified each species into a functional group based on their relocation type (tunnellers or rollers) and beetle size (large or small), according to previous regional publications (see Braga et al., 2013; Doube, 1990; Halffter & Edmonds, 1982; Halffter & Matthews, 1966; Hanski & Cambefort, 1991; Slade et al., 2011). The dweller functional group was not included in the analysis because our literature search did not present independent statistic metrics for this group.

Statistical analysis

We estimated homogeneity between the groups (Q_{between} statistic) to determine the level of heterogeneity between the levels of moderator variables. This statistic has a χ^2 distribution that compares the variation within and between the different levels of moderators (Higgins et al., 2003). We used this statistic because it is the best fit for analysing random models (Borenstein et al., 2009). Finally, we performed meta-regression models (see Thompson & Higgins, 2002), separately for dung removal and seed dispersal, using richness and total abundance as the continuous variables to determine the effect of richness and abundance on the ecological functions performed by dung beetles. Given that there may be asymmetries associated with the sample size between some moderator levels, we recommend caution when interpreting the results with those levels of moderators with less than 10 cases. (Bohada-Murillo et al., 2020).

Publication bias

Studies with neutral or negative results are less likely to be published, so we estimated the numbers of these that would be necessary to obtain non-significant effects in our analyses using the Rosenthal test (see Fontúrbel et al., 2015). Furthermore, since we did not find an equal number of positive, neutral and negative cases, we also performed a 'trim-and-fill' analysis. This analysis evaluates the bias in the cases' distribution asymmetry and recalculates the effect's global average and confidence intervals (Duval & Tweedie, 2000). Bias analyses were carried out for all evaluated metrics. However, we advise caution in interpreting the results for specific metrics with low frequency in the literature, that is, percentage of dung removal, percentage of seed dispersal and rate of excavated soil. All analyses were performed with the Comprehensive Meta-Analysis 3.0 software (Borenstein et al., 2005).

3 RESULTS

Overview database

Of the 48 articles that were analysed, we found 455 comparisons for dung beetles. The total number of comparisons species richness and total abundance were the best represented with 170 and 146 comparisons, respectively; secondary forest was the best represented cover with 173 comparisons. All other metrics were represented for 5–60 comparisons, that is, percentage of dung removal, percentage of seed dispersal, rate of excavated soil and biomass (Tables S1 and S2). These comparisons were distributed mainly in tropical latitudes, particularly in Brazil, Indonesia and Malaysia (Figure 1).

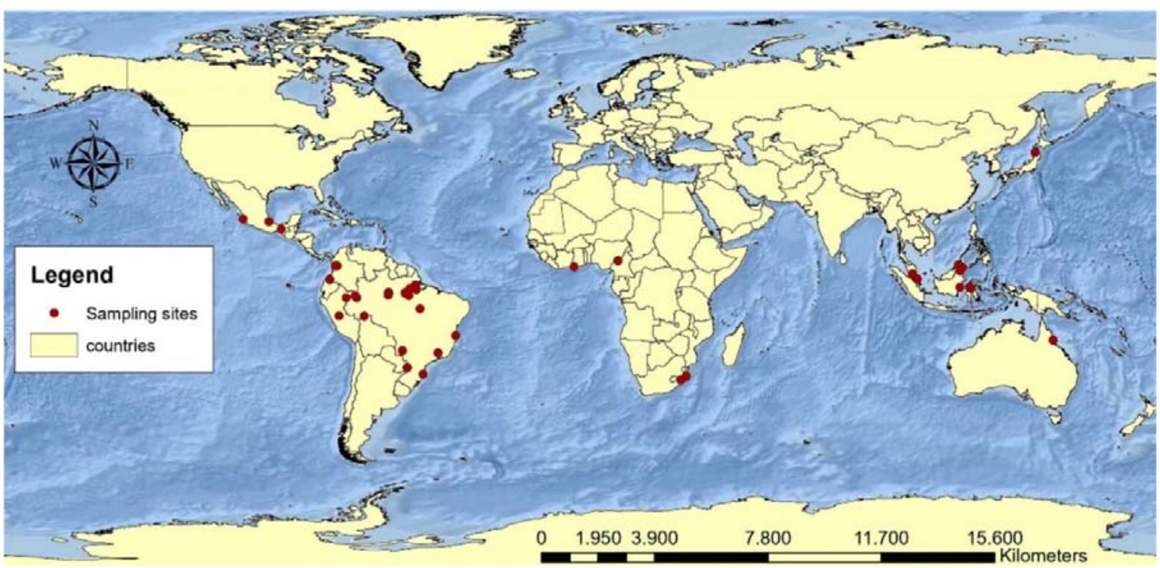

FIGURE 1. Number of articles evaluated in the current meta-analysis organized by countries and different included metrics

