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REVIEW

Importance of restoration of dung beetles in the maintenance of ecosystem services

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Abstract

1. Dung beetles have key roles in ecosystems including accelerating dung decomposition, improving nutrient cycling and influencing physical (such as structure) and chemical (such as pH and available nutrients) soil properties. Without dung beetles, dung decomposition slows, nutrient cycling is impaired, and water infiltration decreases.
2. Dung beetles face various threats, including climate change, anthropogenic chemicals and habitat degradation. However, there is limited information on the restoration of dung beetles in areas where they have been lost.
3. The restoration framework utilized in this review considers three primary facets: environmental conditions, which encompass crucial abiotic features; biotic characteristics, which involve all other species; and focal species, which denote all native functional groups of species that require reintroduction or re-establishment.
4. This review aims to examine the ecosystem services provided by dung beetles, highlight the threats they face and conceptualize a restoration framework for these crucial organisms.

KEYWORDS
dung beetles, ecosystem functions, restoration

1 | INTRODUCTION

Dung beetles (Coleoptera: Scarabaeidae) are among the most recognizable of the dung fauna. Dung beetles occur globally (Frank et al., 2018) and contribute to important ecosystem functions (Thomas, 2001) but are facing multiple threats (Tocco et al., 2021). Despite their importance, very little attention has been paid to the restoration of these charismatic insects where they have been lost.

Dung beetles can be classified into functional groups by how they utilize dung for breeding and feeding. These functional groups are endocoprids (dwellers), paracoprids (tunnelers), and telecoprids (rollers) (Halffter & Edmonds, 1982; Hanski & Cambefort, 2014). Each of these functional groups is comprised of multiple species. Dwellers use dung as their primary habitat and for breeding (Figure 1). Tunnelers live in soil under dung and transfer small quantities of dung into the soil for breeding. Rollers move balls of dung a distance away from the original deposition site and bury them in the soil for feeding and breeding. These functional groups accelerate decomposition by creating pores or channels throughout the dung and increasing fungal and bacterial decomposition (Doube, 1990; Figure 1).

Dung beetles are ubiquitous in many ecosystems and environmental factors such as soil texture, temperature, cover and land use affect the abundance and activity of dung beetles. Dung beetle

