The Effects of
Dung Beetles
on Ecosystem Functioning:
From Global Trends to New Zealand Pastures

A thesis

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This thesis is dedicated to my little bug, Shevonne

ABSTRACT

Dung beetles are amazing. Their diverse nesting behaviours affect a suite of important biotic and abiotic ecosystem processes, or functions. However, the dynamics of these functions across different ecosystems and over time remain largely unknown. This PhD thesis investigates the relationships between dung beetles and ecosystem functions, from global-scale trends to the introduced dung beetle communities in pastures of Aotearoa New Zealand. In the first chapter, I provide an overview of the research topic. I go on to describe ecosystem functioning, and in particular the biotic drivers that shape these processes which ultimately lead to ecosystem multifunctionality and the delivery of ecosystem services that benefit humans. I then emphasise the natural history of dung beetles as a springboard to posit whether we can use dung beetles to enhance ecosystem functioning in human modified landscapes, such as agricultural livestock pastures.

The ecosystem functions and services delivered by dung beetles are wide-ranging, including dung removal, nutrient cycling, plant growth enhancement, bioturbation, secondary seed dispersal and trophic regulation. In a meta-analysis of the relationships between dung beetles and ecosystem functions and services (chapter two), I reveal significant positive relationships between dung beetle presence on all measured ecosystem functions, with mixed nesting behaviours showing greater enhancement of ecosystem functioning. Additionally, the findings highlight the significant gaps in our understanding of the mechanisms by which dung beetles contribute to ecosystem functioning, particularly in relation to primary productivity and trophic regulation. Next, in a comparative analysis of dung beetle community characteristics (chapter three) I examine the potential of community structure, community-weighted functional traits, and metabolic rates in predicting dung removal. My findings show that the use of a nesting behaviour index serves as a reliable functional trait for predicting dung removal.

In a mesocosm experiment (chapter four), I attempt to disentangle the mechanisms through which dung beetle temporal diversity drives direct and indirect changes in ecosystem multifunctionality. By comparing methods including individual ecosystem functions, ecosystem multifunctionality metrics, and structural equation modelling, I demonstrate that a causal inference approach best describes ecosystem multifunctionality. In the concluding chapter (chapter five), I synthesise the overarching significance of the findings obtained in the preceding chapters and examine the potential of dung beetles as a nature-based solution in agricultural

landscapes. I propose that the introduction of dung beetles can be viewed as a means of ecological intensification, offering potential advantages for multitrophic diversification. Overall, the findings of this thesis have positive implications for nature-based management, offering promising prospects for fostering self-sustaining agroecosystems that can benefit future generations.

Format of chapters

The thesis comprises five chapters, the middle three of which are data chapters.

Chapter one:	Introduction
Chapter two:	Ecosystem functions and services provided by dung beetles: a global meta-analysis.
Chapter three:	Comparing community structure, functional traits, and metabolic rates of dung beetles as predictors of ecosystem functioning.
Chapter four:	Dung beetles enhance direct and indirect changes in ecosystem multifunctionality.
Chapter five:	Synthesis

The research presented here is my own work, and was done under the direction of my supervising committee, which included Dr. Andrew Barnes, Dr. Kiri Joy Wallace, Professor Louis Schipper, and Dr. Simon Fowler. The presentation of references immediately after each chapter in this PhD thesis deviates from the traditional format of having a bibliography and appendices at the end of the entire thesis. This arrangement was chosen to align with the specific requirements of journal publications, as the chapters have been prepared as standalone research papers. Therefore, these individual chapters have been adapted and consolidated into the thesis format such that they are easily adaptable for publication.. None of the chapters included in this thesis have been submitted to any journal at the present time.

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Chapter One. INTRODUCTION

1.1 Research Topic

This thesis delves into the ecological world of dung beetles and their effects on ecosystems, from evaluating global trends to characterising the functions delivered by introduced species in Aotearoa New Zealand (Aotearoa NZ). The literature on dung beetle-mediated ecosystem processes is rich and varied, from the pristine and biodiverse primary tropical rainforests of Borneo (Davis & Scholtz, 2001) to the humble livestock paddocks of Wales (Beynon et al., 2012a). Despite these differences in ecosystems, there is consensus that dung beetles have an overall positive contribution to a broad range of ecosystem functions and services (Nichols et al., 2008). Therefore, establishing the extent and specific mechanisms through which dung beetles impact ecosystems is beneficial, as this can advance our understanding of natural systems and guide land management strategies that promote the provisioning and stability of multiple functions in ecosystems (Noriega et al., 2021).

The emergence of the term 'function' in functional ecology can be traced back to Calow (1987), which not only underscored the significance of ecological processes over properties, but also highlighted the pivotal role of species adaptation, or traits, in the study of ecosystems. As a result, functional ecology came to focus on the functions performed by species and the interactions between them, rather than simply describing their properties or characteristics of ecosystems. Functional traits are adaptations found among species and individuals (Díaz et al., 2013; Violle et al., 2007) and the range of functional traits within a community, also known as functional diversity, can significantly impact community structure and ecosystem functioning (Laureto et al., 2015). While a large body of evidence has demonstrated that greater levels of biodiversity in naturally-assembled communities positively drives various ecosystem functions (Tilman et al., 2014; van der Plas, 2019), research from the past 25 years of investigating the physiological mechanisms that determine an organism's function within an ecosystem, has shown that the relationship between biodiversity and ecosystem functioning is more complex (Eisenhauer et al., 2019; Hooper et al., 2005).

Land-use alterations and changes in the composition of the atmosphere on a planetary scale have defined a new epoch in geological time known as the Anthropocene (Lewis & Maslin, 2015). Conversion of native forest habitats into pastures have resulted in changes to vegetation and soil, impacting soil carbon and nutrient cycles, leading to increased atmospheric carbon dioxide, altered soil physical properties, and reduced biodiversity (Smith et al., 2016). This ongoing decline of natural systems has raised concerns and an urgent interest in determining how naturally-assembled communities facilitate and maintain ecosystem functions (Bengtsson et al., 2000), as well as how best to replicate species and community attributes that promote ecosystem functioning in human-modified landscapes, such as pastures, to ensure sustainable ecosystems (Evans 2016).

Nature-based solutions refer to practices that use natural processes in ecosystems to address various societal challenges, such as climate change, biodiversity loss, water scarcity, and urbanisation (Girardin et al., 2021; Seddon, 2022; Seddon et al., 2020). These solutions seek to enhance the capacity of ecosystems to provide essential services, such as carbon sequestration, water purification, soil fertility, and natural hazard mitigation (Babí Almenar et al., 2021; Keesstra et al., 2018). Examples of nature-based solutions include reforestation and afforestation, wetland restoration, green infrastructure, sustainable agriculture, and conservation of biodiversity and ecosystem services. These solutions may offer a more sustainable and cost-effective approach to addressing societal challenges, compared to traditional methods that rely solely on human engineered solutions (Seddon et al., 2020). For example, rather than relying on synthetic fertilisers to boost the nutrient content of pasture, such as phosphorus, natural approaches like using organic compost (Bonanomi et al., 2016), companion planting (Reddy, 2017) or introducing potentially beneficial insects like dung beetles (Hughes et al., 1975) can be considered.

Dung beetles deliver ecosystem functions through physically removing dung from the above-ground environment and depositing it belowground, thus enhancing dung decomposition (Slade et al., 2007). This facilitates the regulation of carbon and methane fluxes (Penttilä et al., 2013), nutrient cycling (Evans et al., 2019), plant growth (Barragán et al., 2022) and enhanced foliar nutrient content (Santos-Heredia et al., 2016). Moreover, differences in the provision of these functions may be attributed to various community level to individual level factors, including dung beetle abundance or richness, morphological (e.g., body size), as well as behavioral traits (e.g., nesting behaviour) (deCastro-Arrazola et al., 2022). Understanding how these factors influence ecosystem functioning may enhance our ability to predict how ecosystems will respond to environmental changes, allowing us to make management decisions that promote dung beetles and their ecosystem functions.

The capacity for dung beetles to provide crucial ecosystem functions and services has made them ideal for introduction into human-modified environments, such as pastures in Australia (Hughes et al., 1975), the USA (Fincher et al., 1983) and Aotearoa NZ (Dymock, 1993; Forgie et al., 2018). However, engineering dung beetle communities to optimise continued delivery of key ecosystem functions, such as dung removal and its cascading processes, throughout all seasons can be challenging. In temperate Australia, the lack of introduced dung beetle species which are active during late winter and early spring has been shown to result in a reduction of up to 25% in ecosystem functions, such as dung removal, and prompted initiatives to address this issue and bridge the seasonal shortfall, commonly known as the "spring gap"(Wright et al., 2015). Furthermore, community structure, morphological traits and behavioural traits are continually responding to environmental conditions, such as warming, which can affect consistent desirable delivery of ecosystem functioning (Holley & Andrew, 2020).

Therefore, it is essential to quantitatively synthesise our current understanding of dung beetle effects on ecosystem functions. By doing so, we can pinpoint the ecosystem processes that occur in relation to dung beetle activity and uncover the functional characteristics that are linked to communities and individual species (deCastro-Arrazola et al., 2022). This knowledge will enable us to forecast rates of ecosystem functioning in diverse scenarios, including novel environments such as pastures in Aotearoa NZ. When combined with ongoing monitoring of population and community dynamics of introduced species in specific settings, this predictive knowledge can facilitate effective management strategies for promoting sustainable and functioning ecosystems for generations to come.

1.2 The biotic drivers of ecosystem functioning

Ecosystem functions refer to the variety of biotic and abiotic processes that occur within an ecosystem, serving as the fundamental basis for ecosystem services (Reiss et al. 2009). From the functioning of marine ecosystems where small phytoplankton, as primary producers, regulate trophic interactions and contribute to biogeochemical cycles (Priyanka et al., 2021), to the much larger Asian elephant's ability to disperse the seeds of up to 48 morphospecies of dipterocarp, thereby sustaining rainforest diversity (Tan et al., 2021), numerous examples demonstrate the essential roles of various organisms in ecosystem functioning. In addition to this, there are still threatened ecosystems that we have limited knowledge of, such as ecosystem functioning in the soils of Antarctica (Wall, 2005). It is therefore important to ensure we understand ecosystem functioning and the key drivers that influence the magnitude and direction of functioning because ecosystems are inherently valuable and provide key processes that contribute to human health and ecosystem services (Brauman et al., 2020). In doing so, humans can work with nature, as part of nature, to ensure the continued functioning of these ecosystems (Seddon, 2022).

Biotic drivers are forces originating from living organisms, which can help us to better understand ecosystem functioning. These drivers include biodiversity, which is defined as the variety of species within an ecosystem (Harper & Hawksworth, 1994), as well as species traits, which are any morphological, physiological or phenological feature measurable at the individual level that can have unique and critical roles in regulating ecosystem functioning (Violle et al., 2007). Hence, understanding the complex interplay between biotic drivers is essential for determining the mechanisms underlying ecosystem functioning (Reiss et al., 2009).

Biodiversity is the variety of life, ranging from molecular genetic diversity, through to whole-organism diversity, and ecosystem diversity (Wilson & Peter, 1988). This variety is essential for maintaining ecosystem functioning, but it is threatened by human activities such as ecosystem destruction, pollution, and climate change, all which drive species loss (Malhi et al., 2020). Biodiversity has been a key focus of the development of our understanding of ecosystem functioning, so much so that it has developed into its own sub-field known as biodiversity-ecosystem functioning (B-EF)(Loreau et al., 2001). For a long time, high levels of biodiversity were considered the key driver in regulating ecosystem functioning, which led to the prioritisation of the preservation, conservation, and restoration of "biodiversity hotspots" which are areas with a high concentration of unique species that are at risk of habitat loss (Myers et al. 2000) and areas with irreplaceable and vulnerable biodiversity (Brooks et al. 2006). While these hotspots contain a large proportion of the world's species, they only occupy a small percentage of the Earth's land surface (Reid 1998), which is concerning for the remaining protection of earth's ecosystems and ecosystem functions.

Research has shown that biodiversity plays a role in driving ecosystem function, with high-diversity mixtures of plants exhibiting approximately twice the productivity of monocultures of the same species (Tilman et al. 2014). Furthermore, positive effects of biodiversity have been found to persist under various types of global environmental change drivers, consistent across taxonomic groups including microbes, phytoplankton, and plants (Hong et al. 2022). As the list of the benefits of biodiversity to ecosystem function goes on, many questions remain unanswered. For example, in a meta-analysis of experimental work spanning 50 years, Balvanera et al., (2006) demonstrated that biodiversity had a positive effect on ecosystem functions and most ecosystem services. However, the effects of biodiversity change on processes were weaker at the ecosystem level compared with the community level and were negative at the population level. Increasing diversity shows a positive relationship with individual ecosystem processes (Hector & Bagchi, 2007) however, this relationship has been shown to be highly variable across studies (Wardle et al., 1997). Considering biodiversity solely from a species perspective may be an oversimplified and possibly inaccurate perspective as it assumes all species to be equal in their contribution to ecosystem functioning (Giller & O'donovan, 2002). Therefore, it could be that biodiversity is not the most critical determinant of a functioning ecosystem (which is not to say it is not important), instead, specific biological and ecological traits of species that play a role in the functioning might be more helpful for understanding the complexities of ecosystem functioning (Díaz et al., 2013; Grime, 1997).

A functional trait is any measurable attribute of an individual organism, such as its morphological, biochemical, physiological, structural, phenological, life history, or behavioral characteristic, that can be compared across different species (Díaz et al., 2013). Functional traits are important because they are at the intersection of an organism's response to the environment and its effect on ecosystem properties, which make them excellent tools to predict ecosystem functioning (Nock et al., 2016). The significance of an animal's body size in shaping its biology and ecology is widely recognized, and body size is often quantified as a functional trait (Reiss et al., 2009). Other morphometric traits, such as the size of certain body parts, can be used to predict an organism's functional role within an ecosystem. A study by Pigot et al., (2020) examined nine morphological traits in birds, including body mass, beak length, primary feather length, and avian trophic diversity. They showed that these traits can be accurately described using a four-dimensional trait space, mapping species positions (with 70 - 85% accuracy) to major niche axes, including trophic level, dietary resource type, and fine-scale variation in foraging behaviour. This work highlighted that morphological traits can be useful in predicting ecological functions delivered by organisms.

However, despite ongoing research, there are still gaps in our understanding of the effects of morphological traits and their effects on movement and behaviour. For example, insect body size may have substantial influence on the dynamics and consequences of species interactions and trophic regulation (Kalinkat et al., 2015). Although functional trait studies of beetles and other arthropods present several benefits, they also come with certain conceptual and practical hurdles, including a limited understanding of trait-function relationships, blurred boundaries between traits, potential misidentification of species, and insufficient knowledge of natural history (Fountain-Jones et al., 2015). Furthermore, trait-based approaches vary across species, for example, eusocial taxa like ants and termites require consideration of the potential effects of different traits at both the individual and colony level (Ohyama et al., 2023). While phylogenetic diversity has been suggested as a predictor of functional traits (Srivastava et al., 2012) there are challenges faced in predicting functional similarity solely based on phylogenetic relatedness, as convergent evolution can result in similar traits even among distantly related species (Winemiller et al., 2015).

Metabolism is another trait that could be a strong predictor of ecosystem functioning. Brandl et al., (2022) proposes that metabolic traits, such as resting metabolic rate (RMR), maximum metabolic rate (MMR), and aerobic scope (AS), can be used to better understand the energetic basis of species coexistence and the assembly, and functioning of animal communities. The authors discuss that these traits integrate across various typical trait proxies for energy acquisition and allocation in animals, yielding a smaller suite of continuous quantities that can be precisely measured for individuals in a standardised fashion and applied to all animals regardless of their body plan, habitat, or taxonomic affiliation. While the metabolic theory of ecology established a theoretical framework for the field of ecology by leveraging fundamental principles of biology, physics, and chemistry (Brown et al., 2004) the integration of metabolic traits as a means to explain variation in ecosystem functioning is a relatively novel approach. While there has been significant research on the relationship between biodiversity and ecosystem processes, the explicit incorporation of metabolic traits (such as RMR, MMR, and AS) to elucidate the energetic basis of species' coexistence and community assembly is not commonly used. In comparison to trophic and life history trait dimensions, Gonçalves-Souza et al. (2023) show that the frequency of studies employing metabolic traits to predict ecosystem functioning is very low. Therefore, the proposal made by Brandl et al. (2022) represents an innovative and potentially valuable avenue for understanding the mechanisms underlying community assembly and ecosystem functioning.

In addition to morphological traits and metabolic rates, animal behaviour can also influence ecosystem functioning, such as shaping the distribution and abundance of organisms, altering resource availability and nutrient cycling dynamics, and modifying energy flow within food webs (Davies et al., 2012). Furthermore, behaviour is responsive to environmental changes, such as temperature changes, and can be a key driver of ecosystem responses to warming. For example, warming temperatures can disrupt ecological interactions, causing mismatches between plants and pollinators, impacting plant reproduction and pollinator populations, altering predator-prey dynamics, and affecting species interactions, such as the expansion of the mountain pine beetle's range and its impact on the white bark pine, a crucial food source for grizzly bears (Traill et al., 2010). Hence, taking behaviour into consideration enables a comprehensive assessment of ecosystem functioning, facilitating better management and conservation under global change scenarios.

Selecting the specific traits that can effectively predict ecosystem functioning has been challenging (Mlambo, 2014). While species-based evaluation relies on taxonomic identification to assess the effects on ecosystem processes, the assessment of functional traits requires a broader understanding of species biology, considering specific traits, and their relationship to ecosystem functioning. Therefore, it is important to recognise which specific functional traits contribute to the desired functions in order to accurately predict ecosystem functioning. By further developing our understanding of organisms' functional traits, we can uncover novel and invaluable information that goes beyond the scope of species-based studies (Dawson et al., 2021).

1.3 Ecosystem multifunctionality and the provisioning of multiple ecosystem services

Focusing solely on individual ecosystem functions may limit our understanding of the complex interactions, synergistic effects, trade-offs, and dynamic nature of ecosystems (Evans et al., 2012). The limitations of focusing on individual ecosystem functions prompted the development of the concept of ecosystem multifunctionality (EMF) which is defined as the simultaneous provisioning of multiple ecosystem functions (Garland et al., 2021). The simultaneous measurement of multiple individual functions within an ecosystem can assist in ecosystem monitoring, understanding ecosystem responses to environmental changes, identifying potential trade-offs or synergies among functions, and informing conservation and management strategies for the sustainable provision of ecosystem services (Byrnes et al., 2014). Examining EMF may enable us to get a comprehensive perspective on the overall functioning of the ecosystem (Manning, Van Der Plas, et al., 2018), however, there are varying opinions on the most suitable approach to quantifying EMF, and no consensus has been reached on the preferred method. Multiple metrics have been developed to quantify EMF, where individual ecosystem functions are measured and then converted into a standardised unit scale (Garland et al., 2021). One example of an EMF metric is the averaging approach, which calculates an average score across each measured ecosystem function. Another example is the single threshold approach, which involves the calculation of the number of functions that are delivered above a predefined threshold percentage (Byrnes et al., 2014; Gamfeldt et al., 2008; Oliver et al., 2015). The Hill numbers approach metric, meanwhile, calculates a diversity index that incorporates both the number of functions or services that an ecosystem performs and the relative abundance of each function (Byrnes et al., 2021). Overall, EMF metrics condense multiple dimensions of ecosystem functioning into a single value, which can oversimplify the complex processes that take place in an ecosystem (Hines, 2019). In addition to this, EMF metrics do not allow for a direct comparison between results because they aggregate and condense multiple dimensions of ecosystem functioning into a single value (Hines, 2019). This aggregation can result in the loss of specific details and nuances of individual functions, making it challenging to make meaningful comparisons between different studies or ecosystems (Giling et al., 2019). The choice of EMF metrics and the weighting assigned to different functions can vary between studies, further complicating direct comparisons. Therefore, while EMF metrics provide a useful tool for assessing overall ecosystem functioning, they have limitations in facilitating direct comparisons between results.

Manning et al. (2018) propose a framework for the development of multifunctionality measures that are relevant to both fundamental ecological science and ecosystem management. They suggest that the multifunctionality concept needs to be redefined as a property that exists at two levels: ecosystem function multifunctionality (EF-multifunctionality) and ecosystem service multifunctionality (ES-multifunctionality). For example, EF-multifunctionality is the array of biological, geochemical, and physical processes that occur within an ecosystem. These processes include nutrient cycling, water purification, climate regulation, and pollination, the foundations for ecosystem service provision. ES-multifunctionality encompasses the simultaneous provision of multiple ecosystem functions in relation to human demand, including benefits like food, water, and recreation derived from ecosystems. The quantification of ES-multifunctionality for human needs further require upscaling ecosystem functions, considering stakeholder perspectives, and accounting for supply-benefit relationships. While this comprehensive approach is pivotal in establishing appropriate weightings for measures of ES-multifunctionality, this can still be subjective and lacking standardisation.

Another approach for investigating ecosystem multifunctionality is the framework proposed by Giling et al., (2019) who emphasise *a priori* identification and explicit testing of the biotic and abiotic mechanisms that lead to EMF through structural equation modelling (SEM). SEM is a causal inference method that can disentangle the individual functions that contribute to overall ecosystem multifunctionality, thus providing a systems-based overview of the ecosystem (Grace, 2006). Using SEM in EMF research can enhance our understanding of causal relationships among multiple variables, improving predictive power and enabling a deeper understanding of how individual ecosystem functions influence ecosystem multifunctionality. Furthermore, SEM may help to enhance our understanding of complex ecological interactions by the identification of the key drivers and pathways affecting EMF, surpassing the capabilities of EMF metrics, and better informing effective management of conservation and restoration initiatives by identifying crucial factors necessary for maintaining or enhancing EMF.