Species richness and abundance of dung beetles

We found a negative global effect on dung beetle richness and total abundance associated with undisturbed primary forests conversion (degradation and deforestation) (Figures 2a and 3a). Moreover, this effect was less severe in degraded primary forest than in secondary forests, forestry plantations and forestry restoration (Figures 2b and 3b). In general, species richness and abundance displayed different responses depending on latitude, zoogeographical region and biodiversity hotspots. For example, a neutral or slightly positive effect on species richness was shown in non-tropical latitudes (Figures 2c and 3c). Moreover, the Australasia, Neotropical and Oriental regions displayed a negative effect on species richness and total abundance instead of a neutral–positive effect shown in the Afrotropical and Nearctic regions (Figures 2d and 3d).

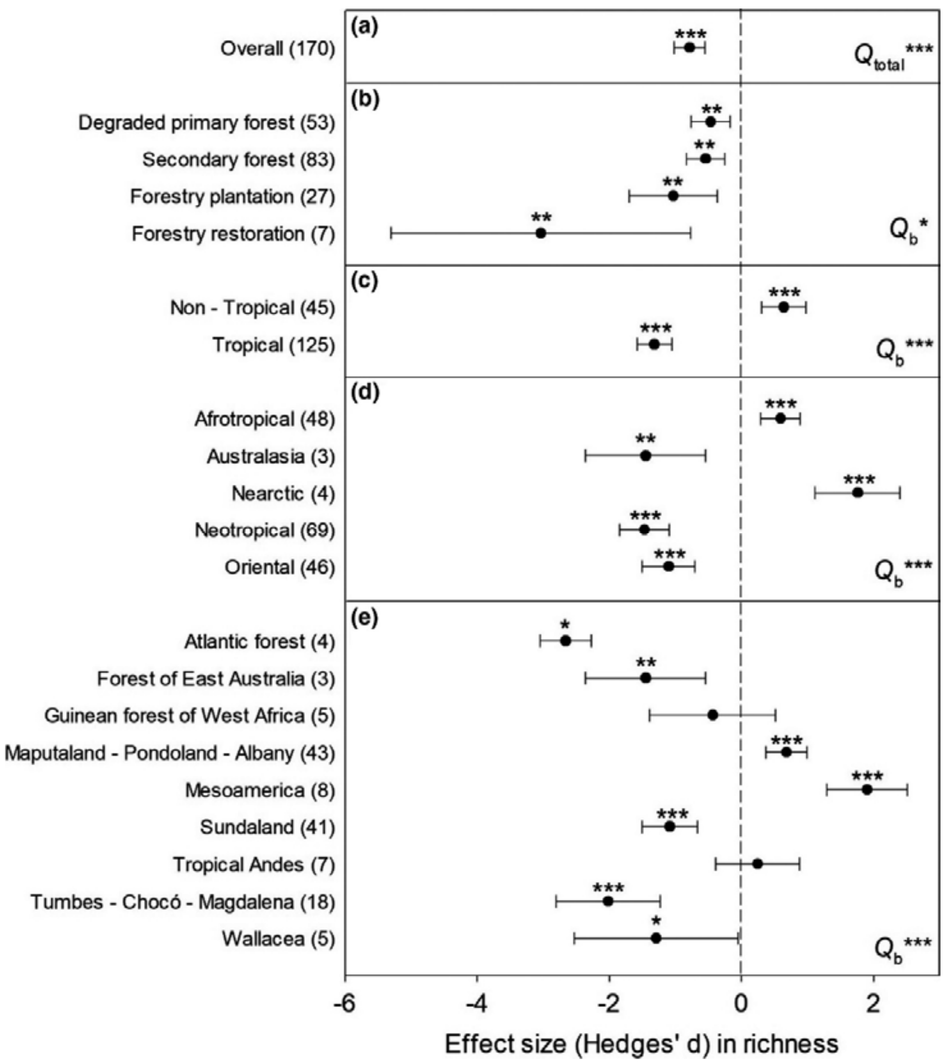

FIGURE 2.
Effects on dung beetle species richness attributed to the replacement of primary forests. The average and 95% confidence intervals are shown for: (a) general effect, (b) type of vegetation cover, (c) latitude, (d) zoogeographical region and (e) biodiversity hotspots. The number of case studies per level of the moderator is given in parenthesis. Asterisks denote confidence intervals that are significantly different from zero. Qb represents the homogeneity between the groups in comparisons. Significance levels were determined as: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