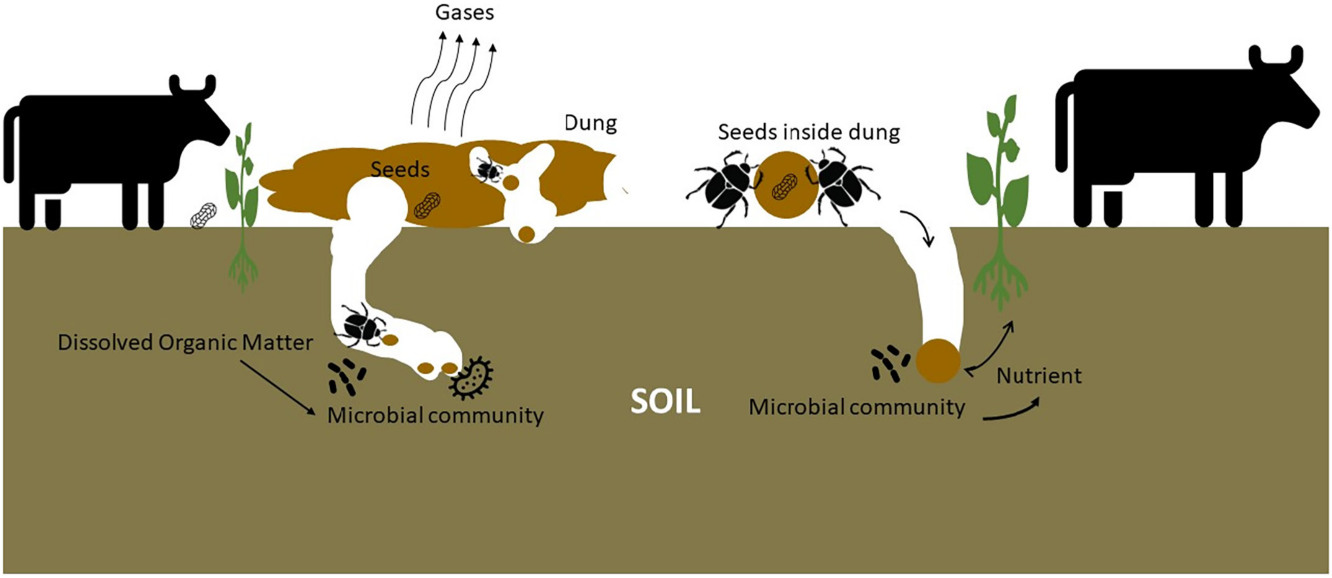

FIGURE 1 Different functional groups of dung beetles including tunnelers (live in the soil under the dung pats and use the dung for brooding), dwellers (use the dung for living and nesting) and rollers (live in the soil and use the dung for brooding) and their effects on different ecosystem services such as improving chemical and physical properties of soil, altering microbial community, promoting plant growth and reproduction and reducing greenhouse gas emissions.

abundance and activity are higher in sandy soils (von Hoermann et al., 2020); in warmer temperatures (Gotcha et al., 2021), and at lower latitudes (Hortal et al., 2011). Moreover, smaller dung beetles are more abundant in grasslands compared with forests (Korasaki et al., 2013). Grazing by cattle positively affects the abundance of dung beetles and species richness (Wagner et al., 2021).

Dung beetles are currently facing numerous threats, and their potential loss will have significant impacts on ecosystem function (Beynon et al., 2012), thereby reducing ecosystem sustainability (Nervo et al., 2017). Due to their significance, it is crucial to incorporate dung beetles into restoration planning (Buse & Entling, 2020).

2 | ECOSYSTEM SERVICES PROVIDED BY DUNG BEETLES

Dung beetles play a significant role in many functions and components of ecosystems (Jones et al., 2018) from soil (Beynon et al., 2015; Evans et al., 2019), to biological pests including pathogens and parasites (Milotić et al., 2017), and plant communities (Griffiths et al., 2015). The effectiveness and efficiency of dung beetles in providing ecosystem functions is linked to their diversity and abundance (Davies et al., 2020). Maintaining high species richness is crucial for sustaining ecosystem functions (Reich et al., 2001). Cumulatively, the ecosystem services provided by dung beetles have considerable economic value estimated annually at $5.9 billion (2005 US dollars) in the United States (Losey & Vaughan, 2006) and $425.9 million (2014 US dollars) in the United Kingdom (Beynon et al., 2015).

Dung beetles play a significant role in soil dynamics, impacting nutrient cycling and greenhouse gas fluxes. They accelerate the decomposition of dung pats (Davies et al., 2020; Ortega-Martínez et al., 2020) and transport nutrients from pats into soil (Menéndez et al., 2016). For example, dwellers increase organic matter and phosphorus concentrations at the soil surface by 50%, rollers increase NH_4^+ in deep soils by 60%, and tunnelers increase organic matter, total nitrogen and phosphorus throughout the soil profile by 50% in a semiarid pasture (Maldonado et al., 2019). Through their activities, dung beetles can reduce the emission of CO_2 by 7%, N_2O by 2%, and CH_4 by 14.5% from dung pats during the grazing season (Iwasa et al., 2015; Piccini et al., 2017; Slade et al., 2016) which can scale up to substantial pasture-level impacts (Slade et al., 2016).

Dung beetle activity leads to a substantial reduction in pests affecting livestock and wildlife, including approximately 70% of flies (Ix-Balam et al., 2018), 60%–90% of nematodes (Bryan, 1976; English, 1979; Fincher, 1975) and protozoa (Nichols et al., 2008) through the reduction of dung on the landscape. Dung beetles reduce these pests during feeding activities that incidentally ingest pest eggs and larvae present in dung (Holter & Scholtz, 2007). Furthermore, rollers bury dung balls and pest larvae emerging from the ball cannot return to the surface following hatch (Gregory et al., 2015).