Ecosystem multifunctionality can be a valuable concept for comprehending and managing ecosystems as it emphasizes the interconnectedness of various functions. The development of precise, comparable, and easily-measurable indicators of ecosystem function can be challenging, but it holds great potential for gaining valuable insights into the factors influencing ecosystem functioning and for identifying essential trade-offs and synergies among ecosystem functions. Furthermore, taking alternative quantitative approaches like SEM may enhance our understanding of the underlying mechanisms and interactions that support ecosystem services (Brauman, 2010; Mace et al., 2012).

1.4 The natural history of dung beetles and their ecological significance

As one of the most prosperous and widespread animal groups on Earth, the beetles (Coleoptera) can be found in nearly every type of terrestrial ecosystem (Crowson, 1981). Beetles are commonly holometabolous (Crowson, 1981) where individuals emerge from eggs as larvae, develop through several instars, pupate, and eventually emerge as adults (Figure 1.1; McGavin, 2001). Dung beetles are not confined to a single taxonomic group, and dung-feeding behaviour can be found in the Geotrupidae and Scarabaeidae families, as well as the Scarabaeinae and Aphodiinae subfamilies, suggesting that the use of dung as a resource did not originate from a single evolutionary event (Arillo & Ortuño, 2008). The subfamily commonly referred to as the "true dung beetles" sits within this hyper-diverse group (Coleoptera: Scarabaeidae, Scarabaeinae) and current records estimate that there are 6200 species across 267 genera with up to 50 % of species that remain undescribed (Tarasov & Génier, 2015). Interestingly, the geological history of Aotearoa NZ has led to depauperate insect assemblages (Foottit & Adler, 2009) with only one family of dung beetles, the ancient flightless Canthonini (Sole & Scholtz, 2010) represented by ~ 16 species from two genera (*Saphobius* and *Saphobiamorpha*). This unique dung beetle fauna is adapted to feeding on the dung of flightless birds and reptiles, which has been shown to create a trophic link between marine and terrestrial systems (Stavert et al. 2014), and they can be captured using rotting squid-baited pitfall trapping. As a result of their evolutionary and ecological significance, dung beetles have emerged as a highly esteemed model taxon, and Tarasov & Génier (2015) found that they hold the distinction of being the second most referenced subfamily of beetles on Google Scholar.

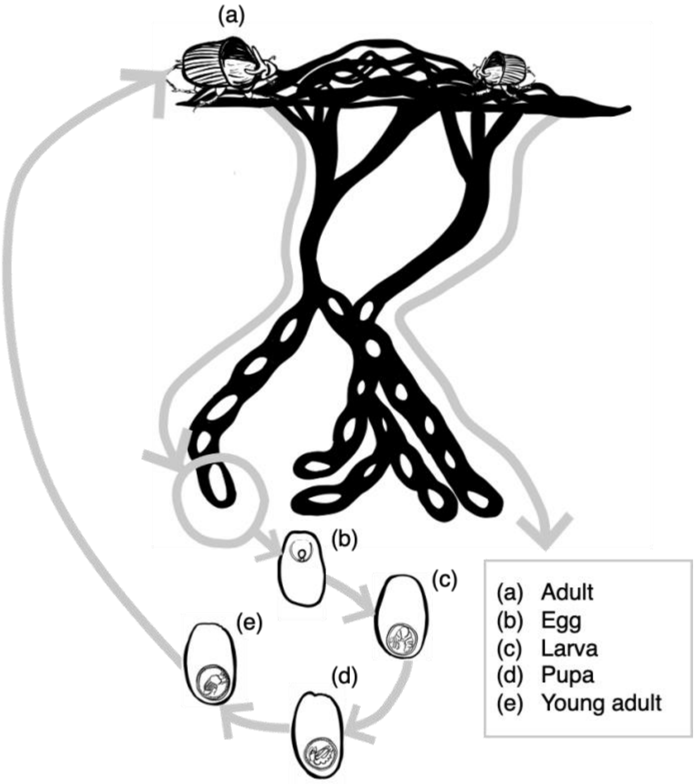

Figure 1.1 The life cycle of *Onthophagus* spp. dung beetles, a paracoprid (nesting tunneller). The completed nest is located below-ground, containing brood masses in the soil directly beneath the dung pad. The figure illustrates the various stages of the life cycle, including (a) adult, (b) egg, (c) larva, (d) pupa, and (e) young adult on the verge of emerging. The young adult breaks out of the brood mass and excavates its way through the soil.

While the phylogeny of dung beetles remains largely uncertain, recent studies suggest that dung beetles may have originated during the time of the dinosaurs in the Mesozoic era (Tarasov & Génier, 2015). According to molecular evidence by Gunter et al. (2016) dung beetles likely emerged during the middle of the Cretaceous period and may have coevolved with dinosaur dung. This timing also coincides with the emergence of angiosperms, which may have indirectly facilitated the proliferation of dung beetles due to their increased palatability to mammalian herbivores (Benton et al., 2022). This evolution of dung beetle coprophagy has led to the radiation of a variety of nesting behaviours as a result of niche partitioning of dung as a valuable resource (Arillo & Ortuño, 2008). Nesting behaviour can be categorised into non-nesters, telecoprids, paracoprids, and endocoprids (Tonelli, 2021). These groups are regarded as functional traits due to their distinct dung relocation strategies, which greatly influence the level of ecosystem function. For thousands of years, human civilizations have held an enduring recognition and deep appreciation for the myriad benefits arising from the behaviours exhibited by dung beetles. The life history of dung beetles was once seen as a manifestation of divine intervention, with the Egyptian scarab beetle, *Scarabaeus sacer*, as the only insect species known to be raised to the level of a deity (Cherry & Kritsky, 1985). In ancient Egyptian mythology, the god Khepri was associated with the telecoprid nesting behaviour and was believed to push the sun across the sky in the same way that *S. sacer* rolls its ball of dung away and buries it (Kenawy & Abdel-Hamid, 2015). As a result, the scarab beetle symbolised rebirth and resurrection, both critical elements of ecological energy transfer.

Dung beetles' use of dung through the variety of nesting behaviours contributes to ecological energy transfer (Hanski & Cambefort, 1991), delivering several key ecosystem functions and processes (Nichols et al., 2008). For example, they contribute to decomposition and nutrient cycling by consuming dung which in turn facilitates the return of organic matter and essential nutrients to the soil (Aarons et al., 2009). Their burrowing activities enhance soil structure and water infiltration (Brown et al., 2010; Keller et al., 2022), and some species of dung beetles assist in seed dispersal and seedling survival by transporting seeds found within the dung (Almeida et al., 2022; Braga et al., 2017; Griffiths et al., 2016). Dung beetles also facilitate the supply key ecosystem services, such as parasite control by reducing populations through dung removal and dispersal (Sands & Wall, 2017), and reduced greenhouse gas emissions (Slade et al., 2016). Overall, dung beetles have the capacity to deliver multiple simultaneously occurring ecosystem functions that benefit nutrient cycling, pest control, soil health, and seed dispersal, influencing ecosystem dynamics and resilience.

1.5 Using dung beetles to enhance ecosystem functioning and services

Unprocessed livestock manure on the pasture surface has led to the pollution of both land and water in Aotearoa NZ (Collins et al., 2007). Much like the highly specialised dung beetles that use marsupial dung as a resource in Australia, the 16 species of endemic Aotearoa NZ dung beetle do not have generalist feeding habits, and there are no records of their attraction to herbivorous mammal dung in Aotearoa NZ livestock pastures as a resource to provision their offspring. The by-and-large absence of dung-associated species such as dung beetles, has culminated in environmental degradation at the above-belowground interface in pasture systems, causing decreases in vegetation growth and severe degradation of freshwater ecosystems due to eutrophication (Julian et al., 2017).

This year (2023) marks 30 years since the initial proposal to introduce dung beetles to Aotearoa NZ pastures in an effort to mitigate the effects of dung pollution (Dymock, 1993; Forgie et al., 2018). One of the significant challenges faced by this dung beetle introduction program is related to socio-political factors, particularly the concerns and attitudes surrounding the introduction of new species into Aotearoa NZ (ERMA, 2011). Given the historical challenges associated with managing introduced species in the country, there is a notable societal apprehension towards introducing non-native species intended for benefit that may later become invasive (Norton, 2009). Examples of non-native species that are currently being targeted for eradication in an effort to restore native ecosystems include rabbits, possums, rats, and heather, and a *Phytophthora* species causing death of the native kauri tree (*Agathis australis*), an iconic tree that is sacred in Māori (indigenous peoples) culture (Bradshaw et al., 2020). In light of impacts from these non-native species introductions, introducing non-native dung beetles is sometimes viewed as a potential threat to Aotearoa NZ's native biodiversity.

Nature-based solutions are often an effective approach to improve ecosystem functioning to tackle human-induced environmental challenges (Seddon, 2022a). This approach is fundamentally based on adapting mechanisms from natural systems to overcome environmental challenges and to facilitate a sustainable and regenerative suite of simultaneously-occurring functions to improve long-term ecosystem service delivery (Grelet & Lang sam, 2021; Keesstra et al., 2018). Given the significant evidence supporting the advantages of enhanced ecosystem services through dung burial in pasture systems, the potential negative outcomes of not introducing dung beetles to Aotearoa NZ were deemed more severe. Consequently, in 2011, eleven species of dung beetles were introduced to Aotearoa NZ (ERMA 2011). Although the outcomes of dung beetle release programs in various countries, such as Australia, have so far demonstrated favourable results in terms of ecosystem service provision (Doube, 2018), significant knowledge gaps remain in our understanding of how dung beetles introduced to agricultural systems influence the ecosystem services of those systems.

1.6 Thesis objectives

In this thesis, I aim to: (1) enhance collective knowledge of the effects of dung beetles on ecosystem functioning on a global scale; (2) determine how biotic drivers, such as dung beetle community structure and functional traits can predict ecosystem functioning; and (3) quantify the temporal direct and indirect effects of introduced dung beetles on ecological functions that occur simultaneously and contribute to ecosystem multifunctionality. In doing so, my thesis integrates analyses from the global scale to the local level, across multiple spatial and biological scales ranging from individual traits to ecosystem functions and services (Figure 1.2).

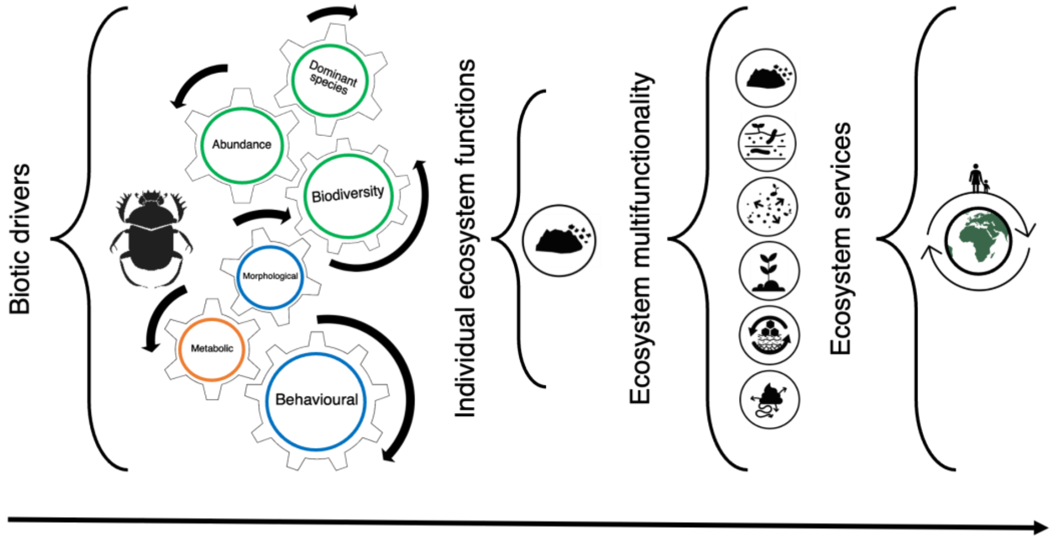

Figure 1.2 Overview of the main concepts of the thesis, where I will investigate dung beetle effects on ecosystem functions and services, with a particular focus on the biotic drivers of single ecosystem functions (e.g. dung removal) and their relationship with ecosystem multifunctionality and the provisioning of multiple ecosystem services.

In the following chapters, I synthesise current evidence of the global patterns of dung beetle-mediated ecosystem functioning. I then test the effects of community traits and propose the use of quantifying community energy use to expand the arsenal of dung beetle functional traits as predictors of ecosystem functioning; and finally, I attempt to disentangle the direct and indirect cascading consequences of dung removal using causal inference methods. This thesis contributes to the growing body of research investigating dung beetles and ecosystem functioning by using quantitative models to understand how dung beetles effect ecosystem functioning, ranging from all published evidence to the analysis of traits within communities and finally in a controlled experimental mesocosm setting. Chapter one establishes the context and outlines the scope of the thesis. Chapter two offers a comprehensive summary of the existing research on the global significance of dung beetles in promoting ecosystem functioning, using a meta-analytic approach. Chapter three examines and compares community weighted traits and investigates whether community energy use can be considered a reliable functional trait for predicting dung removal. Chapter four evaluates techniques for measuring the effect of dung beetles and their subsequent direct and indirect effects on ecosystem multifunctionality, using dung beetles as a model system.

1.7 Thesis overview

In chapter one I provide an introduction and background of my thesis. In chapter two, I investigate the ecosystem functions and services provided by dung beetles using a global meta-analysis. I attempt to answer the questions: do dung beetles have an overall positive effect on ecosystem functioning and does paracoprid (tunnelling) behaviour show the greatest rates of ecosystem functioning? Is there greater ecosystem function by dung beetles depending on ecosystem type? For example, tropical versus temperate latitudes, intact versus wild landscapes, and a range of habitats ranging from forest to agriculture? And finally, are there methodological differences in dung beetle-mediated ecosystem functioning, for example, between native versus introduced dung beetles, laboratory versus field studies, and observational versus experimental studies?

I then go on to chapter three, comparing community structure, functional traits, and metabolic rates of dung beetles as predictors of ecosystem functioning. The key research questions I am interested in here are: what is the role of community structure in shaping dung removal in introduced communities? How do functional traits of introduced dung beetles affect dung removal? And can dung beetle community energy use predict their resource use and therefore determine ecosystem functioning?

In chapter four I investigate whether dung beetles enhance direct and indirect changes in ecosystem multifunctionality. Specifically, how do introduced dung beetles improve individual ecosystem functions, such as dung removal, associated physicochemical soil processes, and pasture growth? Will the enhancement of individual functions lead to overall increases in ecosystem multifunctionality metric values? And can the use of structural equation modelling help provide a mechanistic understanding of dung beetle mediated ecosystem multifunctionality, specifically the flow-on effects of dung removal on interconnected soil processes and pasture biomass production? Finally, in chapter five, I present a synthesis of learnings from all thesis chapters and discuss whether non-native dung beetles a suitable nature-based solution for Aotearoa NZ.

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Chapter Two. ECOSYSTEM FUNCTIONS AND SERVICES PROVIDED BY DUNG BEETLES: A GLOBAL META-ANALYSIS

Abstract

Dung beetles are known to carry out a range of ecosystem functions such as secondary seed dispersal, bioturbation, nutrient cycling, plant growth, pest and parasite control, and trophic regulation, many of which support key ecosystem services. Despite the globally purported significance of this group of insects for ecosystem functioning, there has been no quantitative synthesis to establish the extent of dung beetle effects on ecosystem functions at global, regional, and habitat scales. To address this knowledge gap, I conducted a meta-analysis using 455 effect sizes collected from 66 published studies. The analyses evaluated the overall effects of dung beetles on 24 ecosystem functions, with additional subgroup analyses investigating (i) variation in dung beetle nesting behaviour, (ii) ecosystem type, and (iii) study methodology. Trophic regulation was found to be the ecosystem function most strongly enhanced by dung beetles, followed by nutrient cycling, plant growth enhancement, dung removal, bioturbation, and secondary seed dispersal. However, my analysis revealed considerable biases across the type of function assessed, with a significant focus on dung removal (57% of measured ecosystem functions) compared to nutrient cycling (20%) and less focus on other processes such as bioturbation, secondary seed dispersal, plant growth enhancement, and trophic regulation (<10%). My findings confirm that dung beetles have a net positive effect on multiple ecosystem functions, but with uneven distribution in the measurement of these functions across countries and latitudes, which could potentially lead to biased estimates of the impact of dung beetles on ecosystem functioning. These results emphasize the importance of quantifying a range of ecosystem functions beyond just dung removal, so as to gain a better understanding of the effects of dung beetles on multiple ecosystem services. By explicitly measuring multiple ecosystem functions, future ecological research on dung beetles will better describe the global contributions of dung beetle biodiversity to ecosystems and people.

Key words

Insectageddon, evidence synthesis, ecology, effect size, Scarabaeinae, geographic distribution, biodiversity, dung removal

2.1 Introduction

The stability and functioning of ecosystems occurs through the complex interaction of species, leading to beneficial processes enhancing nature's contributions to people (Díaz et al., 2018). Insects are of great significance in maintaining fundamental ecological processes that underpin ecosystem functioning, such as enhancing decomposition, nutrient cycling, and plant productivity (Hartley & Jones, 2008), facilitating seed dispersal (Chen et al., 2017), and regulating harmful parasite populations (Sands & Wall, 2017). However, the intensification of land use and changing climate patterns are posing increasing pressures on these insect communities and their capacity to contribute to ecosystem functioning (Outhwaite et al., 2022). Furthermore, our current understanding of the ecosystem services provided by insects is still limited and often biased, with significant gaps in knowledge regarding the least-studied functional and taxonomic groups (Noriega et al., 2018). There are potentially concerning negative trends in biodiversity and population abundance among insects, surpassing the rates observed compared with other taxonomic groups (Van Klink et al., 2020). This so-called "insectageddon" has raised significant concerns about the future functioning and stability of ecosystems (Cardoso et al., 2020; Eggleton, 2020; Thomas et al., 2019).

Dung beetles (Coleoptera: Scarabaeoidea) are a functionally significant group of insects due to their utilisation of dung to feed and protect offspring. This behaviour has cascading effects on ecosystem functions such as bioturbation, nutrient cycling, decomposition, and plant growth enhancement. These functions are vital to the stability and resilience of ecosystems (Nichols et al., 2008). The decline in insect biodiversity and biomass at large is mirrored in reports specifically on dung beetle communities, with dung removal, soil excavation and seed dispersal having been shown to decline with forest degradation, which has been attributed to decreased dung beetle biomass (López-Bedoya et al., 2022). In tropical regions, habitat fragmentation has led to large vertebrate defaunation. This has had cascading negative effects on associated dung beetle communities and ecological processes they drive (Andresen & Laurance, 2007; Nichols et al., 2009; Raine & Slade, 2019). Similarly, Bogoni et al. (2019) found that, alongside environmental factors such as climate and vegetation, decreases in diversity of medium- to large-bodied mammals in the South American Atlantic Forest biome seemingly led to a reduction in dung beetle species richness. In temperate regions, decline of telecoprid dung beetles from the Iberian Peninsula has been observed in areas with increased urban development since 1950 (Lobo, 2001) and in Italy, populations of telecoprid dung beetles have changed over the course of the 20th century, with nine species experiencing a decline in the past 30 years, also linked with changes in land use (Carpaneto et al., 2007). Overall, these trends threaten the essential ecosystem functions and ecosystem services that dung beetles provide (Noriega et al. 2021).

Nesting behaviour is one major factor contributing to the variation of ecosystem functions delivered by dung beetles (Halffter & Edmonds, 1982). This behaviour has been classified into four groups including non-nesters, telecoprids, paracoprids, and endocoprids (Tonelli, 2021). These nesting groups are often recorded and analysed as functional traits, due to the different strategies used for dung re-location, which can have strong effects on the level of ecosystem function delivered (deCastro-Arrazola et al., 2022). For example tunnelling and rolling behaviour can enhance dung removal by nearly 50% and have cascading ecological implications for the secondary dispersal of seeds (with reported increases by over 30%; Milotić et al. 2019). For this reason, paracoprid species are often selected for introduction programmes to novel environments, as they have been shown to redistribute dung that would otherwise remain on the pasture surface (Doube et al., 2014c). While many studies quantify the effects of different nesting strategies on ecosystem functions (Hea et al., 2005), our understanding of the overall magnitude and direction of effects of dung beetles and their nesting strategies on ecosystem functions is still limited.

Greater biodiversity of dung beetles can increase rates of ecosystem functioning (Noriega et al., 2021b) and it has been shown that dung beetle specialisation and preference for dung resources varies across regions along the latitudinal gradient, with greater diversity of beetles using dung resources to a greater extent at the equator (Frank et al., 2018). However, the landscape type can affect this considerably. For example, production landscapes such as agricultural fields and pastures are often more homogenous and the use of livestock pharmaceutical products and other agricultural chemicals can result in negative impacts on dung beetle populations and their ecosystem functions (Manning, Slade, et al., 2017; Verdú et al., 2018). In contrast, wild, intact ecosystems such as native forests and grasslands, typically have more abundant and diverse dung beetle assemblages, and have been found to have greater rates ecosystem functioning (Braga et al., 2013). There are unique dung beetle communities in different habitats, such as desert (deCastro-Arrazola et al., 2018) and grassland systems (Evans et al., 2019), which likely also modulate the net functional effects of dung beetle communities due to species-specific effects. Nevertheless, there is still a fundamental lack of any comparative overview of the magnitude and direction of how ecosystem functioning varies across these inherently variable features of native ecosystems.