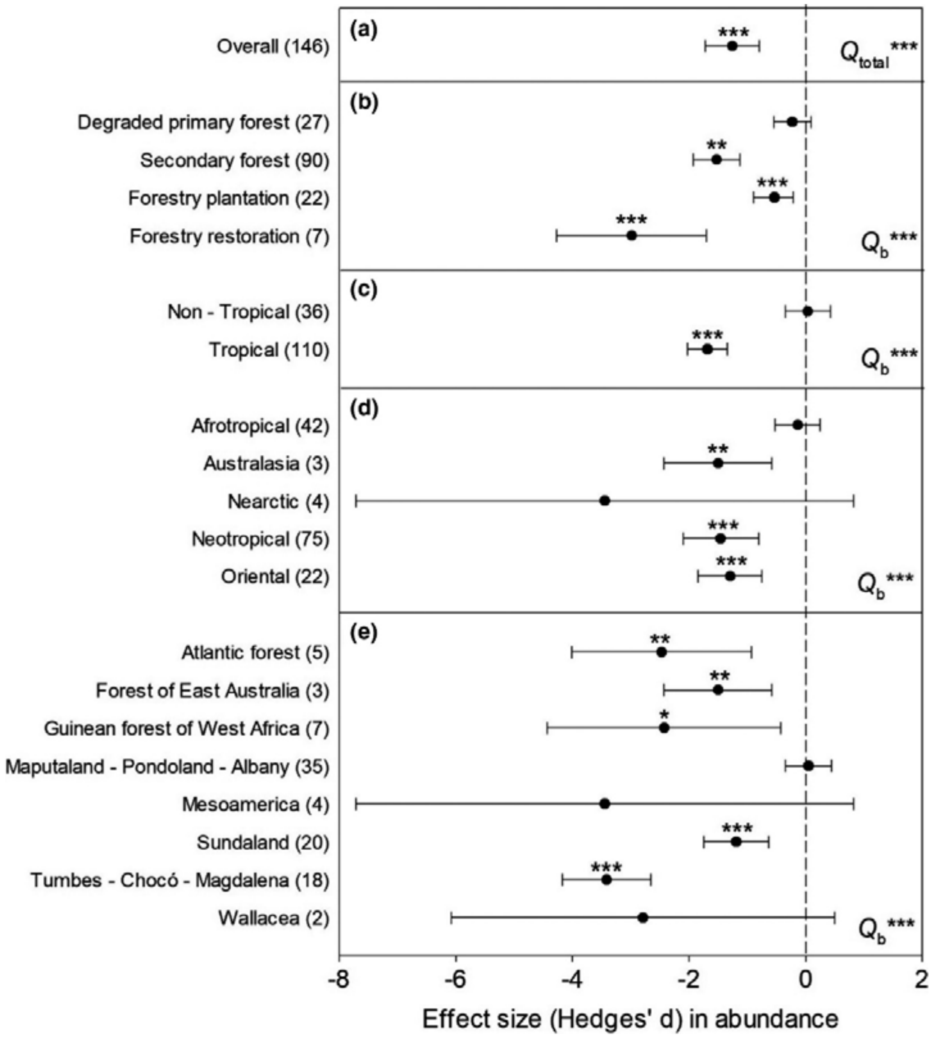

FIGURE 3. Effects on total dung beetle abundance attributed to the replacement of primary forests. The average and 95% confidence intervals are shown for: (a) general effect, (b) type of vegetation cover, (c) latitude, (d) zoogeographical region and (e) biodiversity hotspots. The number of case studies per level of the moderator is given in parenthesis. Asterisks denote confidence intervals that are significantly different from zero. Qb represents the homogeneity between the groups in comparisons. Significance levels were determined as: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

The more severe negative results in the Australasia, Neotropical and Oriental regions were driven by a larger number of case studies with negative results in forestry plantations and forestry restoration. Besides, some biodiversity hotspots in these zoogeographic regions such as Atlantic forest, Forest of East Australia, Guinean forest of West Africa, Sundaland, Tumbes-Chocó-Magdalena and Wallacea presented a more severe negative effect on species richness and/or abundance, compared to the Maputaland-Pondoland-Albany, Mesoamerica and Tropical Andes hotspots, for which a neutral–positive effect was recorded (Figures 2e and 3e).