Water infiltration is improved through biopedturbation by dung beetles (Brown et al., 2010). Biopedturbation by dung beetles arises from their tunneling and digging activities (Hanski & Cambefort, 2014). These actions decrease the bulk density of soil (Nichols et al., 2008), enhance soil porosity that increases infiltration by up to 300% (Keller et al., 2022), and reduce surface water runoff. Tunnels act as channels allowing water to move directly into deeper layers of the soil profile (Manning et al., 2016). Moving water into deeper layers of soil can increase soil moisture by 20% at 0%–30 cm depth (Brown et al., 2010). The enhanced threefold increase in water infiltration rates into soils and improved hydrological functioning through the action of dung beetles influence nutrient cycling and plant productivity (Keller et al., 2022).

Plant growth can also be affected by dung beetle activity through several mechanisms including changes to water and soil nutrients and through seed dispersal and germination. Plants have been observed to respond to dung beetle-driven changes to soil (Santos-Heredia et al., 2016; Yoshihara & Sato, 2015) as evidenced by an increase in leaf tissue N and C content (Johnson et al., 2016). Plants respond to higher moisture in soils due to dung beetle activity through increases in plant growth (280%), leaf emergence (30%) and plant height (200%) under drought conditions in humid subtropical native pasture (Johnson et al., 2016). Moreover, dung beetles have a secondary role in vertical and horizontal seed dispersal of many plant species (Santos-Heredia et al., 2011) which reduces spatial clumping of seeds (Urrea-Galeano et al., 2019) and allows endozoochoric seeds access to a wider variety of safe sites for germination. Furthermore, dung beetles can enhance the germination of seeds inside dung pats by accelerating the decomposition rate of dung that acts as physical barrier for germination (Ishikawa, 2011).

3 | THREATS TO DUNG BEETLES

There are several major threats to dung beetles including climate change (changing temperature and precipitation as well as increasing CO_2), habitat fragmentation and anthropogenic chemical use. Understanding these threats may help improve restoration outcomes.

Climate change can negatively impact dung beetle species richness and abundance (Maldaner et al., 2021) by altering temperature (Sheldon et al., 2020), precipitation (Liberal et al., 2011), biogeochemical cycles (Seddon et al., 2016) and phenology (Forrest, 2016). Dung beetles may respond to increasing temperatures with increased feeding rates (Sheldon et al., 2020) and shrinking body size and overall metabolism to conserve energy (Fleming et al., 2021). These physiological changes can impact dung beetles' abundance by decreasing their reproduction. For instance, within a temperature range of 22–30°C, with a diurnal increase of 2°C and 4°C, the number of broods decreases by 36% and 30%, while dung burial decreases by 25% and 30%, respectively (Holley & Andrew, 2020). The response of the dung beetle community to climate change can also depend on latitude. In northern areas, rising temperatures enhance dung removal and seed dispersal rates by dung beetles (Milotić et al., 2019). But in southern latitudes increasing variability in precipitation may result in lower species richness, abundance and biomass of dung beetles (França et al., 2020).

Increased CO_2 levels above 600 ppm directly impact dung beetles by increasing mortality rates, decreasing adult size and impairing larval development and survival. Additionally, elevated CO_2 levels within dung brood balls decreased larval performance (Tocco et al., 2021). Indirectly, increasing CO_2 levels can lead to an increase in nonstructural carbohydrates and a decrease in N and P in plants (Loranger et al., 2004; Poorter et al., 1997) that negatively impacts the quality of dung pats and dung beetle abundance (Gittings & Giller, 1998). Moreover, rising CO_2 levels contribute to woody encroachment, which decreases the quality of both food and habitat for dung beetles. In the early stages, when shrub cover is less than 10% of the area, shrubs can enhance habitat quality for beetles. However, if encroachment exceeds 10% of shrub cover, it decreases beetle diversity (Hering et al., 2019).

Dung beetles are able, to some extent, to respond to changing climate. For example, dung beetles have the potential to adjust to climate change through their seasonal activity and responses to disturbances (Cuesta et al., 2021; Menéndez & Gutiérrez, 2004). For instance, dung beetle phenology can shift towards earlier seasonal activity or prolonged activity periods, which can help to compensate for adverse changes in their environment (Forrest, 2016). Furthermore, dung beetle ranges may shift northward in response to climate change, and this could lead to an increase in species richness at higher latitudes (Dortel et al., 2013).