With the increasing encroachment of livestock farming into new land areas, the ecology of dung beetles has become a matter of considerable economic concern and ecological significance (Doube et al., 2014), as novel dung beetles are increasingly being introduced to cattle-breeding areas that lack efficient native species that provide critical ecosystem services (Dymock, 1993; Forgie et al., 2018). However, it remains unclear whether dung beetle assemblages introduced to agricultural environments are as functionally effective as when in their native home range because there has been no comparison between the introduced versus native dung beetles and their impact on ecosystem functions. While laboratory studies can provide insights into the mechanisms underlying dung beetle-mediated ecosystem functions (Ortega-Martínez et al., 2016), they can also limit the generalisability of their outcomes to native ecosystems. In contrast, field studies can provide a more realistic assessment of the ecological impacts of the beetles under investigation; for instance field mesocosm experiments that measure rates of dung removal have been shown to be a reliable method for studying ecological impacts *in situ* (Lähteenmäki et al., 2015). Experimental studies aim to establish cause-and-effect relationships by manipulating variables in a controlled setting. However, patterns of dung beetle activity, such as abundance, diversity, and behaviour, identified through observational studies may reveal different patterns of variation in ecosystem functions delivered. As a consequence, there may be variations in outcomes between observational studies and experimental studies when evaluating the effects of dung beetles on ecosystem functions. There is also currently a lack of studies that compare these different methods and assess how they influence our understanding of the effect of dung beetles on ecosystem functions.

In a seminal, qualitative literature review, Nichols et al. (2008) inspired numerous studies investigating the effects of dung beetles on ecosystem functioning. A subset of ecological effects of dung beetles have been investigated using meta-analytical methods. For example, the study conducted by Nichols et al. (2007) found a reduction in dung beetle communities as a consequence of land use change in tropical regions. Similarly, López-Bedoya et al., (2022) reported adverse impacts of forest degradation and deforestation on the essential roles of dung beetles, including dung removal and seed dispersal. In contrast, Fuzessy et al., (2021) showed that the loss of habitat and depletion of large mammals have detrimental effects on dung beetle populations and their associated ecosystem functions. Collectively, these examples underscore the absence of a comprehensive quantitative synthesis of global patterns of dung beetle effects on various ecosystem functions and services.

Here, I investigate dung beetle contributions to ecosystem functioning, and the factors that affect the magnitude and direction of these effects through a meta-analysis approach which includes dung beetle nesting behaviour, ecosystem type, and study methodology. I hypothesise that (1) dung beetles will have an overall positive effect on ecosystem functions and paracoprid (tunnelling) behaviour will show the greatest rates of ecosystem functioning; (2) there will be greater ecosystem function delivery at tropical latitudes, intact landscapes and native habitats; and finally (3) there will be no difference between native versus non-native (introduced) dung beetles on ecosystem functioning, and there will be no difference in the level of ecosystem functions in laboratory versus field, and observational versus experimental studies.

2.2 Methods

2.2.1 Literature search

I used an automated approach to identify search terms that were considered relevant to my overarching question using the 'litsearchr' package (v 0.1.0) in R (Grames et al., 2019). Following this standardised systematic literature search framework, I conducted a naïve search using search terms that I considered relevant to my overarching question: what are the effects of dung beetles on ecosystem functions? I used the following Boolean search string:

dung beetle* AND ecosystem* AND function*

No restriction was placed on publication year, and this process returned a total of 378 unique papers from the Web of Science and Scopus databases (Appendix 2.1). To capture more papers for my meta-analysis, I used a systematic text mining exercise of paper titles, abstracts, and keywords, and generated a list of dung beetle stop words (n = 186) (Appendix 2.2) by manually assessing each word and combining with the standard English stop words. I obtained a pool of 1271 search terms and, to understand their relatedness based on their co-occurrence in papers,Igenerated a feature matrix and visualized word association networks (Appendix 2.3). By detecting commonly appearing terms, I was able to identify important nodes, which allowed me to select 92 key terms, which were then grouped into concept groups following the PICO framework (Appendix 2.1). The automated Boolean search string was:

> \(\(“dung fauna” OR beetle OR biomass OR coleoptera OR “dung beetle” OR “functional group” OR insect OR scarabaeidae OR scarabaeinae OR species\) AND \(manure OR cattle OR dung OR livestock OR mammal\) AND \(“primary

> productivity” OR “carbon sequestration” OR bioturbation OR “seed dispersal” OR “plant growth” OR “secondary seed dispersal” OR “parasite control” OR “fly control” OR “trophic regulation” OR pollination OR decomposition OR dispersal OR “dung removal” OR feeding OR interaction OR “nutrient cycling” OR pasture OR soil OR vegetation\) AND \(abundance OR biodiversity OR conservation OR disturbance OR diversity OR ecological OR ecology OR ecosystem OR functional OR functions OR richness OR “species composition” OR “species richness”\)\)

Using this returned 30,292 papers on WOS and 20,907 papers on SCOPUS. After a first assessment of the search terms suggested by the automated Boolean search string (above), I decided that this cast the net too wide. Thus, based on combined knowledge of the dung beetle ecology literature and assessment of the naïve search, I decided to use the naïve search terms (above) for the final search, as this captured a good sample size and subset from the larger automated search of the most relevant studies for this research question. However, the automated key term search proved to be a beneficial exercise, as it revealed that while the dung beetle ecology literature may briefly mention terms such as “ecosystem functions” or “ecosystem services,” these terms are not reiterated in the abstract or implemented as part of the study design. Instead, the potential outcomes of ecosystem functions and underlying biotic or abiotic mechanisms are described as discussion points and potential outcomes, without explicit measuring and analysis of ecosystem functions.

2.2.2 Abstract and article screening

I assigned each article a unique study ID, and then conducted an abstract screening by reading abstracts using the ‘Metagear’ package (Lajeunesse, 2016). I ensured that the following criteria were met to choose studies for analysis, including (i) explicit quantification of dung beetle-mediated ecosystem functions; and (ii) the reporting of mean values of variables, sample size, and a measure of variability around the mean. In cases where multiple habitats, species, or response variables were examined separately within the same article, I treated them as distinct case studies since they were considered independent. Finally, for response variables that were measured at multiple time points, I included each time point in the analysis and where studies measured responses across seasons, I included each season in my analysis. Abstracts were screened three times to ensure that no papers were missed. Interestingly, many papers stated that they had control treatments, but did not report control treatments in the text, figures or supplementary materials, which created a final sample size of 66 studies (Appendix 2.1).

2.2.3 Data extraction

For each study, I coded details of the article ID, geographic location, environmental variables, and study methodology. I extracted 24 dung beetle associated ecosystem functions by recording means, measures of variability and sample sizes for each response variable from the control (dung beetles absent) and the treatment (dung beetles present) and then re-codified these ecosystem functions by grouping them according to the groups of functions described in Nichols et al. (2008) (Table 2.1). In articles where data were not reported in the text or supplement, I extracted data using the image analysis graphical user interface 'WebPlotDigitizer' V 4.6 (Rohatgi, 2022). To investigate my hypotheses using subgroup analysis, I coded nesting behaviour, ecosystem type, and study methodology factors as categorical variables in the database (Table 2.2).

2.2.4 Effect size calculations

All analyses were done using the 'metafor' package in R version 4.2.2 (Viechtbauer, 2015). I used Hedges' g to calculate standardised mean differences as a measure of treatment effect sizes. Hedges' g takes into account sample size and the inverse of variance, thus correcting for positive bias in standardised mean differences inherent in the Cohen's D value. (Viechtbauer, 2010). This standardised value has a range from $-\infty$ to $+\infty$, where negative and positive values indicate either an increase or decrease in ecosystem functions (respectively), resulting from the presence of dung beetles. A larger effect size implies a more pronounced difference between the experimental control (no dung beetles present) and treatment (dung beetles present), while a Hedges' g of zero suggests no difference in the examined response variables across treatments.

2.2.5 Random effects meta-analysis and subgroup analyses

I first ran a random effects meta-analysis using all individual ecosystem function effect sizes combined to test for overall differences in ecosystem functions between study controls (no dung beetles) and treatments (with dung beetles), hereafter displayed as Q_{overall}. I then grouped data into each ecosystem function category to test responses of each function separately (Table 2.1). To assess the variability of dung beetle-mediated ecosystem functioning across different dung beetle nesting behaviours, ecosystem types and study methodologies, separate random effects meta-analyses were performed for each sub-group (Table 2.2) using the restricted maximum-likelihood estimator (Viechtbauer, 2010). To test the difference ($Q_{\text{difference}}$) between each sub group, I used a random effects meta-analysis, yielding estimates of heterogeneity (I^2) and Q-test of heterogeneity (Q) (Viechtbauer, 2010). Moderator levels with less than four cases are not informative enough and should be interpreted with caution due to their potential unreliability. Despite being aware of the limitations of including ecosystem functions with less than four effect sizes, I made a deliberate choice to include them in the effect displays to explore and highlight the extent of knowledge gaps.

2.2.6 Publication bias

Publication bias is a major limitation of evidence synthesis and meta-analytic research (Osenberg et al., 1999). While I took the appropriate precautions against this at the start of my research (using 'litsearchr' and multiple abstract screenings), I also conducted *post-hoc* tests of publication bias by producing funnel plots to assess any asymmetry (also using the 'metafor' package in R). A funnel plot is expected to have a symmetrical inverted funnel shape when there is no publication bias, with the smaller studies scattered randomly around the effect size estimate, and more extensive studies clustered more tightly around the "true" effect size. However, if publication bias is present, the funnel plot may show asymmetry, where the smaller studies with fewer significant or no effects are missing, resulting in an asymmetrical plot (Viechtbauer, 2010). To assess funnel plot asymmetry, the rank correlation test and the regression test were performed, using the standard error of the observed outcomes as a predictor (Appendix 2.5). The field of ecology is greatly impacted by the "file drawer problem", which refers to a bias towards publishing statistically significant results while neglecting non-significant ones (Rosenthal, 1979). Consequently, a considerable number of effect sizes reporting on ecosystem functions mediated by dung beetles may remain unpublished and as a result are not able to be included here.

Table 2.1 Categories given to ecosystem function effect sizes extracted from the literature following Nichols et al (2008)

Ecosystem Function	Example measured variables from published literature
Dung removal	Dry mass dung removed/remaining on the surface Wet mass dung removed/remaining on the surface
Nutrient cycling	Ammonium N Leachate N Leachate P Microbial respiration Moisture Nitrogen Organic matter Potassium Total carbon Total nitrogen Total phosphorus
Bioturbation	Bulk density
Plant growth enhancement	Foliar nitrogen Foliar phosphorus Number of seedlings Leaf number
Secondary seed dispersal	Seed mimic size (small, medium, large) Burial depth Distance of seed mimic from dung
Pest / parasite control	Adult fly abundance Fly larvae abundance E. coli colony count
Trophic regulation	Bait strip consumption

Table 2.2 Variables that were codified at the study level that could explain variation in the effects of dung beetle presence on measured ecosystem functions

	Study-level factor	Subgroup
Functional trait	Nesting behaviour	Paracoprid Endocoprid Telecoprid Mixed
Ecosystem type	Latitude	Temperate Tropical
	Landscape	Production Wild
	Habitat	Agriculture Desert Forest Grassland
Methodological factors	Dung beetle status	Introduced Native
	Study context	Laboratory Field
	Study method	Observational Experimental

2.3 Results

2.3.1 Database characteristics

After screening the literature and applying the aforementioned selection criteria to screened studies, the resulting dataset comprised 455 effect sizes extracted from 66 peer-reviewed papers (Appendix 2.1), with a notably uneven distribution across countries (Figure 2.1; Appendix 2.6). Dung removal accounted for 57% of effect sizes, nutrient cycling for 20%, bioturbation for 5%, plant growth enhancement for 6%, secondary seed dispersal for 8%, and trophic regulation for 5% (Figure 2.2). The distribution of published effect sizes varied significantly across different geographic regions. Specifically, studies conducted in Brazil contributed the highest number of effect sizes to my analyses on dung removal (n = 39), bioturbation (n = 8), and secondary seed dispersal (n = 13). In contrast, studies from China provided the most effect sizes for nutrient cycling (n = 18), while those conducted in Mexico contributed the most to my analyses on plant growth enhancement (n = 11). Notably, trophic regulation was only reported in studies conducted in the UK, with a total of 23 effect sizes included in my analyses. Further details on the regional distribution of effect sizes are in Figure 2.1 and Appendix 2.6.

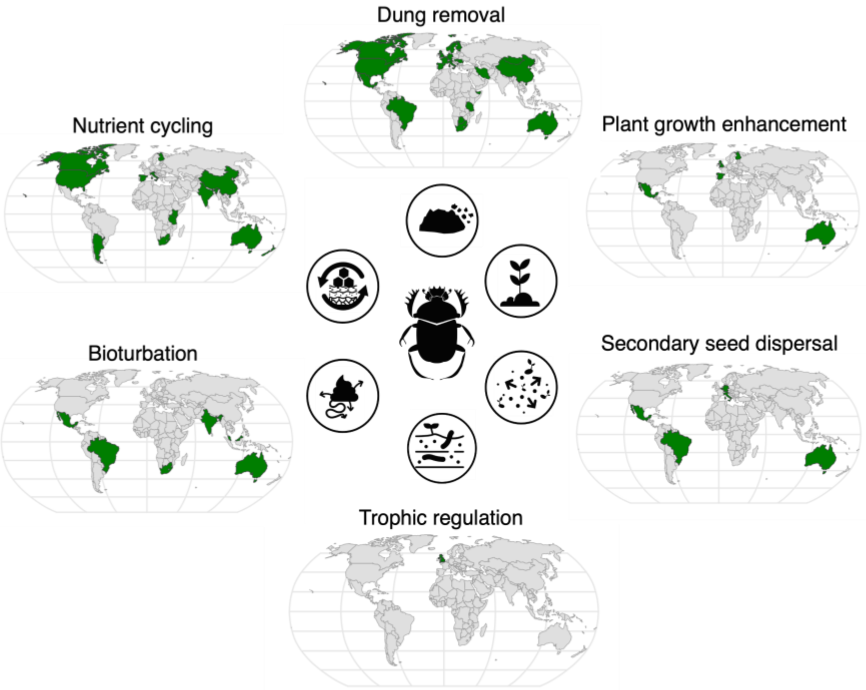
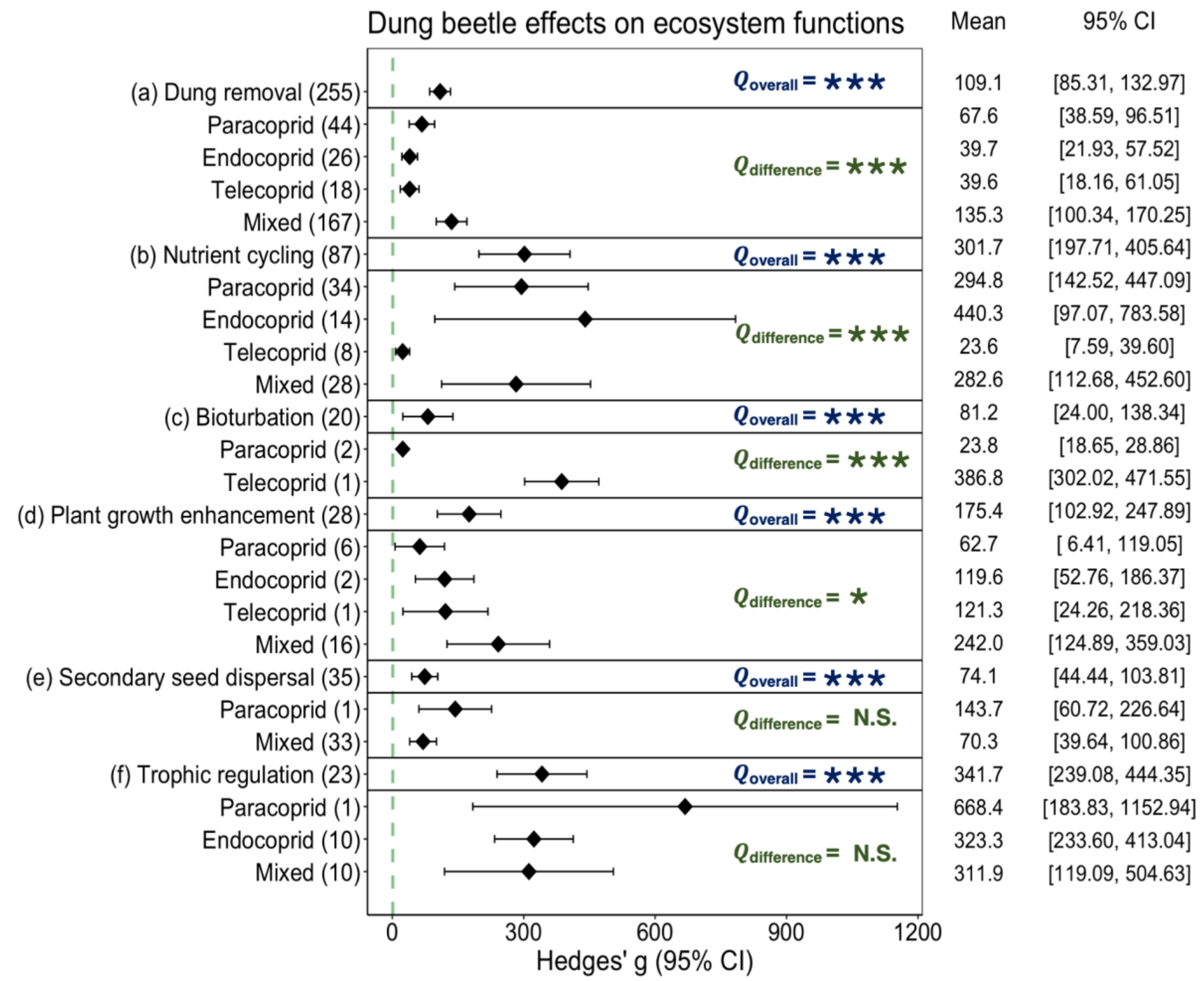


Figure 2.1 The global distribution of effect sizes extracted for each ecosystem function. See Appendix 2.6 for further information regarding individual countries.

2.3.2 Dung beetles enhance overall ecosystem functioning

The aim of this meta-analysis was to quantitatively examine the effect of dung beetles on ecosystem functions, based on published literature to date. I analysed seven ecosystem functions (Table 2.1), six of which had sufficient data for sub-group analysis with 18 moderators (Table 2.2). The results of my analysis show that dung beetles have a positive overall effect on all ecosystem functions reported here (Figure 2.2) Additionally, I found that dung beetle effects on four out of six functions varied significantly depending on nesting behaviour, with no effects of nesting behaviour detected for secondary seed dispersal (Figure 2.2e; Appendix 2.7) and trophic regulation (Figure 2.2f; Appendix 2.7).

The strongest effects of dung beetles on ecosystem functions were found for trophic regulation (Figure 2.2f; Appendix 2.7). This was followed by nutrient cycling (Figure 2.2b; Appendix 2.7), where endocoprid dung beetles contributed significantly to the enhancement of nutrient cycling (Figure 2.2b; Appendix 2.7). Although there was only a marginally significant difference in dung beetle effects between different nesting behaviours on plant growth enhancement, these results provide some indication that a greater level of plant growth enhancement may occur with mixed dung beetle nesting behaviours (Figure 2.2d; Appendix 2.7). Overall, I observed that mixed nesting behaviours had the most pronounced effect on dung removal (Figure 2.2a; Appendix 2.7). With 20 effects found in the literature, bioturbation showed significantly greater effects in studies with telecoprid dung beetles (Figure 2.2c; Appendix 2.7), however this should be viewed with caution since subgroup analyses were based on only three effect sizes (two paracoprids and one telecoprid effect size). Out of all functions quantified in the literature, secondary seed dispersal had the weakest response to dung beetle presence, and there was no difference in secondary seed dispersal between paracoprid and mixed nesting behaviours (Figure 2.2e; Appendix 2.7). Finally, I was unable to conduct any sub-group analyses for pest/parasite control due to insufficient data, so this function was not included in my analyses.



	Mean	95% CI
(a) Dung removal (255)	109.1	[85.31, 132.97]
Paracoprid (44)	67.6	[38.59, 96.51]
Endocoprid (26)	39.7	[21.93, 57.52]
Telecoprid (18)	39.6	[18.16, 61.05]
Mixed (167)	135.3	[100.34, 170.25]
(b) Nutrient cycling (87)	301.7	[197.71, 405.64]
Paracoprid (34)	294.8	[142.52, 447.09]
Endocoprid (14)	440.3	[97.07, 783.58]
Telecoprid (8)	23.6	[7.59, 39.60]
Mixed (28)	282.6	[112.68, 452.60]
(c) Bioturbation (20)	81.2	[24.00, 138.34]
Paracoprid (2)	23.8	[18.65, 28.86]
Telecoprid (1)	386.8	[302.02, 471.55]
(d) Plant growth enhancement (28)	175.4	[102.92, 247.89]
Paracoprid (6)	62.7	[6.41, 119.05]
Endocoprid (2)	119.6	[52.76, 186.37]
Telecoprid (1)	121.3	[24.26, 218.36]
Mixed (16)	242.0	[124.89, 359.03]
(e) Secondary seed dispersal (35)	74.1	[44.44, 103.81]
Paracoprid (1)	143.7	[60.72, 226.64]
Mixed (33)	70.3	[39.64, 100.86]
(f) Trophic regulation (23)	341.7	[239.08, 444.35]
Paracoprid (1)	668.4	[183.83, 1152.94]
Endocoprid (10)	323.3	[233.60, 413.04]
Mixed (10)	311.9	[119.09, 504.63]

Figure 2.2 Global effects of dung beetles on all ecosystem functions reported in the literature. Hedges' g effect sizes +/- 95% confidence intervals are shown for (a) dung removal, (b) nutrient cycling, (c) bioturbation, (d) plant growth enhancement, (e) secondary seed dispersal, and (f) trophic regulation. Sub-group analyses further differentiate the influence of dung beetle nesting behaviour on each ecosystem function, which includes four categories: paracoprids (tunnelers), endocoprids (dwellers), telecoprids (rollers), and mixed (studies with two or more nesting behaviours). Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05.