Genera, functional traits and ecological functions

Different responses to the undisturbed primary forests conversion were found for different genera and functional traits. However, a loss of ecological functions was recorded in all studies. Abundances of *Sulcophanaeus*, *Uroxys*, *Dichotomius* and *Onthophagus* showed negative tendencies to undisturbed primary forest conversion while those of *Copris*, *Diastellopalpus* and *Sisyphus* were neutral or slightly positive effects (Figure 4a). Large and small tunnellers displayed more severe adverse effects in comparison to large and small rollers (Figure 4d), suggesting that this result may be related more to the type of relocation than to the size of individuals. Differences were not found between beetles of different sizes but were attributed to relocation type; tunnellers being more affected by undisturbed primary forests conversion (Figures 4b,c). Biomass, percentage of dung removal and percentage of seed dispersal also showed negative effects (Figures 4e,f,h), whereas those for the amount of excavated soil were neutral (Figure 4g).

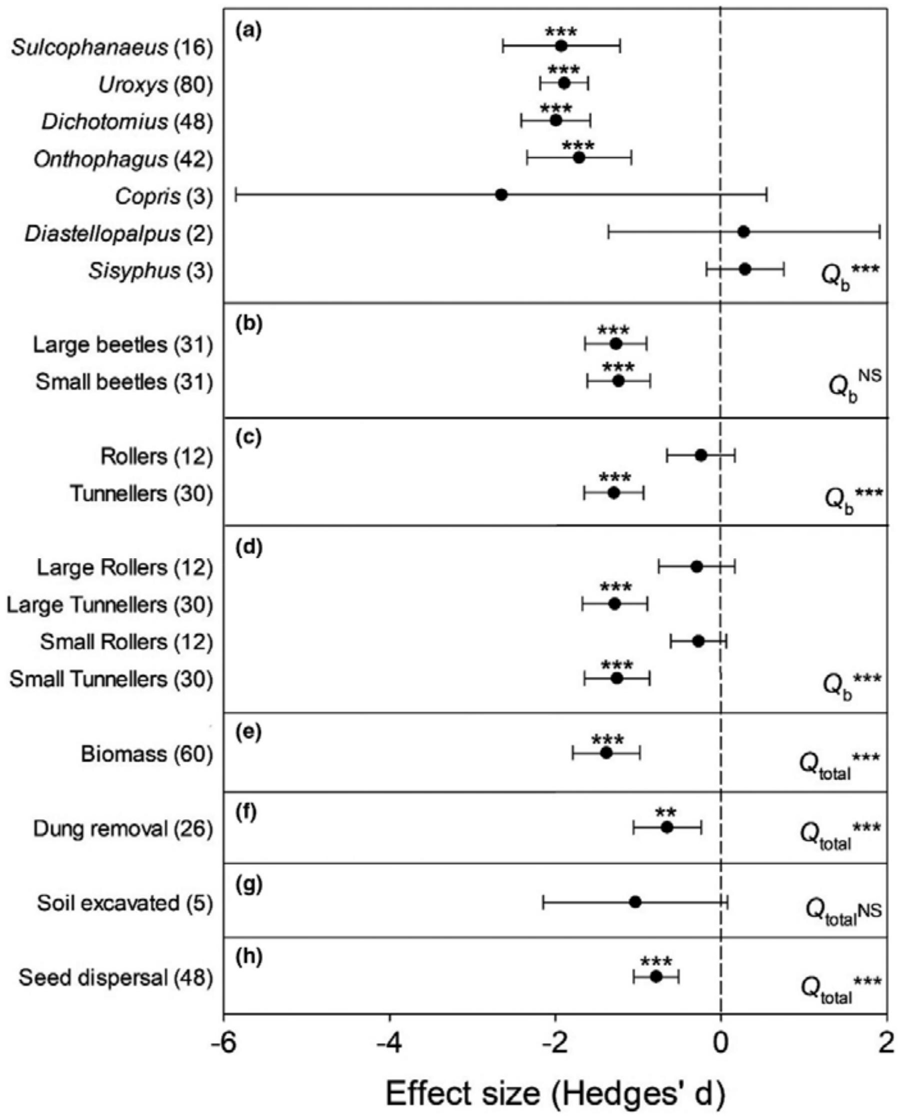