Anthropogenic activities such as fragmentation and chemical use have adverse effects on dung beetles' abundance and richness (Lumaret et al., 2022; Martello et al., 2016). In many areas of the world, habitats are becoming increasingly fragmented (Fahrig, 2003), and when fragmentation leads to habitats becoming isolated dung beetles can be impacted (Mbora & Mutua, 2023). The isolation may result in a failure to sustain large mammal populations (Larsen et al., 2008), potentially leading to a decrease in dung beetle richness, density and biomass (Storck-Tonon et al., 2020). Dung beetles have high dispersal potential and can fly up to 16 km (Thomas, 2001). Thus, fragmentation may be a more serious issue for populations that are more than 16 km apart.

Anthropogenic land-use changes impact dung beetle populations differently based on the disturbance type, extent and species characteristics (Raine & Slade, 2019). Cattle grazing and high wildlife populations benefit abundance and richness of dung beetles (Andresen & Laurance, 2007; Correa et al., 2020). Conversely, removal of wildlife and cattle reduces beetle abundance, community diversity and richness (Fuzessy et al., 2021). In forested areas, diversity of dung beetles is typically lower in logged forests compared with primary forests, and the abundance of dung beetles decreases with canopy openness (Beiroz et al., 2019; Davis et al., 2001). In general, extensive disturbances tend to have negative effects on all dimensions of dung beetle diversity, although certain aspects, such as functional and phylogenetic richness, may be more strongly affected (Rivera et al., 2023).

Anthropogenic chemicals negatively affect dung beetles. Residual parasiticide products in dung decrease the abundance and diversity of dung-associated insects (Pérez-Cogollo et al., 2015) and lead to high adult and larval mortality, low female fertility and a reduction in body size (Lumaret et al., 2022). One common parasiticide, ivermectin, impairs the olfactory and locomotor capacities of dung beetles (Verdú et al., 2015) and affects dung beetle colonization, emigration and biomass (Verdú et al., 2018). In a western

South Dakota rangeland, experimental addition of ivermectin to cattle dung resulted in high mortality of beetles colonizing dung pats (Torabian, unpublished data). The negative impacts of chemicals on dung beetles can lead to losses of ecosystem functions they provide (Kavanaugh & Manning, 2020).

4 | RESTORATION TRIANGLE FOR DUNG BEETLES

A global decline in dung beetles, particularly in the past 30 years, has been documented highlighting the importance of dung beetle restoration (Lumaret et al., 2022; Nichols et al., 2007). A key first step in restoration planning is to identify high-priority habitats and species (Gann et al., 2019). Dung beetle species richness, diversity, and ecological function can serve as important criteria for site selection. Areas with low dung beetle species richness or impaired ecological functions (such as poor dung decomposition and field fouling) are prime candidates for restoration efforts (Sarmiento-Garces & Hernández, 2021).

To conceptualize dung beetle restoration, we propose a restoration triangle framework encompassing environmental conditions, biotic characteristics and focal restoration species (Figure 2: Perkins & Leffler, 2018). Environmental conditions are physical properties of the site that can influence restoration, like soil structure and moisture. Biotic characteristics involve other organisms present at a site, which can aid or impede restoration, including plants, insects and herbivores. Additionally, restoration planning should account for the requirements and traits of focal restoration species (dung beetles), such as seasonal activity and dispersal abilities (Perkins & Leffler, 2018). Whereas the triangle describes the conditions and characteristics of the site, external influences arising from outside the restoration site such as fragmentation and disturbance can also influence restoration success (Perkins et al., 2011). Understanding these factors is crucial for successful restoration.