2.3.3 Dung removal

There were significant differences in dung removal between temperate and tropical ecosystems, with a more substantial effect on dung removal observed in temperate ecosystems (Figure 2.3; Appendix 2.8). Similarly, a significant difference in dung removal was observed between production and wild landscapes, with production landscapes exhibiting a stronger effect on dung removal (Figure 2.3; Appendix 2.8). Dung removal varied significantly across distinct habitat types, with the effects of dung beetles on dung removal being most pronounced in grassland ecosystems, followed by deserts and agricultural lands, while forests displayed the weakest effect (Figure 2.3; Appendix 2.8). In comparison to introduced species, native beetles demonstrated a higher level of dung removal (Figure 2.3; Appendix 2.8). Observational studies exhibited a more substantial impact on dung removal than experimental studies, while there was no statistically-significant difference between laboratory and field studies (Figure 2.3; Appendix 2.8). Similarly, no statistically-significant difference in dung removal was observed between laboratory and field studies (Figure 2.3; Appendix 2.8).

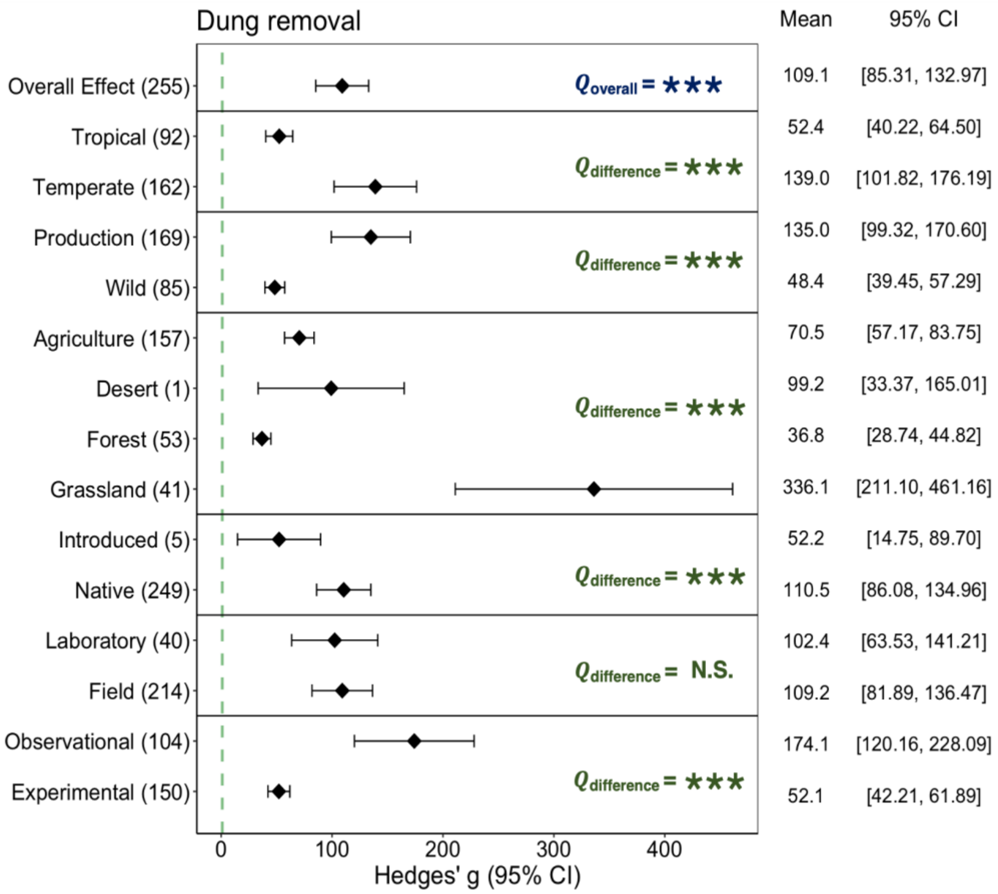


Figure 2.3 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in dung removal by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) introduced versus native dung beetles; (e) laboratory versus field studies; and (f) observational versus experimental studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05.

2.3.4 Nutrient cycling

The effect of dung beetle presence on nutrient cycling was significantly more pronounced in temperate ecosystems when compared to tropical ecosystems (Figure 2.4; Appendix 2.9). In comparison to wild landscapes, production landscapes showed a significantly lower degree of nutrient cycling (Figure 2.4; Appendix 2.9). Grassland habitats exhibited greater nutrient cycling facilitated by dung beetle presence and, surprisingly, the lowest nutrient cycling rates were observed in forest habitat (Figure 2.4; Appendix 2.9). There was no significant difference in nutrient cycling between introduced versus native dung beetles (Figure 2.4; Appendix 2.9). This was also the case for dung beetle effects on nutrient cycling between laboratory and field studies (Figure 2.4; Appendix 2.9), though the number of effect sizes for laboratory (n = 3) and observational (n = 1) studies were low and should be interpreted with caution.. However, there was a significant difference between observational and experimental studies, with higher nutrient cycling effects detected in experimental settings (Figure 2.4; Appendix 2.9).

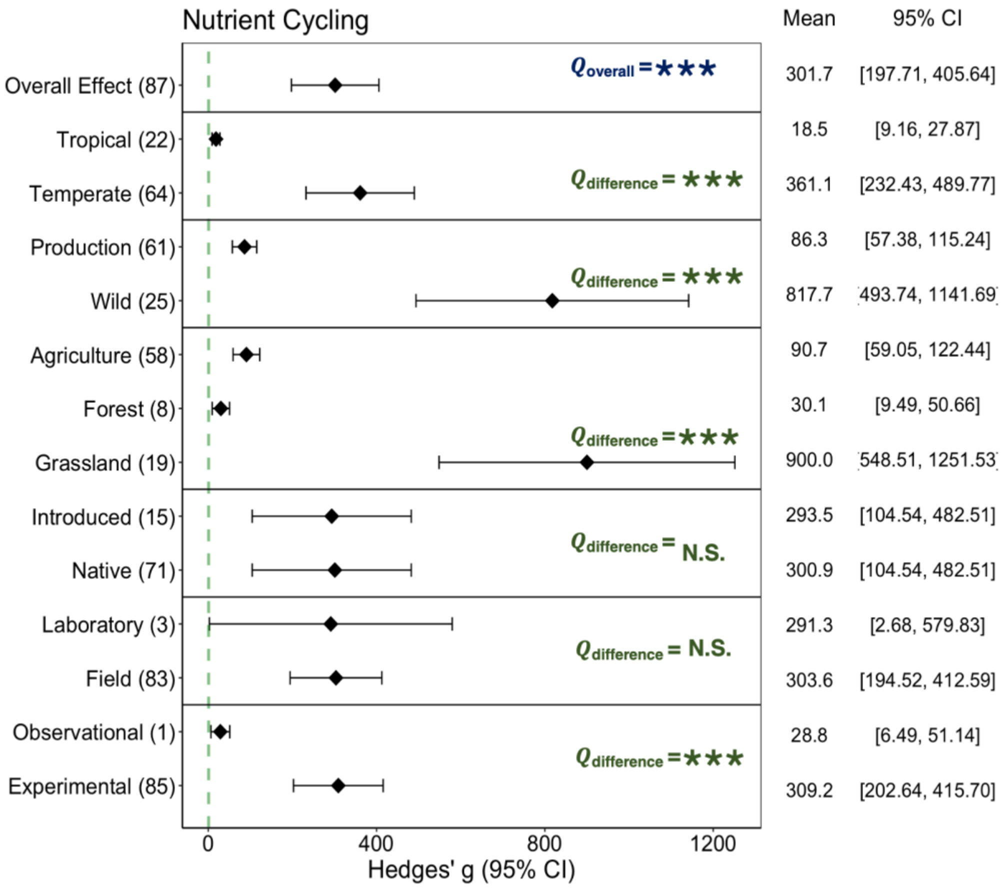


Figure 2.4 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in nutrient cycling by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) introduced versus native dung beetles; (e) laboratory versus field studies; and (f) observational versus experimental studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05

2.3.5 Bioturbation

I found that there was a greater level of bioturbation in temperate than in the tropical ecosystems, which did not support my initial hypothesis (Figure 2.5; Appendix 2.10). A significantly-higher amount of dung beetle-mediated bioturbation was found in production landscapes compared to wild, and there was no significant difference in bioturbation between habitat types (Figure 2.5; Appendix 2.10). Field studies also showed a higher level of dung beetle bioturbation compared to laboratory studies (Figure 2.5; Appendix 2.10), but there was no significant difference in effect sizes between observational and experimental studies (Figure 2.5; Appendix 2.10). I did not find any studies that quantified introduced versus native dung beetle mediated bioturbation, so this factor could not be tested in this meta-analysis. It is noteworthy that there were small sample sizes of the temperate, grassland and laboratory subgroups, which should be taken into consideration in interpreting the outcomes of these analyses (Figure 2.5; Appendix 2.10).

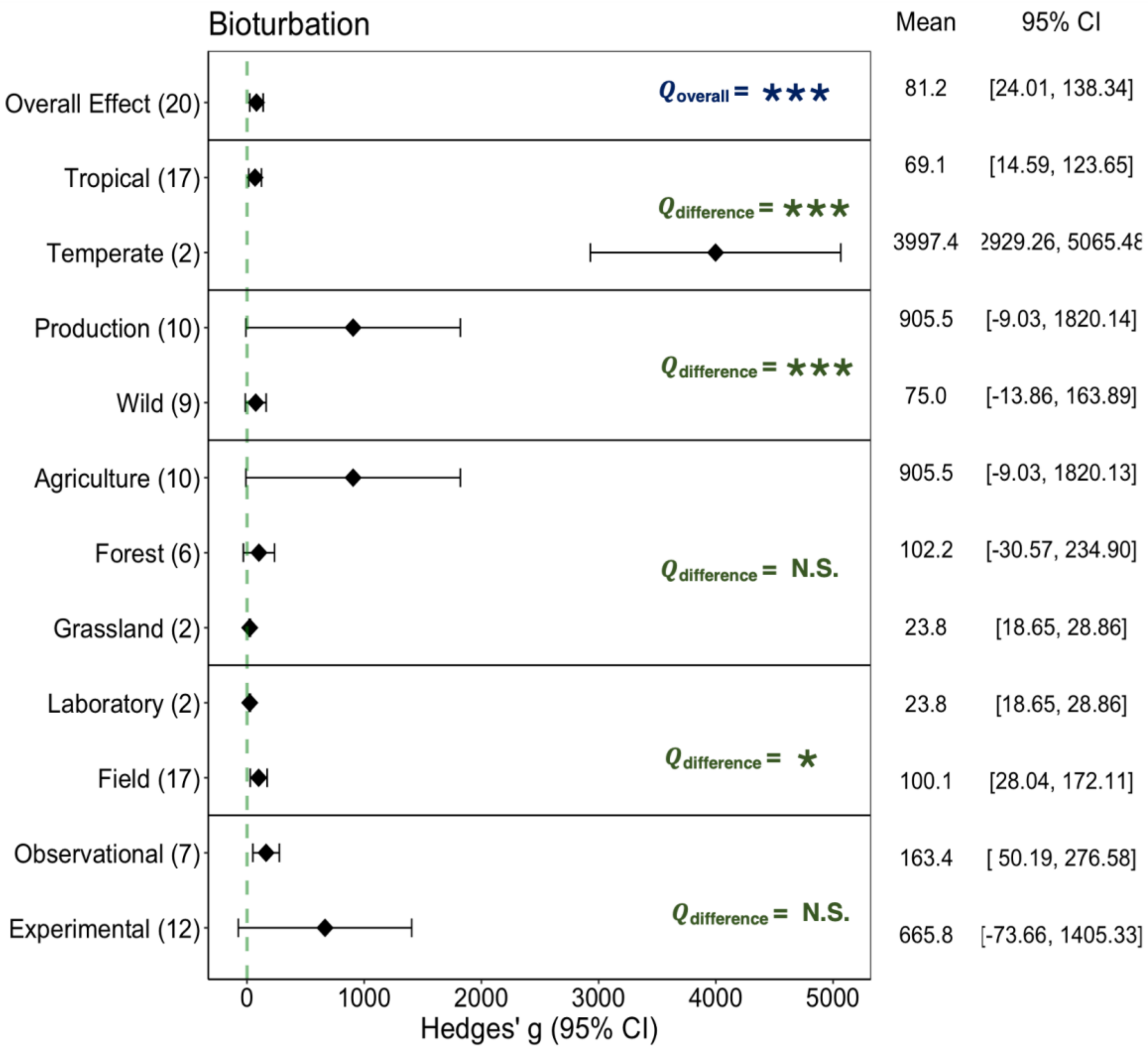


Figure 2.5 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in bioturbation by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) laboratory versus field studies; and (e) observational versus experimental studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05

2.3.6 Plant growth enhancement

My initial hypothesis was that dung beetles would show greater plant growth enhancement on tropical systems in contrast with temperate zones. Interestingly, I found that dung beetles had a positive effect on plant growth enhancement with no difference between both tropical and temperate ecosystems (Figure 2.6; Appendix 2.11). In the same way, dung beetles had similar effects on plant growth enhancement in both production and wild landscapes (Figure 2.6; Appendix 2.11) and there was no differences in dung beetle-mediated plant growth enhancement between agriculture and forest habitat types (Figure 2.6; Appendix 2.11). However, the effects of dung beetles on plant growth enhancement were significantly greater in studies with native dung beetles compared to introduced ones, which were slightly negative. It is important to note that the sample size for introduced species was only three, so these results should be interpreted with caution (Figure 2.6; Appendix 2.11). There was no significant difference in dung beetle mediated plant growth enhancement observed between the effect sizes of laboratory versus field studies and observational versus experimental studies (Figure 2.6; Appendix 2.11).

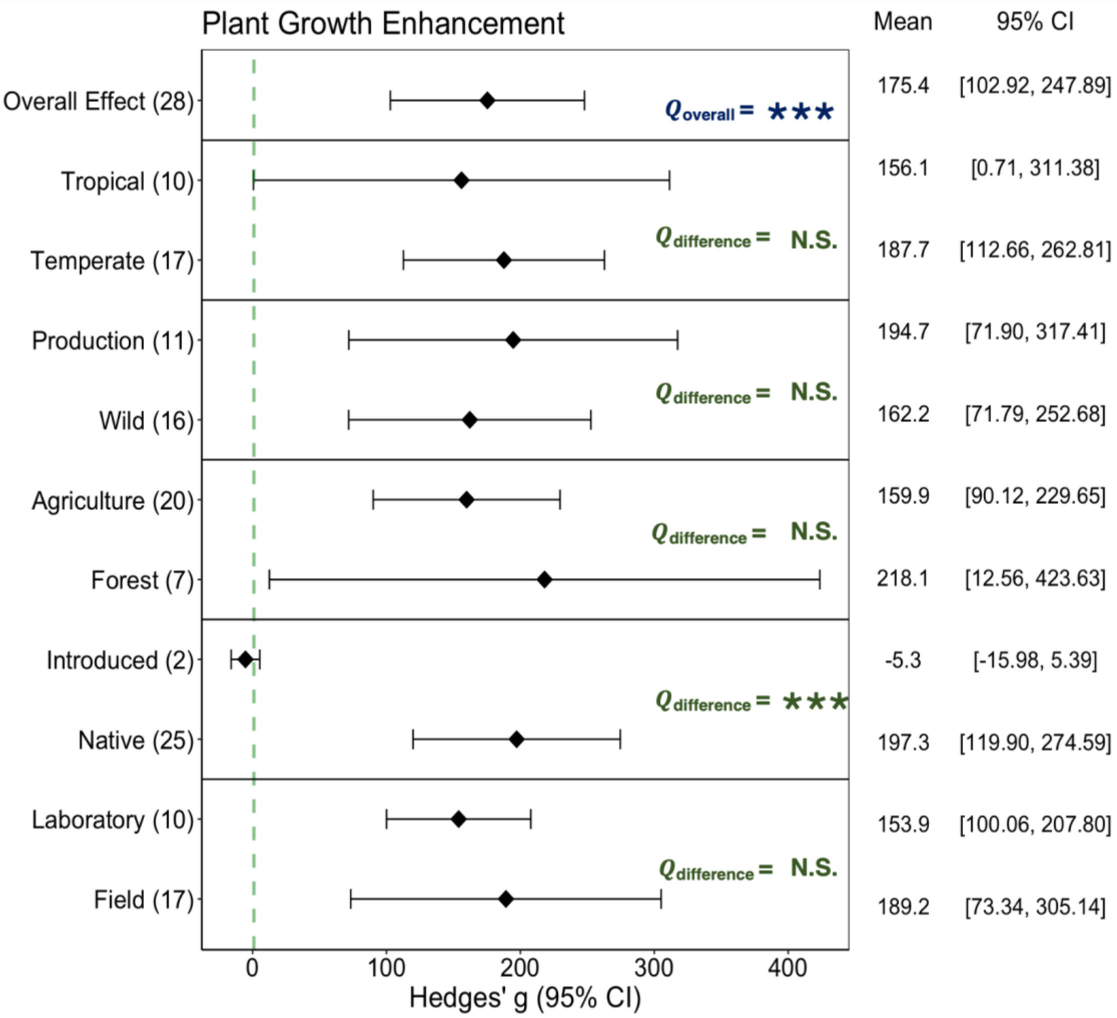


Figure 2.6 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in plant growth enhancement by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) introduced versus native dung beetles; and (e) laboratory versus field studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05.

2.3.7 Secondary seed dispersal

In contrast to all other ecosystem functions, secondary seed dispersal was significantly greater in tropical ecosystems compared to temperate ecosystems (Figure 2.7; Appendix 2.12). Dung beetles appear to deliver similar levels of seed dispersal in both production and wild landscapes (Figure 2.7; Appendix 2.12). Secondary seed dispersal mediated by dung beetles appeared to be greater in agricultural habitats compared to forest and grassland habitats, although the result was not statistically significant and may have been influenced by the small sample size of the grassland habitat (Figure 2.7; Appendix 2.12). There was no significant difference in the effects of dung beetles on secondary seed dispersal between laboratory and field studies. However, it should be noted that the laboratory subgroup had only one effect size, so this inference may not be reliable (Figure 2.7; Appendix 2.12). Finally, there was no significant difference in the effects of dung beetles on secondary seed dispersal between observational and experimental studies (Figure 2.7; Appendix 2.12).

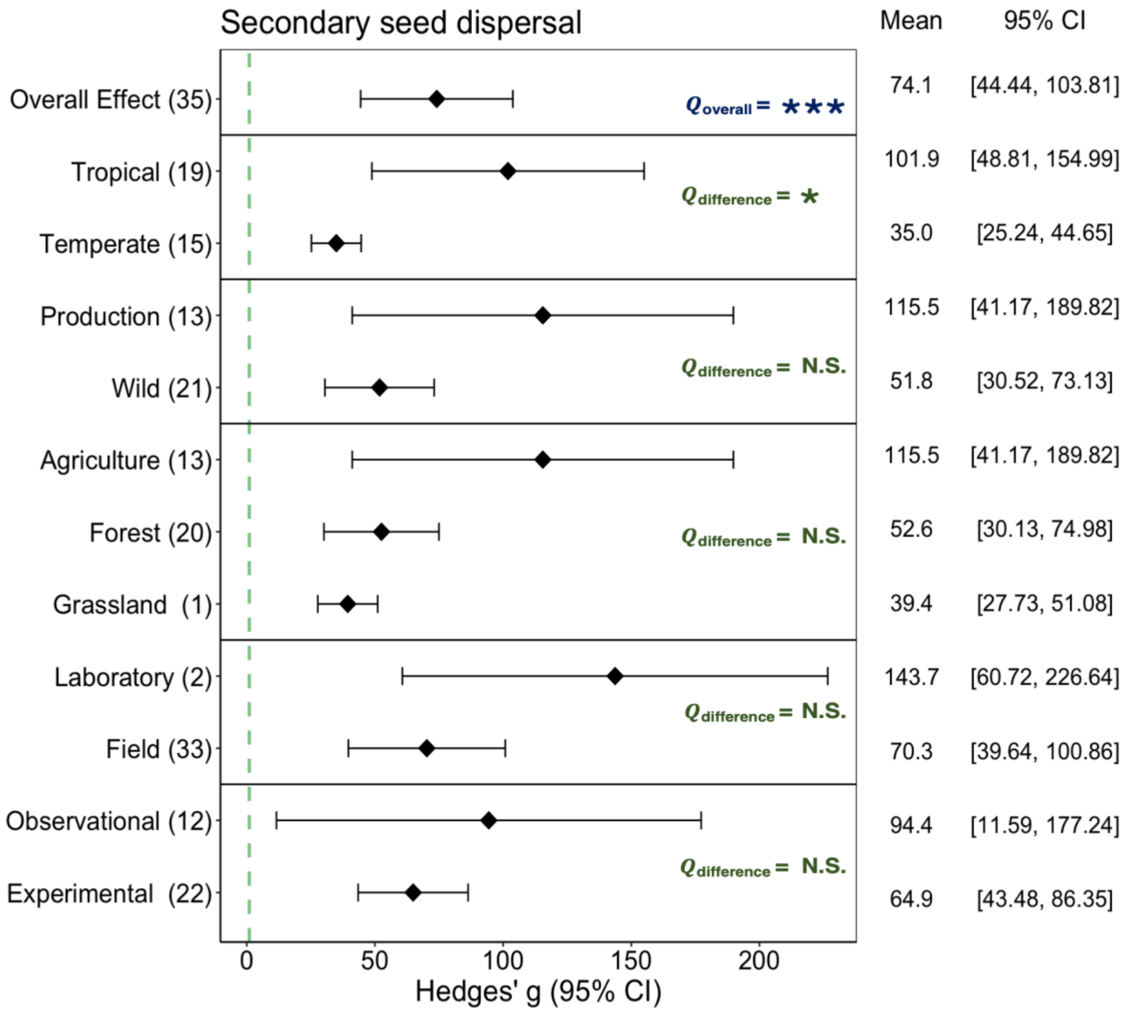


Figure 2.7 Hedges' g effect sizes +/- 95% confidence intervals, illustrating variation in secondary seed dispersal by dung beetles across different ecosystem types and study methodology, including comparisons between (a) tropical and temperate ecosystems; (b) production and wild landscapes; (c) habitat types; (d) laboratory versus field studies; and (e) observational versus experimental studies. Effect moderators are displayed on the y-axis, with number of analysed effect sizes (n) in brackets. Results of tests of significance for Qoverall and Qdifference are indicated on the right as: ***p < 0.001; **p < 0.01; *p < 0.05; N.S. p > 0.05

2.4 Discussion

2.4.1 Dung beetles enhance all ecosystem functions studied

This meta-analysis is the first fully global, quantitative synthesis of dung beetle effects on ecosystem functions. The key outcomes of my study are (1) dung beetle presence has a positive effect on all measured ecosystem functions, with mixed or paracoprid nesting behaviours amplifying these effects (Figure 2.2); (2) contrary to my hypotheses, dung beetle mediated ecosystem functions were greater at temperate latitudes, production landscapes and grassland systems; and finally (3) introduced dung beetles had a slight negative effect on plant growth enhancement, and the magnitude of effect on ecosystem functions varied depending on whether the studies were conducted in the laboratory or field, as well as whether they were observational or experimental.