FIGURE 4. Effects on specific moderators of dung beetle abundance and ecosystem functions attributed to the replacement of primary forests. The average and 95% confidence intervals are shown for: (a) genus, (b) beetle size, (c) relocation type, (d) functional group, (e) biomass, (f) dung removal, (g) excavated soil and (h) seed dispersal. The number of case studies per level of the moderator is given in parenthesis. Asterisks denote confidence intervals that are significantly different from zero. Qtotal represents the total homogeneity value for a given variable, and Qb represents the homogeneity between the groups in comparisons. Significance levels were determined as: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

Effects of species richness and total abundance on ecological functions

The species richness and abundance had a significant effect on ecological functions (Figure 5). Less negative effects for species richness derived in significantly increased dung removal and seed dispersal (slope = 0.466, $p < 0.001$; and slope = 0.714, $p < 0.001$ respectively). Also, less severe effects for dung beetle abundance derived in increased dung removal (slope = 0.351, $p = 0.0035$). However, dung beetle abundance did not influence seed dispersal (slope = 0.054, $p = 0.641$).

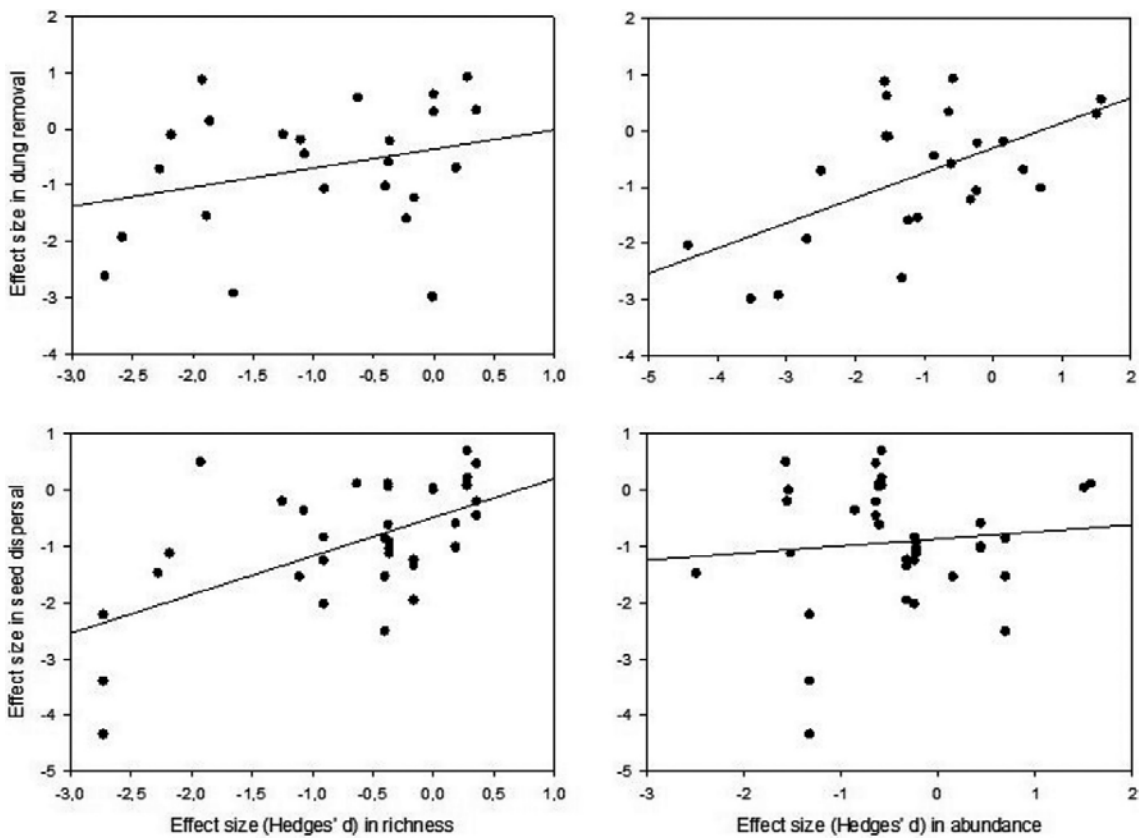

FIGURE 5. Effect on dung beetle species richness and total abundance of dung removal (top panels) and seed dispersal (bottom panels) after disturbance of primary forest