4.1 | Environmental conditions

The environmental conditions of a degraded site play a crucial role in dung beetle restoration (Pessôa et al., 2021). As dung beetles are, in some life stages, soil organisms, the soil abiotic environment is critical (Beiroz et al., 2019). Soil characteristics have an influence on dung beetle abundance (Almeida et al., 2022) owing to their impact on habitat and food sources (Farias & Hernández, 2017). For instance, an increase in soil compaction results in higher penetration resistance, and a rise in penetration resistance from 2000 to 5000 kpa can lead to approximately a 15% reduction in brood ball depth, alongside increased energy consumption by the beetles (Dabrowski et al., 2019). Restoring soil quality may require phyto- or mechanical-remediation (Farrell et al., 2020). Well-drained soil increases dung beetle survival, therefore enhancing soil drainage is a suitable approach (Heneghan et al., 2008; Lal, 2020).

Anthropogenic chemicals, particularly those used to control pest insects, can hinder restoration success due to their broad efficacy and off-target effects (Sánchez-Bayo, 2021). Monitoring and controlling chemicals (Verdú et al., 2018) and minimizing the need for pesticides (Jacobs & Scholtz, 2015) can reduce their impact on non-target species such as dung beetles. Implementing integrated pest management principles, which recommend limited pesticide use and a range of methods to mitigate harm to insects (Stenberg, 2017), is suggested for landscapes where complete pesticide elimination is not feasible due to economic constraints or stakeholder interests. If the landscape is grazed by livestock, minimizing the use of parasiticides such as ivermectin is especially important as these compounds affect dung beetles (Sands & Wall, 2018; Tovar et al., 2023).

4.2 | Biotic characteristics

The presence of other organisms at the restoration site has a significant influence on dung beetle restoration. Primarily for dung beetle

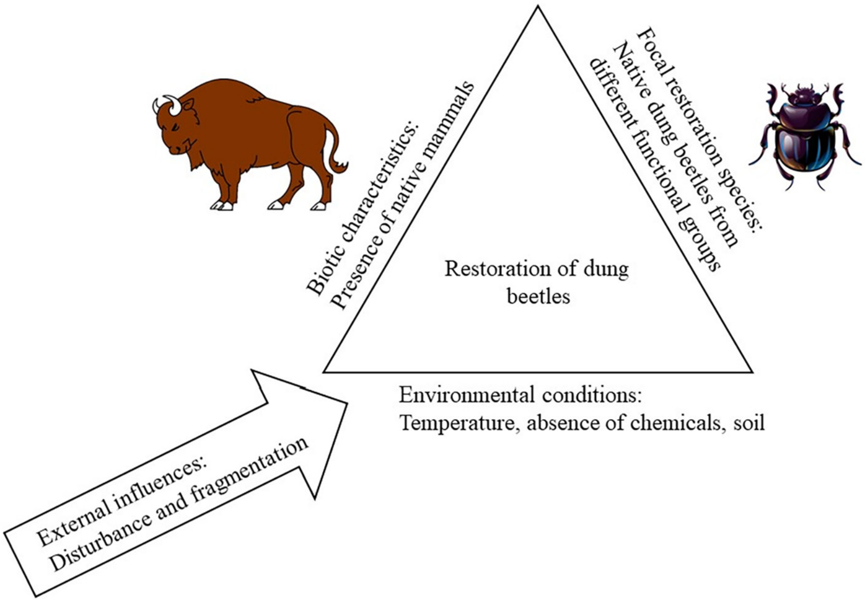

FIGURE 2 Restoration triangle with three principal factors involved in the restoration of dung beetles (adapted from Perkins & Leffler, 2018).

restoration, attention should be paid to mammals. Mammals, as the providers of dung, directly influence dung beetle abundance and indirectly benefit dung beetles by improving habitats and food sources for herbivores.

Re-establishment of native mammals is one effective approach to restoring native dung beetles. Mammal dung is the primary habitat for dung beetles, and native dung beetles prefer native mammal dung (Gigliotti et al., 2023). Without sufficient providers of this habitat, the abundance and richness of dung beetles will be low (Buse et al., 2021). Dung beetle species richness is positively correlated with mammal biomass (Culot et al., 2013), and high diversity of native mammals enhances the resilience of dung beetle–mammal networks (Chiew et al., 2022), leading to increased abundance, richness and diversity of dung beetles (Amézquita & Favila, 2010; Buse et al., 2021; Nependa et al., 2021). Additionally, the abundance of dung beetles may be related to native burrowing mammals (Lindtner et al., 2019) due to their effects on soil structure and interspecies facilitative or commensal relationships.