2.4.2 Differential effects of dung beetle nesting strategies on ecosystem functions

In contrast to my expectation, the presence of mixed dung beetle nesting behaviours resulted in greater dung removal and plant growth enhancement (Figure 2.2). This could be due to niche complementarity, where a diverse range of nesting behaviours allows for varying preferences for dung type, size, and location (Halffter & Edmonds, 1982). A diversified use of available resources can enhance dung removal and, in turn, plant growth (Menéndez et al., 2016). Further studies have shown that the presence of functionally contrasting dung beetles can have a synergistic, positive effect on soil microbial respiration and the decomposition rate of soil organic matter (Cheng et al., 2022), and can promote greater stability and resilience within the dung beetle community (Manning & Cutler, 2018a). This is beneficial for maintaining ecosystem functioning even under environmental disturbances or stressors (Mori, 2016). On the other hand, I observed a decrease in dung removal associated with telecoprid nesting behaviour, which may be attributed to inadequate experimental design in exploring such effects. For instance, Carvalho et al., (2018) suggested that their study on dung burial rates by telecoprid beetles might have used too much dung in the experiment, resulting in incomplete burial of the resource, thereby making it difficult to accurately determine the telecoprids' contribution to dung removal.

The results showed that nesting behaviour is an important trait to consider in dung beetle ecology research, as it could have important implications for decomposition processes. In a meta-analysis by McCary & Schmitz (2021), where they investigated the relationship between invertebrate functional traits and terrestrial nutrient cycling, they found that on a global scale, detritivores, and in particular bioturbators, promoted faster rates of decomposition as well as increased nitrogen pools. Furthermore, they found that decomposer invertebrates had greater predictive power when compared to herbivores or predatory feeding modes. Bioturbation is a key feature that enhances dung beetle decomposition, particularly with paracoprid dung beetles, as they mix organic matter into soil, increasing its surface area and exposure to microbes that can further break it down (Bertone et al., 2006). This highlights the importance of invertebrate functional traits in shaping ecosystem processes and the need to consider the diverse roles that different organisms play in nutrient cycling and decomposition, to best predict how these processes may vary under global change scenarios.

In contrast to my hypothesis, I found that paracoprids had the lowest effect on plant growth enhancement (Figure 2.2), which could be because of their tunnelling behaviour causing a large and rapid influx of dung and other detritus belowground, leading to high concentrations of nutrients at plant roots, which may affect root architecture and overwhelm growth in plants (López-Bucio et al., 2003; Xiao et al., 2020). The amount of time it takes to bury dung could affect subsequent ecosystem functioning, for example, Stanbrook et al. (2021) categorised dung beetles within communities in Tanzania based on their size and their burying speed, with the beetles being divided into fast-burying and slow-burying tunnellers of both large and small body sizes. The study found that the speed of dung burial affected ecosystem functions, with larger beetles moving more macronutrients into the soil given the same time period. Furthermore, the larger dung beetles moved more nitrogen, phosphorus, potassium, and carbon than smaller dung beetles. This demonstrates that plant growth enhancement could depend on the nesting behaviours and sizes of the dung beetle community over time.

In addition to this, my results showed that endocoprid behaviour enhanced nutrient cycling, possibly due to the slower rate of nutrient incorporation into the soil or microclimate and microhabitat conditions created around deposited dung on pasture, fostering a moist environment for an optimum rate of nutrient cycling (Sowig, 1995). While my results showed no difference between nesting behaviours for dung beetle effects on secondary seed dispersal and trophic regulation, this is likely because there were limited data to illustrate these effects. This underscores that there is a very large data gap in the field of dung beetle functional ecology.

2.4.3 Dung beetle effects on ecosystem functions across ecosystem types

Temperate latitudes showed significantly greater effects across dung removal, nutrient cycling, bioturbation, and plant growth enhancement. This was in contrast to my hypotheses, but there are several reasons that could support this outcome. In temperate climates, decomposition rates may be higher due to more pronounced seasonal changes in temperature (Duarte et al., 2016). Van Groenigen et al. (2014) found that earthworm presence showed decreased aboveground biomass in temperate compared to tropical climates, suggesting decomposition is greater in the temperate zone. Furthermore, they discuss implications for this in tropical climates, where decomposition rates may be higher due to the warm and humid conditions year-round, the presence of earthworms may not have as much of an impact on aboveground biomass. They conclude that this could be because the rate of decomposition is already high, and therefore, the contribution of earthworms to the decomposition process is relatively small.

In a meta-analysis by (López-Bedoya et al., 2022) investigating primary forest loss and degradation on dung beetle biodiversity, deforestation that occurred in temperate latitudes led to an increase in dung beetle species richness and no difference in species abundance. In contrast, they found that in tropical latitudes both dung beetle richness and abundance declined significantly under deforestation or degradation. I think this could be because temperate and tropical regions have different ecological characteristics and climatic variation, for example, temperate regions have variable resources due to seasonality, so there could be a lag time before negative effects are detected at different trophic levels (Krauss et al., 2010), when compared to tropical latitudes, which have more constant climatic conditions, which could mean specialised dung beetle species which could be more vulnerable to habitat loss. For example, Englmeier et al., (2022) found that community specialisation of dung-visiting beetles is driven by climate, while diversity is mainly affected by land use intensification.

Anthropogenic factors, such as agricultural practices, may play a role in shaping the latitudinal trends observed in dung beetle-mediated ecosystem functioning. Specifically, it is possible that agricultural landscapes provide greater dung resources for dung beetles due to greater stocking densities. However, while it has been shown that the amount of resource available and dung beetle abundances are related, the response of dung beetles to changes in the amount of resource available depends on the species and the structure of the landscape (Roslin & Koivunen, 2001). Alternatively, it is possible that the trends found in agricultural landscapes here are more related to human agricultural productivity practices (such as mulching) and not dung beetles alone.

The relative contributions to soil microorganism-mediated global nutrient cycling varies spatially. It has been found that soil bacterial genetic diversity is highest in temperate habitats, with fungi and bacteria showing global niche differentiation associated with contrasting diversity responses to precipitation and soil pH, which could be associated with dung decomposition patterns found in my meta-analysis (Bahram et al., 2018). However, further research is needed to fully understand the underlying mechanisms driving these latitudinal patterns of dung beetle effects on ecosystem functioning, as this pattern could be attributed to data gaps from tropical latitudes.

We found dung beetle mediated secondary seed dispersal is significantly higher in tropical latitudes (Figure 2.12). Tropical regions are characterized by high levels of biodiversity and a greater abundance of frugivorous animals and larger seeds that are easier to quantify, which may contribute to greater secondary seed dispersal in tropical ecosystems (Braga et al., 2017; Griffiths et al., 2016). It will therefore be important for future studies to quantify secondary removal of smaller seed sizes that are typically found at temperate latitudes, as dung beetles have been shown to potentially assist in ecological restoration by acting as secondary seed dispersers, potentially increasing the success of projects to restore areas with degraded soil and vegetation cover (Almeida et al., 2022).

Our study compared the effects of production and wild landscapes on dung removal, nutrient cycling, bioturbation, and plant growth enhancement. I found that production landscapes had the highest rates of dung removal and bioturbation, while wild landscapes exhibited the greatest nutrient cycling. Furthermore, although plant growth enhancement was greater in production landscapes, the effect was not statistically significant. These landscape-scale findings provide valuable insights into the trade-offs and benefits of different types of landscapes for ecosystem functioning.

2.4.4 Effects of study methodology on observed outcomes

In agreement with my hypothesis, I found that introduced dung beetle species had a similar influence on nutrient cycling as native species, suggesting that dung beetle introductions are beneficial to ecosystem functioning (Figure 2.9). However, nutrient cycling is a complex process that involves multiple factors, such as the physical and chemical properties of the soil, the presence of other organisms, and environmental conditions like temperature and moisture (Swift et al., 1998). As a result, the impact of introduced species on nutrient cycling may be influenced by these other factors, which could mask or amplify any differences in effects between introduced and native species. The outcome of the subgroup analysis of introduced versus native dung beetles for the remaining ecosystem functions should be interpreted with some caution due to the low sample size for introduced species.

We found a significant positive effect of dung removal by native dung beetle assemblages, suggesting that dung beetles in their natural distributional ranges are better adapted to those environments and may be more functionally efficient as a result. This has been demonstrated in other insects and arthropods, which benefit from access to native vegetation cover in agricultural habitats, providing enhanced ecosystem services, such as pollination (Isaacs et al., 2009). However, habitats where introduced dung beetles are found are subject to ongoing anthropogenic disturbances, such as tillage, pesticide application, and livestock trampling, which may affect the level of ecosystem functions. There has been recent debate about possible unintended consequences of introductions of non-native species (Pokhrel et al., 2020), however this is not based on quantitative evidence to date. While I found a significant negative effect of introduced dung beetles on plant growth enhancement, this is likely because of a small sample size (Figure 2.11). These outcomes highlight the need for further efforts to quantify and compare native versus introduced dung beetle effects on ecosystem functions.

No significant difference was found between lab and field studies for dung removal, nutrient cycling, plant growth enhancement, and secondary seed dispersal, indicating reliable results of dung beetle mediated ecosystem functioning. However, I did observe a greater effect of bioturbation in field studies compared to laboratory experiments (Figure 2.10). This difference could be attributed to variations in the methods used to measure bioturbation which include visual scoring (Leiva & Sobrino-Mengual, 2023), collection of upturned soil from the surface (Ferreira et al., 2023) and bulk density (Maldonado et al., 2019; Manning, Slade, et al., 2017). Furthermore, the volume and substrates used in laboratory experiments may be less compacted, requiring less effort for bioturbation to occur (Reis et al., 2023).

Dung removal was greatest in observational studies, which is likely because the dung was exposed to an uncontrolled diversity and abundance of dung beetles over time, compared to experimental studies which have highly controlled dung beetle biomass, abundance, or diversity. This is similar to the effect I found with mixed nesting behaviour, highlighting the potentially critical role of complementarity effects in driving rates of ecosystem functioning. Another explanation could be due to the methods used to quantify dung removal which could lead to differences in the observed outcomes. For example, observational studies may use different sampling methods or may not be able to account for the fate of dung that is removed by other organisms in addition to dung beetles. I observed no difference in bioturbation or secondary seed dispersal in observational versus experimental studies. This suggests that these ecological processes may be more consistent and independent of the study method, highlighting the robustness of the observed outcomes. Finally, I found nutrient cycling was greater in experimental studies, however this result is not particularly reliable because of the low sample size from published studies (Figure 2.9).

2.4.5 Data limitations and conclusions

Despite intensive efforts to conduct a comprehensive search for primary publications with relevant data, some papers may have been missed due to the limitations of the search terms. While the naïve search generated a large number of studies, the use of natural language processing methods revealed that the terminology used in this field can be rather broad. As a result, not all authors will include terms like "dung beetle" and "ecosystem function" in their abstract or title, and instead may use completely different and more descriptive terminology. Manually searched studies were not included here, which is a limitation to the outcomes of my study. To capture all published research on dung beetle-mediated ecosystem processes, additional manual searches for studies may have been beneficial for identifying research that does not use the common terminology found in the dung beetle ecology literature, but that may be reported in other disciplines such as environmental engineering (Grames et al., 2019).

Studies investigating dung beetle impacts on ecosystem functions often focused heavily on community factors such as dung beetle abundance, richness, and identity. While these attributes are important, they were often discussed in detail without explicit examination of the subsequent ecological processes resulting from dung beetle activity. As a result, 249 papers were excluded from the meta-analysis. This could be mitigated by developing and using a standardized protocol for dung beetle ecology research, which would yield valuable insights into the relationships between dung beetle community factors, as well as provide a more comprehensive understanding of the effects of dung beetles on ecosystem functions and services. Furthermore, adopting a standardized reporting system could assist future quantitative synthesis exercises, such as meta-analyses, by improving reporting transparency and preventing the damaging "file drawer problem" (Koricheva et al., 2013). This would enhance comparative power between different factors, such as ecosystem type.

The meta-analysis method constrained us to consider only studies that report both control (absence of dung beetles) and treatment (presence of dung beetles) outcomes (Osenberg et al., 1999). As a result, the final dataset included studies that reported the outcomes of control treatments, which are necessary for calculating effect sizes. Consequently, I had to eliminate 63 studies which would have contributed 297 effect sizes to my analyses. Most of the studies that were removed were from tropical settings and wild environments, and despite authors mentioning the use of dung-only controls, they did not report this data in a graph or table form in the paper. Obtaining these data by contacting the authors of these studies would be advantageous for future research, especially since they represent the geographical gaps in my analysis, for example from Southeast Asian tropical rainforests, which have a significant amount of literature on dung beetles but were unfortunately excluded due to lack of reporting on control treatments.

Our meta-analysis specifically focuses on the responses of multiple ecosystem functions to the presence or absence of dung beetles. While there are benefits in concentrating on the functions derived from dung beetle presence in particular, I acknowledge some disadvantages to this, in that it removes potentially fundamental mechanisms for evaluating dung beetle mediated ecosystem functioning, such as abundance and richness effects on ecosystem functioning (Barragán et al., 2011, 2021; Manning & Cutler, 2018b; Sarmiento-Garcés & Hernández, 2021). To address this gap, future research could consider data-mining community attributes and using meta-regression methods to assess the effects of abundance and richness on separate ecosystem functions. In addition to this, there may be an impact of varying dung availability on dung beetle resource use rates. A potential future research direction could also investigate the quantity of dung used in experimental treatments. If an excessive amount is used, it may mask the effects of competition among dung beetles and have repercussions for predicted ecosystem functions (Carvalho et al., 2018).

In summary, my findings indicate that dung beetles exert significant effects on various ecosystem functions, such as trophic regulation, nutrient cycling, plant growth enhancement, dung removal, bioturbation, and secondary seed dispersal. The extent to which these functions are enhanced, however, is contingent on factors such as nesting behaviour, ecosystem type, and variation in study methodologies. Since the impacts of dung beetles are highly context-dependent, repeated observations and experiments conducted across multiple geographic locations, ecosystem types and across gradients of anthropogenic disturbance are necessary to enhance our understanding of the mechanisms underlying their effects. Given the rapid pace of environmental change, it is crucial to determine the overall effects of dung beetle-mediated ecosystem processes. Doing so will enable predictions of the functional consequences of changing dung beetle biodiversity, as well as development of targeted strategies for managing ecosystems and the functions and services they provide.

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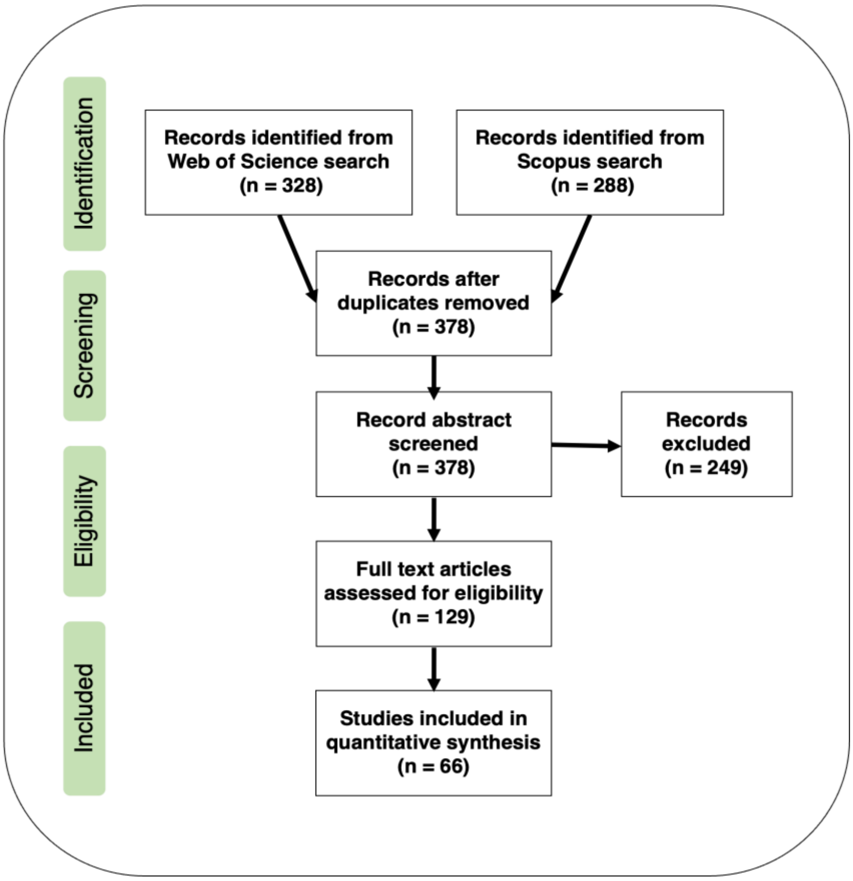
Appendices for chapter two

Appendix 2.1 Prisma flow diagram showing the systematic selection of primary literature.

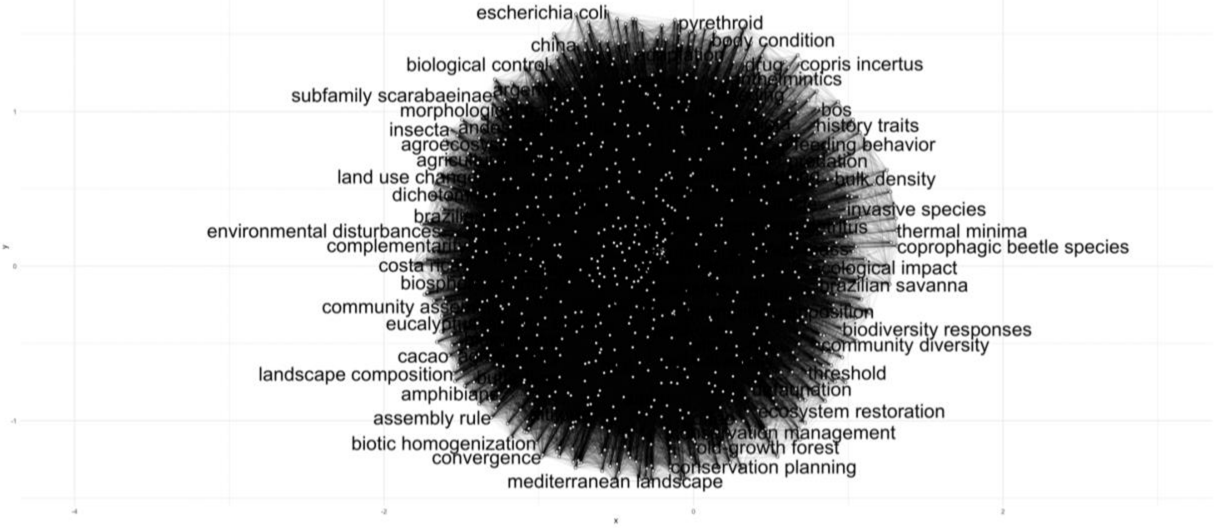


Appendix 2.2 Dung beetle stop words

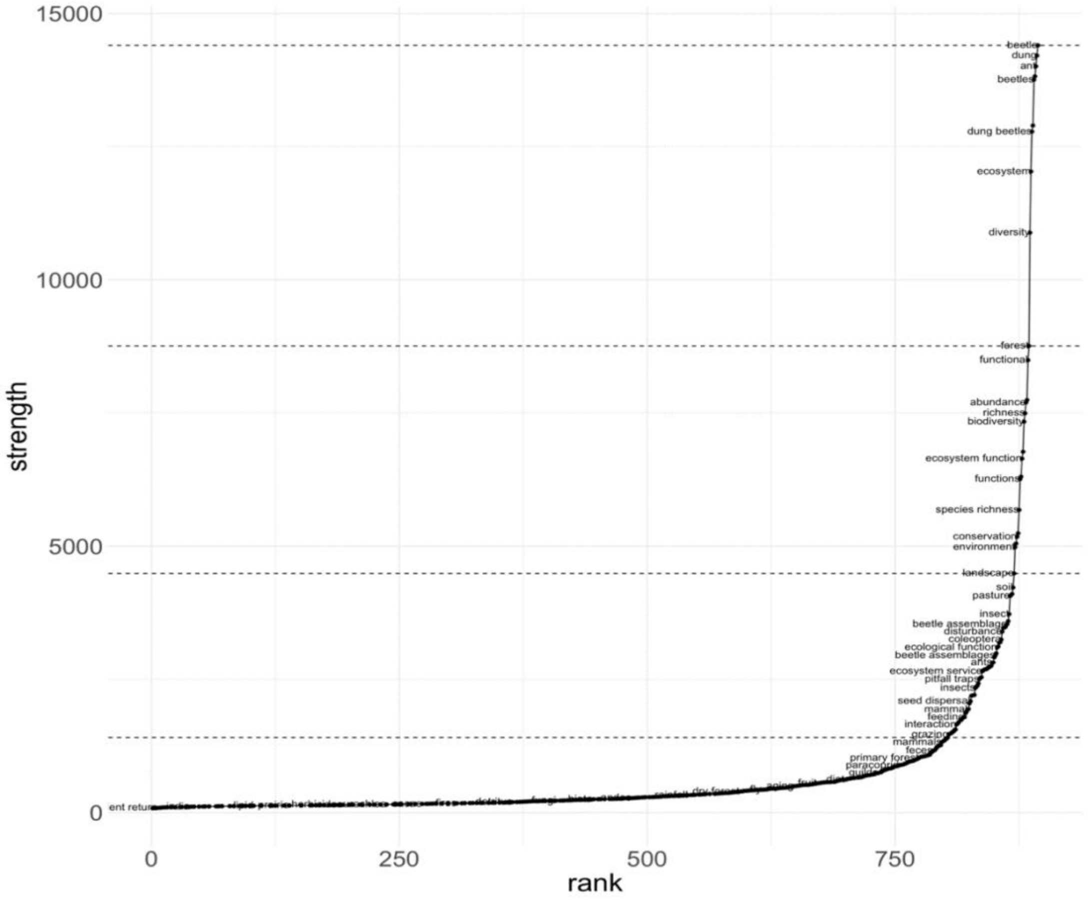
Dung beetle ecology stop words

access
adverse
affected
aimed
amounts
analyses
analysis
appeared
areas
article
aspects
association
attribution
author
balanced
based
belonging
berlin
biotropica
blackwell
british
business
cambridge
causing
challenge
collected
commons
compared
contributed
correlated
correlation
correspondence
creative
critically
current
degrees
delivery
demonstrate
demonstrated
demonstrates
differ
differed
differences
differently
direct
distributed
effect
effects
effort
elsevier
empirical
essential
evaluated
evidence
examined
excellent
exclusive
expansion
explanatory
factors
fewer
findings
focused
found
future
global
greater
group
groups
heidelberg
higher
highlight
identified
impact
implications
important
including
increased
individuals
influence
influenced
information
international
involved
knowledge
large
levels
licence
license
limited
lower
maintaining
major
manipulative
masson
material
media
medical
methods
model
multiple
nacional
needed
negative
number
online
original
oxford
perform
periodicals
periods
permits
points
poorly
positive
positively
potential
predictor
present
press
previous
producing
products
protocols
provide
providers
providing
published
publishing
rapid
reduced
regime
region
related
relationship
remain
remains
represent
research
reserved
respond
results
revealed
rights
royal
sampling
science
sensu
service
shifts
showed
showing
shows
significant
significantly
sites
small
sociedade
society
springer
springer-verlag
standardized
stricto
strong
studied
studies
study
suggest
suggests
support
times
understood
unequally
universidad
university
unknown
unrestricted
urgently
valuable
values
variables
variation
varied
varying
widely
wiley

Appendix 2.3 Key terms co-occurrence network identifying words that are central to the field of study. Terms in the center of the network are of greater importance than those found on the edges.