Publication bias

In general, the Rosenthal security number (i.e. the number of non-published case studies necessary to obtain non-significant results) shows that the different evaluated metrics present reliable results compared to the safety threshold. This confirms that the observed effects are not due to bias associated with the omission of articles with neutral or negative effects. However, given the test results (see Table S3), we advise caution in interpreting our dung removal findings and excavated soil. Besides, the magnitude and direction did not vary substantially across the different metrics evaluated in the 'trim-and-fill' analysis, demonstrating that our results are reliable and not influenced by the asymmetry in the number of positive, neutral or negative case studies (Figure S2; Table S4).

4 DISCUSSION

We performed a meta-analysis on the impact of undisturbed primary forest conversion on diversity and ecological functions, using dung beetles as a model study taxon. Overall, we found support for our research hypotheses, demonstrating that degraded primary forest, secondary forest, forestry plantations and forestry restoration supported lower diversity and ecological functions loss and that geographical location influence these effects. However, degraded primary forest had less negative effect for dung beetles than secondary forest, forestry plantations and forestry restoration. These negative effects were more pronounced in vulnerable areas such as Australasia, Neotropical and Oriental regions. We concluded that undisturbed primary forest conservation is the best fit for dung beetle diversity and ecological function preservation. However, in vulnerable regions and associated hotspots, where undisturbed primary forest is not feasible, degraded primary forest associated with logging managements programs could be the best strategy to reduce negative impacts for dung beetles.

Overall response of species richness and total abundance

Our results demonstrate a negative global effect on dung beetle species richness and abundance associated with undisturbed primary forest conversion. These findings agree with investigations based on different faunal taxa that demonstrate the loss of species richness and abundance in response to undisturbed primary forest conversion (see Barlow et al., 2007; Castaño-Villa et al., 2019; Gibson et al., 2011). Undisturbed primary forest conversion and consequent creation of degraded primary forest, secondary forest, forestry plantations or forestry restoration drives different micro-habitat characteristics to those of undisturbed primary forests, such as a reduced basal area and increased canopy opening (Audino et al., 2017; Barlow et al., 2007; Beiroz et al., 2019; Culot et al., 2013; Parry et al., 2007), a larger percentage of coarse sand in the soil (associated with the degree of soil compaction), lower soil moisture content and higher temperatures (Beiroz et al., 2019; Senior et al., 2017). Furthermore, these coverages may have lower excrement availability due to large vertebrates' defaunation compared to undisturbed primary forests (Barlow et al., 2007; Fuzessy et al., 2021; Parry et al., 2007). This combination of factors may explain the negative effects of dung beetle assemblages in response to the undisturbed primary forest conversion. Also, it should be noted that, responses could be varied according to the specific micro-habitat requirements of different beetle species (Davis et al., 2001), given for a physiological restrictions (França et al., 2018; Salomão et al., 2019), associated with elevated soil temperatures and light intensity, lower soil moisture levels and increased soil compaction impacting on feeding, reproduction and establishment (Chown, 2001; Halffter & Edmonds, 1982; Nyamukondiwa et al., 2018; Osberg et al., 1994; Sheldon et al., 2011).

Differential effects between cover types for dung beetles

Our study shows that degraded primary forest have less negative effects on dung beetle's diversity, comparatively with secondary forest, forestry plantations and forestry restoration. This matches with local studies that emphasize the viability of degraded primary forest for conserving a representative dung beetle assemblage of undisturbed primary forest (Audino et al., 2014; Davis & Philips, 2005; Slade et al., 2011). Depending of logging intensity (selective or conventional) (de Moura et al., 2021) the primary forest may be maintained through time, minimizing the negative effects for biodiversity (Bicknell et al., 2014; Davis et al., 2001; Fuzessy et al., 2021) when compared to the complete removal of undisturbed primary forest.