Dung beetles also utilize livestock dung. Dung beetles can benefit from a combination of game and cattle ranching (Tocco et al., 2020), cattle grazing (Verdú et al., 2007) and re-establishment of large native mammals like bison in grasslands (Barber et al., 2019). In such settings, the presence of both wild game (big herbivorous such as deer and bison) and domesticated cattle results in a diverse range of dung sources, providing dung beetles with a variety of food options. This diversity in dung types can support diverse dung beetle communities, contributing to the overall health of the ecosystem. However, it is important to consider the effect of anthropogenic chemicals that may be present in livestock dung (see discussion above). If the only dung available has levels of chemicals that negatively impact dung beetles, livestock dung could be an ecological trap (Manning et al., 2017) that hinders rather than helps restoration.

Restoration strategies such as revegetation enhance habitats and native dung beetle abundance (Gardner et al., 2008). Although the specific mechanisms by which native plants influence dung beetles are not well-documented, alterations in microclimates are one possible explanation (Gollan et al., 2011). Moreover, native plants associated with native mammals contribute to the functional diversity of dung beetles, potentially through the positive effects of native plants on the quality of mammal dung (Guerra Alonso et al., 2022).

Furthermore, reintroducing different functional groups of native dung beetles can mitigate the negative impacts of invasive dung beetles (Filho et al., 2018). Invasive dung beetles have adverse impacts on native dung beetle populations, including reduced diversity, decreased population size and occasional local extinctions (Génier & Davis, 2017). The invasive dung beetles have a competitive edge over native dung beetles with similar nesting behaviours and phenology. Consequently, these invasions have altered the proportion of different functional groups (Filho et al., 2018).

4.3 | Focal restoration of dung beetles

Dung beetles will either naturally recolonize or will need to be reintroduced to the restoration site. Natural recolonization depends on landscape context and fragmentation (discussed above; Collinge, 2000). Dung beetles can fly almost 16 km (Thomas, 2001) and therefore may naturally recolonize many areas. However, in isolated habitats assisted colonization can be considered (Rivera et al., 2021). Reintroduction can be accomplished either by relocating dung pats containing beetles after ensuring the quality of dung (with no pests, chemical contamination, or seeds of invasive species) or by releasing commercially available dung beetles. Commercially available dung beetles are intentionally bred and marketed for specific purposes. These beetles are obtained from diverse locations, where they are collected from their natural habitats and subsequently reared in captivity for commercial sale. Dung beetle breeding procedure entails housing the dung beetles within a spacious, enclosed container filled with soil, and providing them with an ample supply of manure until their population expands. Assisted recolonization has been undertaken to serve goals such as pest control in grazing systems (Hosler et al., 2021) although care must be taken to consider the physiological requirements of species (Giménez Gómez et al., 2020), investigate species distribution and genetic diversity, determine appropriate release timing and season and conduct post-monitoring (Pokhrel et al., 2021) especially given the potentially negative impacts of non-native dung beetles on native communities described above.

The goal of restoration is to produce a dung beetle community that is similar to that of a reference site. Therefore, both functional diversity and overall dung beetle abundance should be the focus of restoration efforts. Functional diversity improves population stability. High functional diversity can improve population stability, enhance resilience against disturbances (Nelson et al., 2021; Slade et al., 2011) and contribute to the diversity of ecosystem functions, ensuring long-term maintenance of ecosystem processes despite abiotic variation (Gagic et al., 2015). Therefore, postmonitoring and reintroduction measures of diversity and composition are necessary for long-term success.