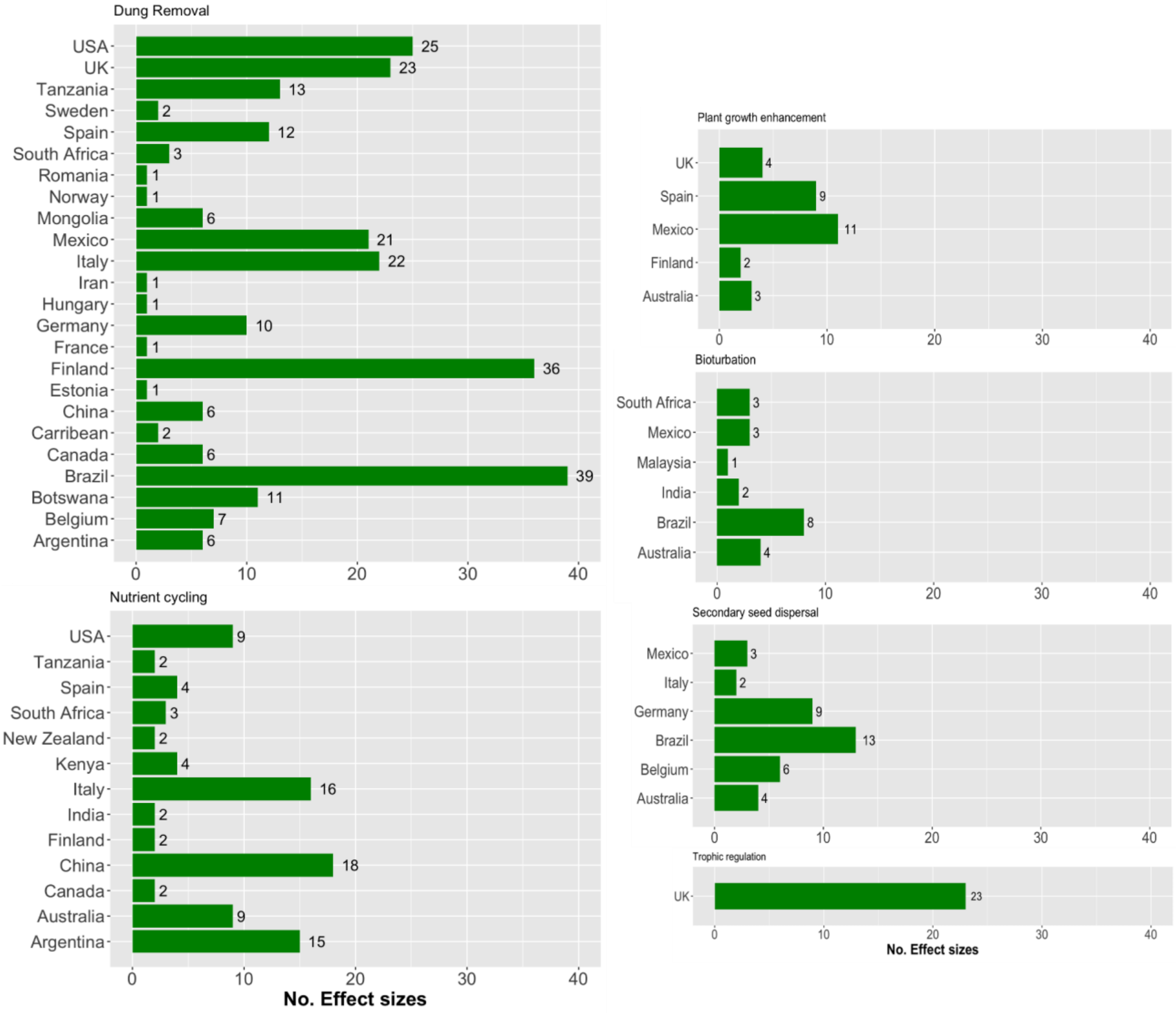
Appendix 2.4 Ranked node strengths of the terms found in the co-occurrence network with cumulative cut off points which returns the minimum number of terms that will give the percent strength of the network. Node strength is a weighted measure of how important a measure is in the network and terms with greater node strengths have more occurrences.



Appendix 2.5 Concept groups following the PICO framework for filtering search terms to produce the final search. Groups were codified as follows: 1 = beetles, 2 = dung, 3 = ecological outcomes, 4 = processes.

Group	Description
1	***Synonyms for dung beetle*** Dung beetle, Scarabaeinae
2	***Synonyms for dung*** Dung, manure
3	***Ecological outcomes relating to dung beetles*** Ecosystem function, ecosystem process, ecosystem service
4	***Potential processes as a result*** Decomposition, bioturbation, nutrient cycling, flux, recycling, primary production, biomass production, plant growth, secondary seed dispersal, pollination

Appendix 2.6 Bar charts showing the number of effect sizes extracted from studies from each country



Appendix 2.7 Results of meta analyses on study-level factors of **overall effect**. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes Hedges' g, the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom (df)and the p-value.

	Effect size				**Test statistics**				
Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
Dung Removal ($Q_{\text{difference}}$)	68.79	[26.08, 111.51]	21.79	0.0016	1719.15	25.80	91.76%	3	< .0001
No Moderators (Q_{overall})	109.14	[85.31, 132.97]	12.16	<.0001	37240.32	13100.05	100.00%	255	< .0001
Paracoprid	67.56	[38.59, 96.51]	14.78	<.0001	9084.99	1902.08	99.99%	44	< .0001
Endocoprid	39.73	[21.93, 57.52]	9.08	<.0001	2021.59	1283.24	99.96%	26	< .0001
Telecoprid	39.61	[18.16, 61.05]	10.94	0.0003	2055.46	636.28	99.88%	18	< .0001
Mixed	135.30	[100.34, 170.25]	17.83	<.0001	52714.43	8885.82	100.00%	167	< .0001
Nutrient Cycling ($Q_{\text{difference}}$)	223.45	[46.15, 400.74]	90.46	0.014	24649.49	26.21	84.30%	3	< .0001
No Moderators (Q_{overall})	301.68	[197.71, 405.64]	53.04	<.0001	487.19	5555.86	100.00%	87	< .0001
Paracoprid	294.81	[142.52, 447.09]	77.70	0.001	204044.46	2226.88	100.00%	34	< .0001
Endocoprid	440.33	[97.07, 783.58]	175.13	0.012	454707.93	1494.75	100.00%	14	< .0001
Telecoprid	23.60	[7.59, 39.60]	8.17	0.0039	503.90	225.54	99.70%	8	< .0001
Mixed	282.64	[112.68, 452.60]	86.72	0.0011	206082.75	1315.21	100.00%	28	< .0001
Bioturbation ($Q_{\text{difference}}$)	202.71	[-153.02, 558.43]	181.50	0.260	98.58	70.20	98.60%	1	< .0001
No Moderators (Q_{overall})	81.18	[24.00, 138.34]	29.17	0.010	14578.49	471.44	100.00%	20	< .0001
Paracoprid	23.76	[18.65, 28.86]	2.61	<.0001	12.45	5.30	61.30%	2	0.0707
Telecoprid	386.79	[302.02, 471.55]	43.25	<.0001	0.00	0.01	0.00%	1	0.9043
Plant Growth Enhancement ($Q_{\text{difference}}$)	123.65	[58.47, 188.83]	33.26	0.000	2662.54	7.70	62.40%	3	0.0527
No Moderators (Q_{overall})	175.41	[102.92, 247.89]	36.98	<.0001	38354.58	1000.05	100.00%	28	< .0001
Paracoprid	62.74	[6.41, 119.05]	28.73	0.029	5527.95	178.30	99.96%	6	< .0001

Endocoprid	119.57	[52.76, 186.37]	34.09	0.0005	3018.51	11.70	89.68%	2	0.0029
Telecoprid	121.31	[24.26, 218.36]	49.52	0.0143	4426.63	9.83	89.83%	1	0.0017
Mixed	241.96	[124.89, 359.03]	59.73	<.0001	58612.49	641.96	100.00%	16	< .0001
Secondary Seed Dispersal ($Q_{difference}$)	96.43	[27.50, 165.35]	35.17	0.010	1677.95	2.65	62.20%	1	0.1036
No Moderators ($Q_{overall}$)	74.13	[44.44, 103.81]	15.15	<.0001	8010.87	914.34	99.80%	35	< .0001
Paracoprid	143.68	[60.72, 226.64]	42.33	0.0007	2563.17	3.30	69.71%	1	0.0692
Mixed	70.26	[39.64, 100.86]	15.62	<.0001	8087.98	878.96	99.85%	33	< .0001
Trophic Regulation ($Q_{difference}$)	330.80	[250.57, 411.01]	40.93	<.0001	0.00	1.93	0.00%	2	0.3813
No Moderators ($Q_{overall}$)	341.72	[239.08, 444.35]	52.37	<.0001	60862.33	631.48	99.70%	23	< .0001
Paracoprid	668.39	[183.83, 1152.94]	247.23	0.0069	106370.91	7.33	86.36%	1	0.0068
Endocoprid	323.32	[233.60, 413.04]	45.78	0.0015	101969.38	272.34	99.99%	10	< .0001
Mixed	311.86	[119.09, 504.63]	98.35	0.0015	101969.38	272.34	99.99%	10	< .0001

Appendix 2.8 Results of meta analyses of **dung removal** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (Hedges' g), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (τ^2), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				Test statistics				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No Moderators	**($Q_{overall}$)**	**109.145**	**[85.31, 132.97]**	**12.160**	**< .0001**	**37240.320**	**13100.047**	**100.00%**	**255**	**< .0001**
Latitude	Tropical	52.367	[40.22, 64.50]	6.193	< .0001	3299.687	3175.553	99.96%	92	< .0001
	Temperate	139.007	[101.82, 176.19]	18.971	< .0001	57894.323	9914.827	100.00%	162	< .0001
	($Q_{difference}$)	93.832	[9.00, 178.65]	43.280	0.0302	3554.112	18.848	94.96%	1	< .0001
Landscape	Production	134.964	[99.32, 170.60]	18.183	< .0001	55509.149	9669.169	100.00%	169	< .0001
	Wild	48.365	[39.45, 57.29]	4.552	< .0001	1602.290	3395.338	99.92%	85	< .0001
	($Q_{difference}$)	89.875	[5.08, 174.66]	43.263	0.0378	3574.017	21.345	95.31%	1	< .0001
Habitat	Agriculture	70.467	[57.17, 83.75]	6.779	< .0001	6924.925	6764.641	99.98%	157	< .0001
	Desert	99.195	[33.37, 165.01]	33.585	0.0031	2118.657	16.096	93.79%	1	< .0001
	Forest	36.784	[28.74, 44.82]	4.103	< .0001	826.919	1880.493	99.86%	53	< .0001
	Grassland	336.132	[211.10, 461.16]	63.793	< .0001	168803.726	4020.353	99.99%	41	< .0001
	($Q_{difference}$)	124.018	[4.75, 243.27]	60.848	0.0415	13660.599	41.137	99.35%	3	< .0001
Introduced / Native	Introduced	52.228	[14.75, 89.70]	19.119	0.0063	1958.134	38.692	98.18%	5	< .0001
	Native	110.527	[86.08, 134.96]	12.470	< .0001	38251.491	12962.311	100.00%	249	< .0001
	($Q_{difference}$)	83.179	[26.15, 140.20]	29.094	0.0042	1438.866	6.523	84.67%	1	0.0106
Study Type	Laboratory	102.377	[63.53, 141.21]	19.816	< .0001	15214.542	1327.201	99.99%	40	< .0001
	Field	109.187	[81.89, 136.47]	13.925	< .0001	41152.816	11764.509	100.00%	214	< .0001
	($Q_{difference}$)	106.936	[84.60, 129.26]	11.393	< .0001	0.000	0.000	0.00%	1	0.7786
Observational / Experimental	Observational	174.130	[120.16, 228.09]	27.534	< .0001	78844.075	6730.774	100.00%	104	< .0001
	Experimental	52.052	[120.16, 228.09]	5.023	< .0001	3537.200	6369.143	99.96%	150	< .0001
	($Q_{difference}$)	110.089	[120.16, 228.09]	60.965	0.071	7059.773	19.025	94.74%	1	< .0001

Appendix 2.9 Results of meta analyses of **nutrient cycling** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators	**($Q_{overall}$)**	301.6822	[197.71, 405.64]	53.0436	< .0001	237352.0825	5555.8576	100.00%	87	< .0001
Latitude	Tropical	18.5173	[9.16, 27.87]	4.773	0.0001	433.9885	476.6099	99.72%	22	< .0001
	Temperate	361.103	[232.43, 489.77]	65.6499	< .0001	273767.9584	4671.848	100.00%	64	< .0001
	($Q_{difference}$)	183.5531	[-151.95, 519.05]	171.1786	0.2836	56516.1622	27.0883	96.31%	1	< .0001
Landscape	Production	86.3159	[57.38, 115.24]	14.7585	< .0001	12433.5223	3305.534	99.98%	61	< .0001
	Wild	817.7227	[493.74, 1141.69]	165.2959	< .0001	663047.1007	2148.8083	99.99%	25	< .0001
	($Q_{difference}$)	433.49	[-282.35, 1149.33]	365.2337	0.2353	253707.6779	19.4243	94.85%	1	< .0001
Habitat	Agriculture	90.7476	[59.05, 122.44]	16.1709	< .0001	14212.8496	2955.1305	99.98%	58	< .0001
	Forest	30.0763	[9.49, 50.66]	10.5033	0.0042	756.313	348.508	98.47%	8	< .0001
	Grassland	900.0261	[548.51, 1251.53]	179.3443	< .0001	616573.2022	1171.1642	99.93%	19	< .0001
	($Q_{difference}$)	313.6796	[-208.16, 835.52]	266.2516	0.2387	202837.2708	32.4116	99.80%	1	< .0001
Introduced / Native	Introduced	293.5306	[104.54, 482.51]	96.4234	0.0023	137226.7262	540.8728	100.00%	15	< .0001
	Native	300.934	[104.54, 482.51]	61.152	< .0001	259194.9418	5013.0458	100.00%	71	< .0001
	($Q_{difference}$)	298.8104	[197.59, 400.02]	51.6421	< .0001	0	0.0042	0.00%	1	0.9483
Study Type	Laboratory	291.2607	[2.68, 579.83]	147.2357	0.0479	82954.2486	65.3948	99.78%	3	< .0001
	Field	303.5581	[194.52, 412.59]	55.6322	< .0001	249168.8102	5411.2495	100.00%	83	< .0001
	($Q_{difference}$)	302.0218	[200.02, 404.02]	52.0412	< .0001	0	0.0061	0.00%	1	0.9377
Observational / Experimental	Observational	28.8178	[6.49, 51.14]	11.39	0.0114	235.2589	10.2999	90.29%	1	0.0013
	Experimental	309.1748	[202.64, 415.70]	54.3507	< .0001	243423.7759	5502.529	100.00%	85	< .0001
	($Q_{difference}$)	163.9594	[-110.60, 438.52]	140.0879	0.2418	37758.1395	25.4886	96.08%	1	< .0001

Appendix 2.10 Results of meta analyses of **bioturbation** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators	**($Q_{overall}$)**	81.178	[24.01, 138.34]	29.169	0.005	14578.487	471.442	100.00%	20	< .0001
Latitude	Tropical	69.125	[14.59, 123.65]	27.820	0.013	13163.144	417.446	100.00%	17	< .0001
	Temperate	3997.373	[2929.26, 5065.48]	544.963	< .0001	0.000	0.196	0.00%	2	0.9067
	($Q_{difference}$)	1995.546	[-1853.35, 5844.44]	1963.762	0.310	7566688.285	51.824	98.07%	1	< .0001
Landscape	Production	905.549	[-9.03, 1820.14]	466.634	0.052	2204993.042	126.767	100.00%	10	< .0001
	Wild	75.014	[-13.86, 163.89]	45.349	0.098	19912.202	337.857	100.00%	9	< .0001
	($Q_{difference}$)	360.431	[-412.66, 1133.52]	394.444	0.361	234992.025	3.138	68.13%	1	0.0765
Habitat	Agriculture	905.549	[-9.03, 1820.13]	466.634	0.052	2204993.042	126.767	100.00%	10	< .0001
	Forest	102.169	[-30.57, 234.90]	67.726	0.131	31122.183	124.639	100.00%	6	< .0001
	Grassland	23.758	[18.65, 28.86]	2.606	< .0001	12.452	5.298	61.30%	2	0.0707
	($Q_{difference}$)	46.378	[-26.54, 119.30]	37.209	0.213	1777.008	4.908	28.32%	2	0.0859
Study Type	Laboratory	23.758	[18.65, 28.86]	2.606	< .0001	12.452	5.298	6130.00%	2	0.0707
	Field	100.076	[28.04, 172.11]	36.751	0.007	19374.174	254.201	100.00%	17	< .0001
	($Q_{difference}$)	53.113	[-19.65, 125.88]	37.129	0.153	2233.474	4.291	76.96%	1	0.0383
Observational / Experimental	Observational	163.389	[50.19, 276.58]	57.752	0.005	24742.009	124.596	100.00%	7	< .0001
	Experimental	665.837	[-73.66, 1405.33]	377.303	0.078	1703056.204	326.396	100.00%	12	< .0001
	($Q_{difference}$)	276.268	[-134.73, 687.27]	209.700	0.188	53380.664	1.733	42.29%	1	0.1881

Appendix 2.11 Results of meta analyses of **plant growth enhancement** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators	**$(Q_{overall})$**	175.411	[102.92, 247.89]	36.984	<.0001	38354.582	1000.046	100.00%	28	<.0001
Latitude	Tropical	156.053	[0.71, 311.38]	79.255	0.049	67709.521	337.986	100.00%	10	<.0001
	Temperate	187.737	[112.66, 262.81]	38.304	<.0001	25138.928	661.151	99.97%	17	<.0001
	$(Q_{difference})$	181.737	[114.14, 249.33]	34.487	<.0001	0.000	0.130	0.00%	1	0.7189
Landscape	Production	194.662	[71.90, 317.41]	62.631	0.0019	45476.239	340.304	100.00%	11	<.0001
	Wild	162.237	[71.79, 252.68]	46.147	0.0004	35087.793	659.660	100.00%	16	<.0001
	$(Q_{difference})$	173.647	[100.83, 246.46]	37.152	<.0001	0.000	0.174	0.00%	1	0.6768
Habitat	Agriculture	159.891	[90.12, 229.65]	35.593	<.0001	25522.408	663.485	99.99%	20	<.0001
	Forest	218.100	[12.56, 423.63]	104.869	0.0375	86043.931	336.104	100.00%	7	<.0001
	$(Q_{difference})$	165.904	[99.84, 231.96]	33.705	<.0001	0.000	0.276	0.00%	1	0.5992
Introduced / Native	Introduced	-5.291	[-15.98, 5.39]	5.454	0.332	85.155	33.828	99.04%	2	<.0001
	Native	197.253	[119.90, 274.59]	39.462	<.0001	39019.472	965.328	100.00%	25	<.0001
	$(Q_{difference})$	92.210	[-106.14, 290.56]	101.202	0.3622	19718.476	25.850	96.13%	1	<.0001
Study Type	Laboratory	153.935	[100.06, 207.80]	27.485	<.0001	7543.649	102.232	95.83%	10	<.0001
	Field	189.246	[73.34, 305.14]	59.134	0.0014	61286.226	580.402	100.00%	17	<.0001
	$(Q_{difference})$	160.208	[111.35, 209.05]	24.925	<.0001	0.000	0.293	0.00%	1	0.5882