On the other hand, although secondary forest, forestry plantations and forestry restoration show more negative effects, in some cases they could maintain dung beetle assemblage in deteriorated or locally eradicated primary forests (undisturbed or degraded) (Andresen, 2008; Arellano et al., 2013; Davis et al., 2003; Derhé et al., 2016). Finally, surprisingly, we found the most negative effect in forestry restoration compared to forestry plantations. Our meta-analysis, forestry plantations included, generally utilized fast-growing tree species, minimizing the direct exposition of soil in early stages (Beiroz et al., 2016), while forestry restoration has implemented generally with a mixture of slow-growing native tree species (Audino et al., 2014). However, forestry restoration could promote higher dung beetle diversity with an increase in age (Audino et al., 2014; Derhé et al., 2016), associated with friendly micro-climatic characteristics (i.e. soil temperature and humidity) presents in older restoration (Audino et al., 2017).

The effect of geographical location

The impacts on species richness and abundance proved to depend on dung beetles' geographical context. Global dung beetle diversity is influenced by the availability of excrement resources produced by mammals (Davis et al., 2002; Scholtz et al., 2009). The most significant negative impact occurred in tropical latitudes, where highly mammal diversity loss and undisturbed primary forests conversion and increases in poaching (Fritz et al., 2009; Gibson et al., 2011), leads to negative impacts on the diversity and structure of dung beetle assemblages (Nichols et al., 2009). Added to the decline in mammals in the tropics, there is a more complicated scenario concerning primary forest deforestation rates and their conversion rates into forestry plantations. According to global statistics, the tropics show the most massive undisturbed primary forest deforestation rates and have the most extensive conversion rates into forestry plantations compared to non-tropical latitudes (FAO, 2020; Keenan et al., 2015; Payn et al., 2015).

The effects of zoogeographical regions were more severe in areas with high diversity and significant conservation interest. In particular, the largest negative impacts were shown in Australasia, Neotropical and Oriental regions and associated hotspots. These regions are characterized by high levels of dung beetle species richness (Davis et al., 2002; Scholtz et al., 2009) and a critical degradation and deforestation of primary forest with over 75% of their original area lost to deforestation (Armenteras et al., 2003; Mittermeier et al., 2004; Myers et al., 2000). The primary forest remnants (undisturbed and disturbed) in these regions are subject to logging managements, in fragmented landscape and isolated by agrarian, livestock development or the establishment of large urban areas. The continuous escalation in these activities threatens to decrease primary forest vegetation even further and may lead to an accelerated loss of biodiversity.

Moreover, although the Australasia, Neotropical and Oriental zoogeographical regions comprise only 20% of global forestry plantations, these are mainly composed of exotic species (FAO, 2020; Payn et al., 2015). For example, in South America, 85% of forestry plantations are of exotic origin (e.g. *Pinus* or *Eucalyptus*), 75% in Oceania and 37% in Asia (Payn et al., 2015). Prospects in the top 10 countries with the most area of forestry plantations (see Payn et al., 2015) are expected to be even more harmful due to the increase in this type of vegetation cover, including Indonesia (associated with the Wallacea hotspot), Thailand and

Vietnam (related to the Sundaland hotspot). Given this situation, South-eastern Asia, Oceania and South America can be considered as extremely vulnerable regions due to the growing threat that primary forests experience regarding the increase in exotic plantations and its consequent negative effect on tropical dung beetles (see Beiroz et al., 2016; Gardner et al., 2008; Ueda et al., 2015).

Genera, functional traits, and ecological functions related to diversity

Although the number of articles related to functional aspects was low compared to species richness and total abundance, we observed a significant reduction in biomass, and impoverishment in assemblage and functional group structure, and a loss of ecological functions (e.g. dung removal and seed dispersal) in response to undisturbed primary forest conversion. As responses differed between genera, some of those genera identified that displayed a negative response (e.g. *Sulcophanaeus*, *Uroxys*, *Dichotomius* and *Onthophagus*) may be used as bioindicators to monitor this functional loss as has been demonstrated in other studies (Audino et al., 2011; Bitencourt et al., 2019; Cajaiba et al., 2017; Daniel et al., 2014; Filgueiras et al., 2015).

Several studies have shown the marked effect of defaunation (i.e. the loss of large mammals) on beetle assemblages' structure (Feer & Boissier, 2015; Fuzessy et al., 2021; Nichols et al., 2009; Raine & Slade, 2019). In functional groups, large tunnellers were the most sensitive to vegetation cover changes in the present study, displaying a substantial decrease in abundance to the undisturbed primary forests conversion. This functional group requires larger quantities of excrement for feeding and nesting that can only be generated by large mammals, which are the first to disappear with vegetation cover changes due to anthropogenic perturbation, potentially explaining the observed sensitivity to changes in tunnelling beetles (Raine & Slade, 2019). The disappearance of large species can exacerbate negative effects for ecosystem functioning since these are the species that make the greatest functional contribution (Piccini et al., 2019).