Finally, in habitat restoration projects for other species (not specifically dung beetles), the recolonization or presence of dung beetles serves as an indicator of success (Gelviz-Gelvez et al., 2023). Dung beetles can be considered an indicator species that respond to habitat restoration and faunal recovery even within a relatively short monitoring period (Gelviz-Gelvez et al., 2023). For example, dung beetles have been examined in response to vegetation restoration (Díaz-García et al., 2022; Gelviz-Gelvez et al., 2023; González-Tokman et al., 2018). The premise of using dung beetles as indicators of successful restoration is that the habitat (vegetation) has been sufficiently restored to support fauna in enough abundance to attract dung beetles. Conversely, the same restoration that would benefit dung beetles should benefit other members of the ecosystem.

5 | EXTERNAL INFLUENCES

External influences are transient dynamics that are not inherent in a site but can impact restoration (Perkins et al., 2011). For dung beetle restoration, these external influences include disturbance and fragmentation. Prior to attempting restoration, it is essential to address stressors and mitigate severe and frequent disturbances impacting the dung beetle community (Barbero et al., 1999; Barnes et al., 2014). Disturbances occurring too frequently compared with historical patterns can decrease functional evenness and dispersion of dung beetles (Mouillot et al., 2013). For example, if fires occur too frequently due to human intervention or climate change, it can disrupt the dung beetle community (Blanche et al., 2001; Smith et al., 2019). Conversely, prolonged periods without disturbance or infrequent disturbances can also negatively affect beetle diversity and evenness, as well as the broader dung fauna (Hosler et al., 2021). For example, in a forest ecosystem, if logging activities cease entirely, it might initially seem beneficial for the ecosystem. However, without occasional disturbances that mimic natural events, the beetle community may become dominated by a few species that are particularly well-adapted to stable conditions. This can lead to reduced overall diversity and potentially disrupt the ecosystem's functioning (Edwards et al., 2017). Therefore, maintaining a balance between the frequency and intensity of disturbances is crucial for preserving the health and diversity of the dung beetle community.

Landscape fragmentation poses a threat to dung beetles and may limit their ability to naturally recolonize a site (Rivera et al., 2022). Creating and restoring corridors between isolated patches (Williams & Snyder, 2005) and establishing buffer zones (420–970 m wide; Deere et al., 2022) are effective strategies to mitigate fragmentation impacts. Corridors facilitate movement through otherwise unsuitable habitat (Christie & Knowles, 2015). Corridors also promote large-scale metapopulations, sustaining gene flow amid rapid environmental changes (Samways et al., 2020). Although corridors improve habitat connectivity, this connectivity may be less critical for dung beetles that can disperse considerable distance than less mobile species. Dung beetles are able to disperse up to 16 km (Thomas, 2001), so corridors can be envisioned as diffuse patches of suitable habitat between existing populations and the restoration area. Corridors might be especially useful in areas impacted or separated by urbanization (Salomão et al., 2019).

6 | CONCLUSION

In this review, we illustrated the importance of dung beetles in ecosystem services, discussed threats to dung beetles and elucidated a restoration framework. Dung beetles are associated with different ecosystem functions that provide vital services and goods for humans, animals and plants. The decomposition process is the primary service dung beetles provide. This service not only clears pastures from dung but also enhances nutrient cycling. Improved nutrient cycling boosts ecosystem productivity which is beneficial for humans. Human activities and ecosystem changes have affected the dung beetle community. Increasing usage of chemicals, climate change and land-use change negatively affect dung beetles and related ecosystem functions, so it is essential to find ways to solve the problem. The conservation and preservation of endemic dung beetle species and native habitats are required to maintain ecosystem functions. Note that conservation can protect populations and communities of dung beetles against land-use change and climate change leading to more sustainable human activities, when conservation is not sufficient restoration is required. To ensure effective restoration practices, we must carefully consider environmental conditions, biotic characteristics and focal restoration and focus on precise restoration methods.

AUTHOR CONTRIBUTIONS

Shiva Torabian conceived, designed, wrote and reviewed the papers; Shiva Torabian, A. Joshua Leffler and Lora Perkins reviewed the manuscript; Shiva Torabian, A. Joshua Leffler and Lora Perkins edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest associated with this manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The authors confirm that this review article does not involve the collection, generation or analysis of original data. The information presented herein is based on a comprehensive review of existing literature, previously published studies and publicly available information.

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