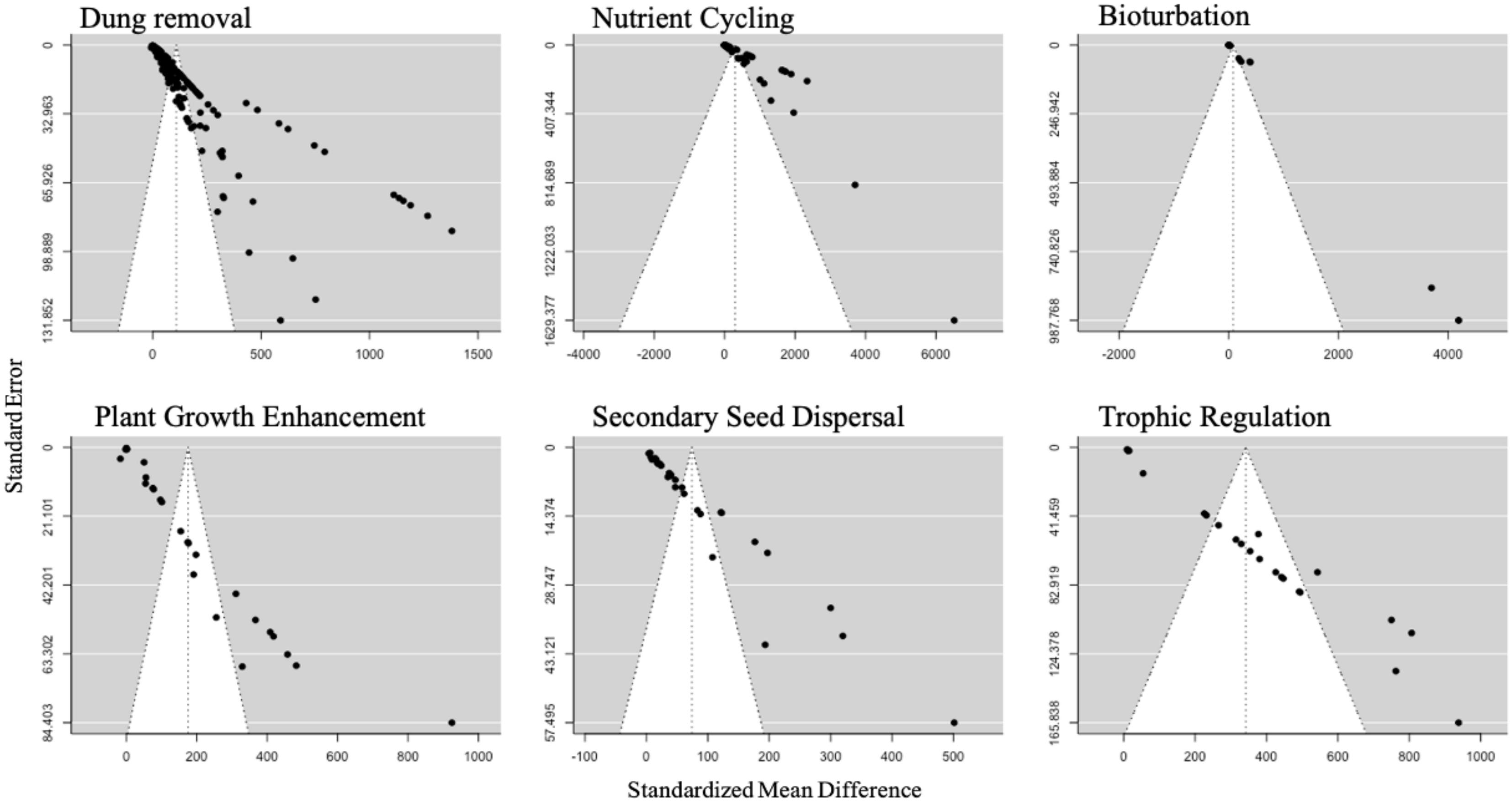
Appendix 2.12 Results of meta analyses of **secondary seed dispersal** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

		Effect size				**Test statistics**				
	Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators	**($Q_{overall}$)**	74.128	[44.44, 103.81]	15.147	<.0001	8010.866	914.339	99.84%	35	<.0001
Latitude	Tropical	101.904	[48.81, 154.99]	27.085	0.0002	14317.615	664.536	99.90%	19	<.0001
	Temperate	34.952	[25.24, 44.65]	4.950	<.0001	329.619	247.120	95.50%	15	<.0001
	($Q_{difference}$)	63.133	[-1.65, 127.91]	33.055	0.0561	1862.274	5.913	83.09%	1	0.015
Landscape	Production	115.499	[41.17, 189.82]	37.923	< .0001	19571.126	437.455	99.91%	13	<.0001
	Wild	51.833	[30.52, 73.13]	10.871	<.0001	2515.848	460.793	99.48%	21	<.0001
	($Q_{difference}$)	73.299	[14.30, 132.28]	30.097	0.0149	1248.477	2.604	61.60%	1	0.1066
Habitat	Agriculture	115.499	[41.17, 189.82]	37.923	0.0023	19571.126	437.455	99.91%	13	<.0001
	Forest	52.560	[30.13, 74.98]	11.440	<.0001	2661.702	445.284	99.52%	20	<.0001
	Grassland	39.408	[27.73, 51.08]	5.956	<.0001	0.000	0.000	0.00%	0	1.000
	($Q_{difference}$)	47.912	[30.47, 65.34]	8.896	<.0001	96.367	4.703	38.80%	2	0.0952
Study Type	Laboratory	143.685	[60.72, 226.64]	42.329	0.0007	2563.169	3.301	69.71%	1	0.0692
	Field	70.258	[39.64, 100.86]	15.618	<.0001	8087.984	878.957	99.85%	33	<.0001
	($Q_{difference}$)	96.431	[27.50, 165.35]	35.168	0.0061	1677.947	2.649	62.24%	1	0.1036
Observational / Experimental	Observational	94.418	[11.59, 177.24]	42.259	0.0255	22782.854	313.209	99.96%	12	<.0001
	Experimental	64.920	[43.48, 86.35]	10.938	<.0001	2595.001	572.875	99.71%	22	<.0001
	($Q_{difference}$)	66.772	[46.01, 87.52]	10.589	<.0001	0.000	0.457	0.00%	1	0.4992

Appendix 2.13 Results of meta analyses of **trophic regulation** on different moderators. The first random effects model fit shows the difference between sub-groups and the second shows the overall effect of dung removal. The effect size section includes the standardised mean difference (SMD), the 95% confidence interval (CI) and the standard error (SE). The test statistics include total heterogeneity (Tau Squared), the test for heterogeneity (Q), the degrees of freedom and the p-value.

	Effect size				**Test statistics**				
Random Effects Model	**Hedges' g**	**95% CI**	**SE**	**p-value**	**Total Heterogeneity (τ^2)**	**Test for Heterogeneity (Q)**	**I^2**	**df**	**p-value**
No moderators ($Q_{overall}$)	354.971	[250.65, 459.28]	53.223	<.0001	59990.167	624.373	99.97%	22	<.0001

Appendix 2.14 A funnel plot of the estimates (Standardized Mean Difference = Hedges' g) for the overall effects (no moderators) of each ecosystem function. Both the rank correlation and the regression test indicated potential funnel plot asymmetry at p < 0.0001 and p < 0.0001 for (a) dung removal; (b) nutrient cycling; (c) bioturbation; (d) plant growth enhancement; (e)secondary seed dispersal; and (f) trophic regulation.



Appendix 2.15 Data sources (alphabetical-order) list of 66 studies

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Chapter Three. COMPARING COMMUNITY STRUCTURE, FUNCTIONAL TRAITS, AND METABOLIC RATES OF DUNG BEETLES AS PREDICTORS OF ECOSYSTEM FUNCTIONING

Abstract

The influence of dung beetles on ecosystem functioning is well-studied, with evidence that abundance, diversity, and a suite of life history traits can facilitate the removal of dung, promoting overall ecosystem functioning in both natural and human modified landscapes. However, there is a paucity of research investigating the relative importance of the biotic drivers that shape dung beetle community characteristics including (i) community structure, (ii) functional traits, and (iii) community energy use, on ecosystem functioning such as dung removal. To address this knowledge gap, I conducted a field experiment to quantify dung beetle community characteristics and associated dung removal rates at 16 sites across two locations in the North Island of Aotearoa New Zealand. To determine community structure, I quantified abundance, richness and dominant species. I then measured individual-level morphological features from each beetle (including the length and width measurements of body, thorax, head, eye, abdomen, and tibia) which I then used to quantify functional traits including: fresh body mass, reproductive capacity, nesting behaviour, and activity period. I then estimated the metabolic rate of each beetle (J hr^{-1}) using published allometric scaling relationships. To conduct a community-level trait analysis, I calculated the community weighted mean (CWM) values for each functional trait. To evaluate the energy demand of the community, I summed the metabolic rates of the dung beetles within each community to calculate community energy use (CEU). I used mixed effects models of community structure, functional traits, and community energy use to explore the relationships between community characteristics and ecosystem functioning. According to my findings, nesting behaviour was an important functional trait in predicting dung removal rates. However, in contrast to my expectations, community structure and community energy use were found to be poor predictors of dung removal. These findings emphasise the significance of taking into account relevant functional traits, in addition to typical community structure measures, when conducting biodiversity-ecosystem function research. Furthermore, my study highlights the need for a targeted exploration of functional traits in order to better understand their impact on ecosystem functioning and to improve our ability to predict the consequences of changes in community structure on ecosystem processes.

Key words

Trait-function relationship, metabolic theory of ecology, biodiversity-ecosystem functioning

3.1 Introduction

The interconnection between biodiversity and ecosystem functioning (B-EF) is complex. Although biodiversity has been shown to enhance the functioning of ecosystems and the provision of broader-scale ecosystem services (Mace et al., 2012), other studies have shown that there is not necessarily a positive linear relationship between species richness and ecosystem functioning. The functioning of ecosystems is largely influenced by the organisms present, and thus, community composition and species traits play a crucial role (Reiss et al., 2009). Community characteristics can be divided into a set of biotic factors that have the potential to drive ecosystem functioning. For example, classical metrics of community structure, including richness, abundance and dominant species (Larsen et al., 2005), functional traits (Díaz et al., 2013) and more recently, community energetic demand (Brandl et al., 2022).

Dung beetles have been used as a model organism for studying the relationship between biodiversity and ecosystem functioning, and studies testing the effects of community structure has revealed different patterns associated with dung beetle abundance (Jargalsaikhan et al., 2023) and richness (Manning et al., 2016; Nunes et al., 2018; Slade et al., 2007) in predicting dung removal, a key ecosystem function. Furthermore, the effect of dominant dung beetle species has been shown to contribute to greater resource use through competitive advantages and its use of broader trophic niches than other species (Salomão et al., 2014) enhancing ecosystem functioning.

Early B-EF research focused on investigating the relationship between taxonomic diversity and ecosystem functioning to establish the functional consequences of changing biodiversity (Tilman et al., 2014). However, traditionally used taxonomic diversity indices that describe community structure may present limitations when it comes to predicting variation in ecosystem functioning (Gagic et al., 2015; Reiss et al., 2009). To improve predictions of ecosystem functioning, researchers have suggested measuring the functional traits of organisms, a method derived from the field of plant ecology (Dawson et al., 2021; Eisenhauer et al., 2016, 2019). Recent advances in trait-based approaches for understanding the trait-mediated effects of dung beetles have identified 66 dung beetle traits that respond to the environment and affect ecosystem processes, covering a wide range of spatial, temporal, and biological scales (deCastro-Arrazola et al., 2022). Yet, identifying the relevant traits that have a greater potential of predicting the functioning of ecosystems within communities remains to be a challenging task (Mlambo, 2014; Violle et al., 2007b).

Body size is considered a fundamental and universal trait that plays a central role in determining various biological processes (J. H. Brown et al., 2004). As a result, body size is often described as a 'super-trait', because it is strongly correlated with life history traits including fecundity, behaviour, and dispersal ability (Bribiesca et al., 2019). Body size has been shown to be a significant predictor of dung removal by dung beetles (Gebert et al., 2022). For example, individuals of *Onthophagus* spp. dung beetles with larger body sizes have demonstrated greater likelihood of tunnelling behaviour compared to those with smaller body sizes (Palestrini et al., 2001). Furthermore, previous studies investigating the relationship between dung beetle body size and ecosystem functioning have identified that larger beetles typically remove a larger quantity of dung, with positive effects of both body size (Kenyon et al., 2016; Nervo et al., 2014; Tonelli et al., 2020) and behaviour, such as nocturnal activity (Slade et al., 2011) on the amount of dung buried.

The morphological features of beetles can reflect behaviour, which can potentially predict resource use (Fountain-Jones et al., 2015). Morphological measures can therefore be used to calculate an index indicating the level of adaptation of certain behavioural traits, such as reproductive capacity (Srygley & Chai, 1990), nesting behaviour (Raine et al., 2018), and activity period (Caveney et al., 1995), which is useful because directly quantifying behavioural traits can be difficult as they require observation of living individuals. Raine et al. (2018) showed that dung beetle morphological traits can be used to calculate dung beetle behavioural traits, providing a reliable foundation to assess functional trait information for species lacking natural history information.

Moreover, employing a quantitative technique for behavioural traits based on morphological measures on an individual level allows for the calculations of the community-weighted mean of a trait (CWM), which is a widely used index of functional diversity that is defined as the mean of values present in the community weighted by the relative abundance of individuals bearing each value (Lavorel et al., 2008). For example, if a dung beetle community exhibits an index indicating a greater reproductive capacity, this could mean that more individuals can produce more offspring, leading to more brood balls being provisioned with dung. Similarly, if a dung beetle community exhibits an index that reflects greater nesting behaviour, this reflects how and where the dung beetle species' eggs are deposited and provisioned (Hanski & Cambefort, 1991; Rössner, 2012). This can result in a greater rate of dung removal and burial, which has important implications for nutrient cycling and other ecosystem processes. However, the boundaries between certain calculated functional traits, such as reproductive capacity and nesting behaviour could be related or overlapping (deCastro-Arrazola et al., 2022) making it difficult to distinguish between. For example, the index for reproductive capacity is based on abdomen and thorax measurements (Srygley & Chai, 1990), and nesting behaviour is based on measurements of hind tibia length and width (Raine et al., 2018). While the quantification methods are independent, the inferences my not be as clear. Could it be that variation in abdomen size indicates a dung beetle's capacity to support the weight of its hind legs, which may be mistaken for adaptations related to reproductive capacity? In other words, a beetle with a proportionally larger abdomen will not necessarily be better suited for reproduction. On the other hand, some traits may be more distinct, such as activity period, because it is calculated through eye measurements (Caveney et al., 1995). For instance, activity period can indicate whether a community is more active during the day (diurnal), night (nocturnal), or dawn and dusk (crepuscular). This can provide valuable insights into complementarity effects that contribute to enhanced ecosystem functioning over time, for example enhanced dung burial and microbial activity (Menéndez et al., 2016).

One trait with little coverage in the dung beetle literature is metabolic rate. According to the metabolic theory of ecology (MTE), individual metabolic rate constrains the structure and function of ecological communities (Brown et al., 2004). The correlation between body mass and metabolic rate implies that it could serve as a reliable predictor of a species' functional role within ecosystems (Reiss et al., 2011) and a valuable tool for studying ecosystem functioning. Metabolic traits, which describe an organisms' energetic demands, can provide a way to link energy acquisition and allocation. However, while traits related to energy and nutrient acquisition and expenditure have been used to understand plant communities, the use of such traits in animal communities has been limited (Brandl et al., 2022). To date, there has been insufficient research examining the relationship between energetic traits like metabolic rate and ecosystem functioning in animals, such as dung removal carried out by dung beetles (Brandl et al., 2022; Enquist et al., 2003).

Early work by Chown & Steenkamp (1996) studied body size-abundance relationship in dung beetles over 16 months and tested the impact of metabolic rate and population growth scaling on assemblage structure, but did not test for any association with dung removal. Energetic constraints of telecoprid, paracoprid and endocoprid dung beetles have been discussed as a possible factor in patterns of dung removal in the afrotropics (Krell et al., 2003) but no measurements of individual or community metabolic rates have been explicitly quantified to address this. Similarly, Dangles et al. (2012) tested how dung and carrion beetles of different body sizes affect ecosystem functioning in a removal experiment, with speculation that metabolic constraints would be the underlying mechanism explaining the variation observed. However, while their results showed that body size positively affected dung removal, they did not quantify metabolic rate or further discuss their results through the lens of their initial hypotheses. Barnes et al. (2014) evaluated the impact of dung beetle body mass on dung removal rate by considering both body mass and biomass as variables in their model and found a negative relationship between body mass and mass-specific dung removal rates but did not account for the role of metabolic constraints in their findings. As a result, there has been no mechanistic connection between dung beetle metabolic rate and ecosystem functioning, leaving us with the question: is dung beetle energetic demand (or, community energy use, CEU) capable of predicting dung removal rates and, therefore, ecosystem functioning?

Intentionally designing agricultural landscapes to support the ecological functions of arthropods, like dung beetles, can lead to the provision of better ecosystem services (Doube, 2018; Forgie et al., 2018; Haan et al., 2021). Disentangling the relative importance of dung beetle community structure, functional traits, and community energy use can help in understanding how these organisms contribute to ecosystem functioning and how they can be better supported through agricultural management practices. Traits have been shown to be useful to assess plant community dynamics and ecosystem properties, with multivariate analysis found to be the most effective method of evaluating these effects (Miller et al., 2019). In this study, I aim to examine the effect of community characteristics of dung beetles on ecosystem functioning. Specifically, I test whether dung beetle community structure (abundance, richness, and species dominance), functional traits (fresh body size, reproductive capacity, nesting behaviour, activity period) and community energy use can predict dung removal, a key ecosystem function (Figure 3.1).

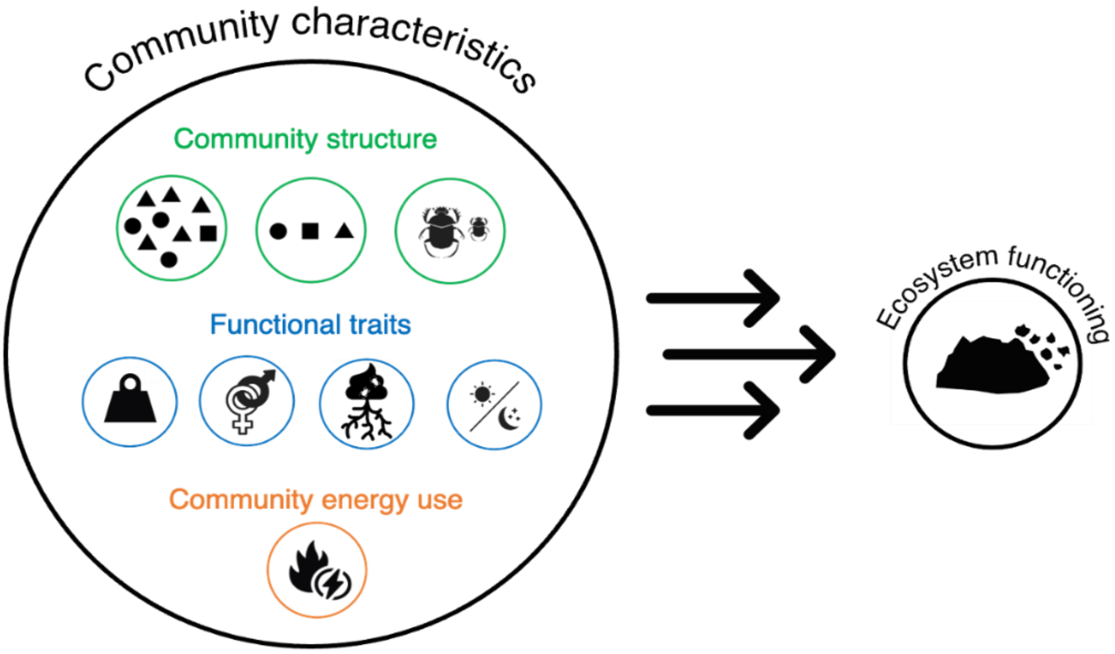

Figure 3.1 Conceptual diagram illustrating the community characteristics and biotic drivers that may contribute to shaping dung beetle mediated ecosystem functioning, in this case, dung removal.

Using a paired pitfall trapping and dung removal experiment, my study tests three primary hypotheses that: (i) dung beetle abundance and richness will be positively associated with dung removal, but this may be affected by the dominant species in the community, leading to variations in dung removal; (ii) community weighted mean functional traits, including body size, reproductive capacity, nesting behaviour, and activity period will play a significant role in determining dung removal rates; and (iii) the total community energy use, which is the sum of the metabolic rates of individual dung beetles in each community, will predict dung removal rates in dung beetle communities.

3.2 Methods

3.2.1 Field site

To investigate the relationships between dung beetle community structure, functional traits, and community energy use with ecosystem functioning, dung beetle assemblages were surveyed in the North Island of Aotearoa NZ, from December 2020 to December 2021. Sampling was done at two farm locations, Shelly Beach Farm in Kaipara Harbour (36°34'05.0"S, 174°21'01 . 7"E) and Miromiro Farm in Taupo (38°26'03.4" S, 175°58'00.9"E) (Figure 3.2). These regions primarily consist of agricultural pasture for grazing livestock and both farms had well established communities of introduced dung beetle populations. To characterise the environmental variables at each location, mean annual temperature and total annual precipitation were used from the New Zealand Environmental Data Stack v 1.0 (NZEnvDS) (McCarthy et al., 2021). The mean annual temperature at Shelly Beach was 14.6°C and 12.5°C at Miromiro, with total annual precipitation of 1163 mm and 1376 mm, respectively. At each farm, four sites were established giving a total of eight sites, where data collection was conducted each month. To avoid shade effects in tree-lined pastures, a minimum distance of 200 m was maintained between sites and pasture edges.