Our study is the first global analysis to evaluate ecosystem functions performed by an arthropod taxon and its response to undisturbed primary forest conversion. According to our analysis, dung removal and seed dispersal are strongly and negatively affected by vegetation cover changes. Our global pattern agrees with previous local studies evaluating these metrics (see Audino et al., 2014; Braga et al., 2012; Horgan, 2005; Larsen et al., 2005; Slade et al., 2011). The effect is related to decreased abundance, species richness, biomass and functional groups of the dung beetle assemblage (Buse & Entling, 2019; Derhé et al., 2016; Milotic et al., 2018; Slade et al., 2007). Various studies have shown that assemblages with high functional richness values maintain a larger number of ecosystem functions and offer greater resilience to anthropogenic perturbation events (Beynon et al., 2012; Manning et al., 2016; Menéndez et al., 2016; Milotic et al., 2018), whereas reduction in species richness or abundance leads to profound negative effects at multiple levels in the ecosystem functioning (Larsen et al., 2005). In contrast, the neutral response of soil removal may be associated with the broad range of values or the low number of studies for this variable (e.g. Amezquita & Favila, 2010; Amore et al., 2018; Frank et al., 2017). Nevertheless, this response will likely be negative in the future studies given that degraded primary forest, secondary forest, forestry plantations or forestry restoration soils show a higher degree of compaction, lower moisture and a smaller amount of leaf litter (Gries et al., 2012). All of these factors have been previously demonstrated to hinder soil removal by beetles (Sowig, 1995).

Some authors have proposed that undisturbed primary forest conversion by these coverages may be less disruptive to ecological functions than when replaced with heavily perturbed or open areas such as grasslands (see Brockerhoff et al., 2008; Derhé et al., 2016; Estrada & Coates-Estrada, 2002; Neita & Escobar, 2012; Slade et al., 2011). To better understand the pattern found in the current study, we recommend experimental field evaluation on a global scale for the different ecological functions provided by dung beetles (e.g. dung removal, seed dispersal) in undisturbed primary forest, degraded primary forest, secondary forest, and forestry restoration or plantation types.

5 CONCLUSIONS

The results show that undisturbed primary forest conversion (degradation or deforestation) has a negative effect on species richness and abundance, alteration in the assemblages' functional structure and a reduction in ecological functions. Moreover, we demonstrate that these effects are dependent on geographical context, particularly with the most obvious negative effects in tropical latitudes and biodiversity hotspots. Our results show a priority of focusing conservation efforts on remaining undisturbed primary forests, especially in tropical latitudes and countries located in regions with high biodiversity such as Borneo, Brazil, Colombia, Ecuador, Indonesia, Malaysia, New Guinea and Peru. However, where undisturbed primary forest conservation is not feasible, we recommend implementing logging managements for these undisturbed primary forest (selective or conventional) as the best strategy for conservation of diversity and ecological functions of dung beetles. Besides, in landscape where primary forest (undisturbed or degraded) has been extirpated, secondary forest creation could be a good strategy for dung beetle diversity conservation. Finally, we propose the necessity for future studies to consider the intensity of logging, secondary forest or forestry age or connectivity for dung beetles. The above determines which management characteristics can moderate less severe responses with the conversion of primary forests over biodiversity.

ACKNOWLEDGEMENTS

The authors thank Wallace Beiroz for facilitating dataset information to develop the analyses. They thank Juan Mateo Rivera for their help in generating the map. They also thank Estefani Martínez Sánchez and Erika Alejandra Cardona for their valuable comments on the manuscript, and Javier H. Santos and David Morris from English Syntax for their thorough English revision. CNPq supported L.D. Audino, proc. PDJ 150776/2017-9.

AUTHORS' CONTRIBUTIONS

P.A.L.-B. and J.A.N. designed the research; P.A.L.-B. collected, cleaned and filtered the data; P.A.L.-B. and M.B.-M. analysed the data; P.A.L.-B., M.C.Á.-V., L.D.A. and J.A.N. led the writing of the manuscript, assisted by A.L.V.D. and G.G. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.4tmpg4fc0 (López-Bedoya et al., 2022).

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