Figure 3.2 The North Island of Aotearoa New Zealand. The two farms where data were collected are shown by red dots (4 data collection sites were established at each farm).

3.2.2 Experimental design

To quantify the proportion of dung removed from the pasture surface by dung beetle action, a dung removal trial (n = 8) was conducted concurrently with pitfall trapping (n = 8) at each farm site each month for 12 months (Appendix 3.1). The dung removal trial was carried out at a distance of 5 meters from each pitfall trap. Fresh dung was collected and homogenised in 10L buckets in the early morning to prevent other insects being present in the dung. A sub sample of two 1 kg fresh dung pads were then placed into coarse 2 mm mesh bags (bagged) to exclude dung beetles, and two 1 kg fresh dung pads were left in the open on the pasture surface (unbagged) (Appendix 3.1a). The bagged and unbagged dung samples were collected after 24-hours and dried at 65°C for up to three days until there was no change in dry weight and then a final weight was recorded. The proportion of dung removed by dung beetles was calculated by subtracting the unbagged initial dry weight from the ending dry weight after being in the field.

To sample the dung beetle community, a baited pitfall trapping protocol was implemented using trays baited with 1 kg of dung in a fine fly screen mesh bag placed on the flattest area of the paddock for a 24-hour period. The trays were filled with food-grade propylene glycol, with a steel grid placed on top of the tray to ensure that beetles fell into the liquid and remained there until collection. The tray and steel grid were secured using tent pegs at four corners (Appendix 3.1b). After 24 hours, the dung beetle pitfall samples were collected by straining the beetles through a 125 μm plankton sieve and preserving them in 80% ethanol.

3.2.3 Dung beetle species and community structure

All beetles were identified to species level at the University of Waikato using a custom ID guide of introduced dung beetle species. In total, our sampling campaign captured 350 individuals from seven species, comprising *Geotrupes spiniger, Copris incertus, Onthophagus binodis, Onthophagus taurus, Bubas bison, Digitonthophagus gazella,* and *Onthophagus granulatus.* To examine the potential effects of community structure on ecosystem functioning, the abundance (i.e., total number of individuals), richness (i.e., number of species) and dominant species (i.e., the species with the highest abundance) from each sample were quantified. If two or more species had equally high abundance within a community, the dominant species was classified as 'even'.

3.2.4 Individual morphological measures

Eleven morphological traits of the dung beetles were measured using a LEICA microscope, including body length, body width, thorax length, thorax width, head length, head width, eye length, eye width, tibia length, tibia width, and abdomen length.

3.2.5 Individual functional traits

I then used these morphological measurements to calculate the fresh body mass, reproductive capacity, nesting behaviour and activity period of each individual dung beetle. To calculate fresh body mass of each dung beetle, I used an allometric scaling regression model for Coleoptera (Sohlström et al. 2018) with the formula:

$$log10(Bodymass) = intercept \ + \ slope_L \cdot \ log_{10}(L) + slope_W + \ log_{10}(W) \tag{3.1}$$

Where L is the body length and W is the body width of the beetle.

I then quantified functional traits indicating reproductive capacity, nesting behaviour and activity period, which are considered key behavioural traits associated with ecosystem functioning. For reproductive capacity, I calculated the ratio of thorax length to abdomen length, where a value close to 1 indicates that a beetle's abdomen is as large as its thorax, suggesting a greater reproductive capacity (Srygley & Chai, 1990). Dung beetle nesting behaviour was calculated through assessing hind leg robustness, where I divided the tibia width by the tibia length, where a ratio close to 1 suggests that the leg is proportionally wider and shorter indicating the presence of more muscle mass, indicating greater adaptation to tunnelling, moving and burying dung (Raine et al., 2018). To quantify the activity period of dung beetles, I calculated the relative size of the eyes by dividing the length of the eye by the length of the body, where a value close to 1 indicates that the individual has relatively large eyes in proportion to its body size, and is better suited to nocturnal activity (Caveney et al., 1995).

I then calculated individual metabolic rates (J h^{-1}) of each dung beetle using regression parameters taken from an allometric scaling relationship for Coleoptera and using the formula

$$\ln I = \ln i_{oPG} + a_{PG} \cdot \ln M - E_{PG} \left(\frac{1}{kT}\right)$$

(3.2)

where *I* is the whole-organism metabolic rate, *E* is the activation energy (eV), *k* is the Boltzmann constant ($8.62 \times 10^{-5} \cdot \mathrm{eV} \cdot \mathrm{K}^{-1}$), *T* is the average annual temperature for each site, *a* is the allometric exponent, *M* is the fresh body mass, and i_o is a normalisation factor (Ehnes et al., 2011).

3.2.6 Community weighted calculations

To assess overall effects of dung beetle functional traits and metabolic rate, I calculated community weighted values from the individual level data. The community-weighted mean (CWM) values for body mass, reproductive capacity, nesting behaviour and activity period for each dung beetle community, weighted by abundance as

$$CWM_{j,y} = \sum_{k=1}^{n_j} A_{k,j}.Z_k$$

(3.3)

where n_j is the number of species that were sampled within dung beetle community, j ; and $A_{\mathrm{k,j}}$ is the relative abundance of species k in community j, and Z_k denotes the average value of species k. I then calculated community energy use by summing the individual metabolic rates ($\mathrm{J\ h}^{-1}$) of all dung beetles for each community (Barnes, Jochum, et al., 2014).

3.2.7 Statistical analyses

To understand how community structure, functional traits, and community energy use explains variation in dung removal, I created two linear mixed-effects models using the 'lme4' package using the lmer() function (Bates et al. 2022) in R (R Core Team, 2022). To ensure that model assumptions were met, including normality and homogeneity of variance, I logit transformed the proportion of dung removed. In the first model, I examined the influence of dung beetle community structure, using abundance, richness and dominant species, and their interaction to predict the proportion of dung removed. Because I pooled all data collected from the two farms for analyses, I specified sampling location (farm) as a random effect. I then scaled the three variables: dung removed, abundance and richness, with a mean of 0 and a standard deviation of 1, to reduce structural multicollinearity. However, high levels of multicollinearity arising from the interaction term between species richness and dominant species were still detected using the variance inflation factor (VIF), so I revised the model to exclude this interaction term. I then compared the model fits with and without the interaction term using AIC, which further supported its exclusion (i.e. this reduced the AIC score by > 2 units). In the second model, to test the effects of functional traits and community energy use (CEU) on dung removal, I used the community weighted mean values of fresh body mass, reproductive capacity, nesting behaviour, activity period, and CEU with sampling location (farm) specified as a random effect. All model assumptions were satisfied, and no additional modifications were made. The models were fitted with the restricted maximum likelihood method (REML = TRUE).

3.3 Results

3.3.1 Community structure effects on dung removal rates

The model of community structure showed that there were no significant effects of abundance, richness or dominant species on dung removal rates (Figure 3.3; Appendix 3.1). Although I observed differences, I did not detect a significant effect, possibly due to the limited number of replicates for some dominant species, such as *C. incertus* (Figure 3.3; Appendix 3.1).

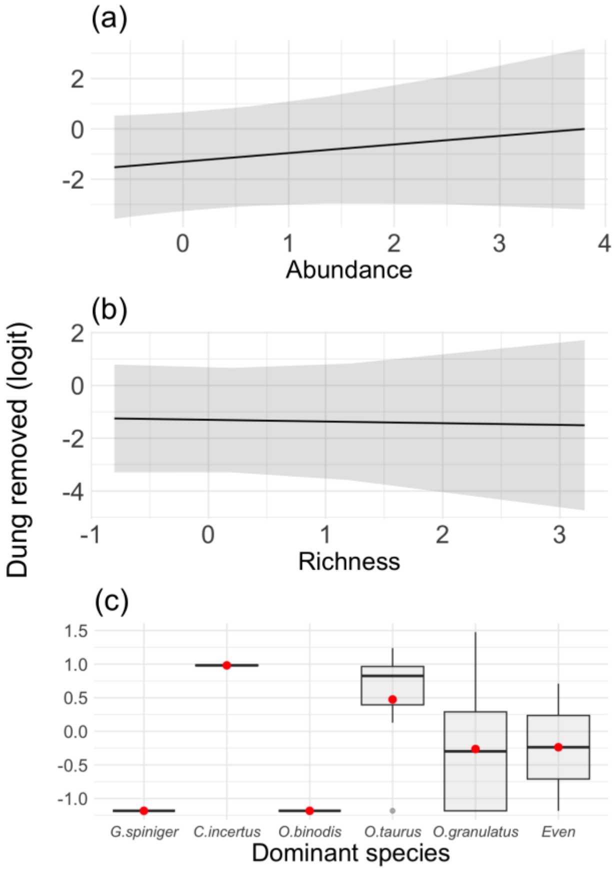

Figure 3.3 Estimated marginal effects (± 95% CI) of three community variables including (a) abundance; (b) richness and (c) dominant species on dung removal.

3.3.2 Individual level patterns of functional traits

On the individual level, there was variation of functional traits including fresh body mass, reproductive capacity, nesting behaviour, activity period, and metabolic rate (Figure 3.4). For example, the mean fresh body mass of dung beetle species ranged from 26.82 g (*O .granulatus)* to a maximum of 875.08 g (*G. spiniger*) (Figure 3.4a; Appendix 3.4). In line with this, *G. spiniger* also exhibited a relatively larger abdomen compared to its thorax, with a reproductive capacity value close to 1, while *B. bison* had a mean reproductive capacity value of 2.09, indicating a relatively smaller abdomen compared to its thorax and a possibly lower reproductive capacity (Figure 3.4b; Appendix 3.4). *C. incertus* had the lowest mean nesting behaviour (hind leg robustness) ratio of 0.11 compared to *B. bison* with the greatest mean nesting behaviour ratio of 0.20, indicating that *B. bison* has relatively wider tibia compared to their length. I expected nocturnal species to have a higher ratio of eye length to body length, suggesting a greater capacity to operate in the dark. *C. incertus* had the average activity period closest to 1 (Figure 3.4d). On the other hand, *B. bison* had a mean activity period of 0.01, a value further from 1, suggesting it is adapted to daytime activity (Figure 3.4d). Finally, I found that the average metabolic rate for each species strongly correlated with average fresh body mass (Figure 3.4e; Appendix 3.4), where the lowest metabolic rate was *O. granulatus* at 0.14 J h^{-1} and the highest mean metabolic rate was by *G. spiniger*, at 1.88 J h^{-1}.

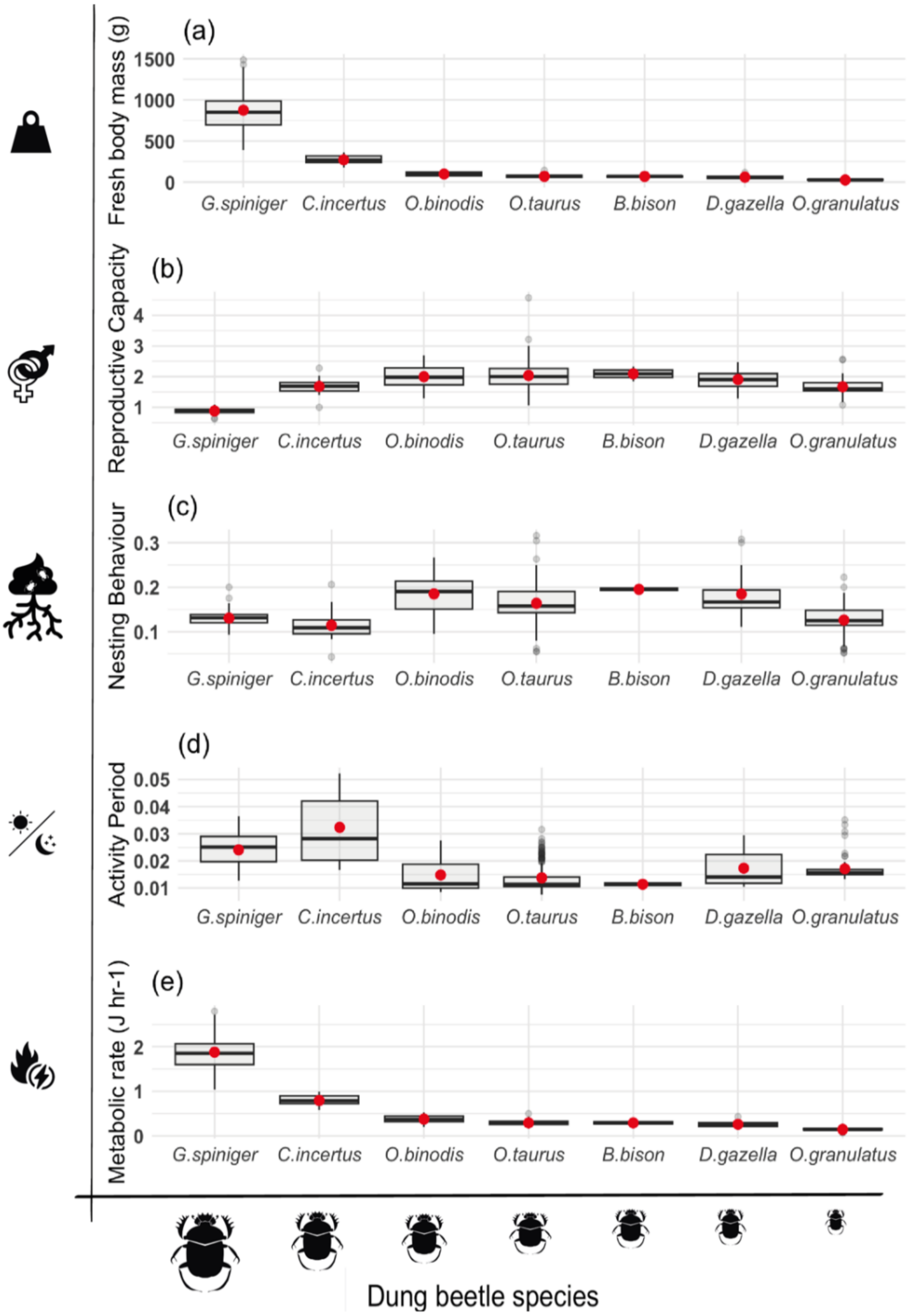

Figure 3.4 The mean, median, and distribution of individual-level functional traits of the seven dung beetle species captured across monitoring sites, including: (a) fresh body mass, (b) reproductive capacity, (c) nesting behaviour, (d) activity period and (e) metabolic rate. The red point in each plot denotes the mean value for each species.

3.3.3 Community weighted functional traits and energy use as predictors of dung removal

I examined functional traits and their impact on dung removal (ecosystem functioning) and observed no significant associations with fresh body mass, reproductive capacity, activity period, and community energy use (Figure 3.5; Appendix 3.5). However, nesting behaviour had a significant effect on dung removal ($p < 0.05$) (Appendix 3.5).

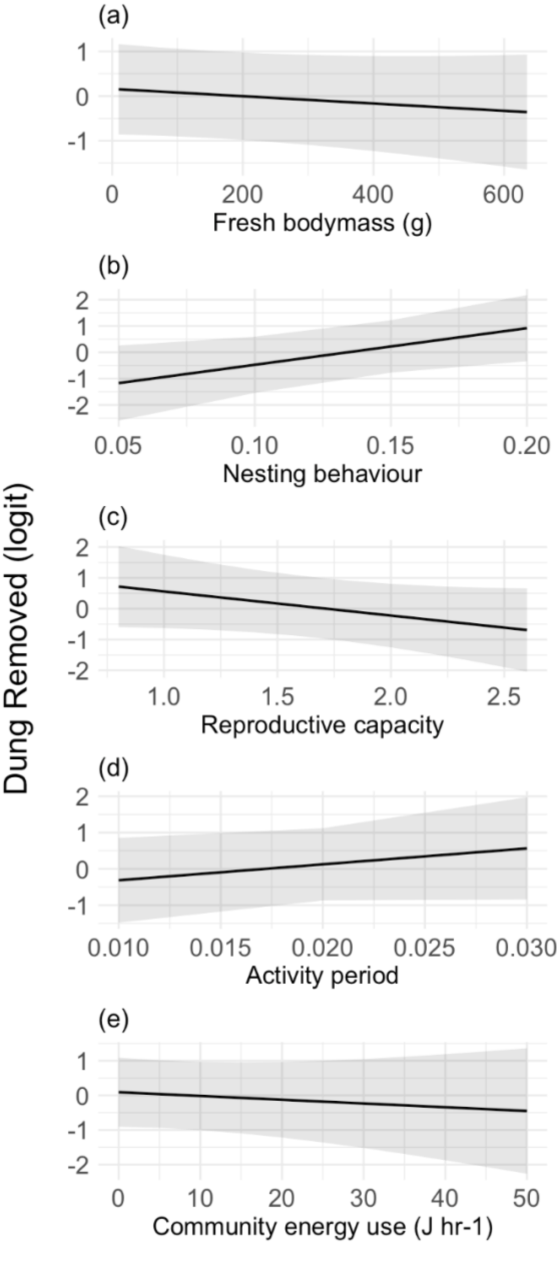

Figure 3.5 Estimated marginal effects (± 95% CI) of the relationship between dung removal rate and (a) fresh body mass; (b) nesting behaviour; (c) reproductive capacity; (d) activity period; and (e) community energy use.

3.4 Discussion

This study aimed to investigate whether dung beetle community characteristics, namely community structure, community weighted mean functional traits and total community energy use, could predict dung removal, an important ecosystem function (Figure 3.1). My findings revealed that community structure based indices did not predict ecosystem functioning compared to community weighted trait values. Specifically, community weighted mean nesting behaviour (hind leg robustness) was found to be a significant predictor of dung removal, possibly quantitatively disentangling the closely associated trait boundaries of reproductive capacity. On the other hand, the results showed that community energy use was not effective in predicting ecosystem functioning, which was contrary to my hypothesis. Hence, adopting a more focused trait selection approach based on the relevant function appears to yield higher predictive potential in dung beetle ecosystem functioning research.

3.4.1 Community structure and dung removal

Abundance indices have been found to be ineffective predictors of ecosystem functioning not only for dung beetle-mediated processes such as dung removal and seed dispersal, but also for other organisms such as bee pollination, ground beetle biocontrol, earthworm bioturbation, and nematode nutrient cycling (Gagic et al., 2015). However, the importance of dung beetle abundance for ecosystem functioning may vary depending on the habitat, as studies have shown that reductions in abundance due to agricultural intensification can have more significant consequences than reductions in species richness. (Manning & Cutler, 2018c). Similar results have been seen in a mesocosm experiment, where Tixier et al. (2015) examined dung beetle assemblages and their effects on dung and leaf litter processes, finding interactive effects between species identity and abundance on dung removal, revealing enhanced ecosystem functioning with greater biomass and beetle abundance. This shows the limitations of using abundance alone as a predictor of ecosystem functioning, as the relative contribution of effects are likely dependent on a variety of factors. The model found no effect of richness on dung removal. This could be because on the species level, the dung beetles are appearing to be functionally redundant, making it difficult to distinguish their relative contributions to dung removal effects. This explanation could also account for the fact that there was no effect of dominant species on dung removal, because on the species level they are functionally even. While functional redundancy may promote ecological resilience and stability, as ecosystem function of communities with more redundant species should be buffered against the loss of individual species (Biggs et al., 2020) it also raises the question of whether introducing a more diverse assemblage of nesting strategies could be necessary to maintain functional pasture ecosystems in Aotearoa NZ. Future research could quantify other functional indices, including functional evenness (Villéger et al., 2008).

3.4.2 Community trait values predict dung removal

I found nesting behaviour to be the strongest predictor of dung removal. This is logical since nesting behaviour is the primary mechanism for dung redistribution (Halffter & Edmonds, 1982), which can contribute to direct or indirect effects on other associated ecosystem functions, such as nutrient cycling and primary productivity (Nichols et al., 2008). It is noteworthy that reproductive capacity did not predict dung removal, because this may help distinguish the relative importance of nesting behaviour and reproductive capacity, which can be difficult to differentiate due to overlapping trait boundaries (deCastro-Arrazola et al., 2022).

Nesting behaviour (also sometimes referred to interchangeably throughout the literature as reproductive behaviour) being identified as an important trait is not a new concept. In fact, it was the original trait used to categorize functional guilds of dung beetles based on their nesting strategy (Halffter & Edmonds, 1982; Tonelli, 2021). Nesting behaviour involves creating tunnels and burying dung, which requires strong and well-developed leg muscles, which is why it is quantified as leg robustness. Other studies that measure the traits directly related to resource use have yielded similar findings. For example, a weevil's elongated rostrum is directly related to its function, as it allows it to penetrate plant tissues and extract nutrients, with the length of the rostrum shown to be a significant predictor of the extent to which it can access resources (Toju & Sota, 2006). Therefore, by focusing on the traits that allow organisms to acquire and use resources that lead to the ecological processes in question, we can make more accurate predictions of how organisms will interact with each other and their environment to better predict ecosystem functioning.

I found that dung beetle activity period did not predict dung removal, and this is likely due to the little variation in the species within the communities surveyed here. Thus, this approach could potentially be more suitable for investigating dung beetle communities in tropical rainforests with high biodiversity, abundance, and range of activity periods, instead of agricultural pasture ecosystems. Quantifying activity period could be an effective way to test hypotheses of niche complementarity over time rather than predicting overall dung removal patterns. This approach could enable the differentiation of the varying contributions of diurnal, nocturnal, and crepuscular dung beetle behaviours to the process of dung removal, which could help to determine how changes in environmental conditions such as temperature, could influence their foraging behaviour and subsequent dung removal at different times.

While there was a good range of body sizes present in this study, body size was insufficient to determine any effects on dung removal probably due to the different ways in which dung beetles use energy. As far as I know, no previous study has examined the relationship between dung beetle community energetic demand and ecosystem functioning. While the outcome of the model did not show a significant effect of community energy use and dung removal by dung beetles, the findings of the study have raised interesting points for discussion and potential directions for future research. For example, I hypothesised that adult metabolic rate would predict dung removal, but the relationship between dung beetle metabolic rate and dung removal may be more complex. Firstly, dung beetles require energy to perform activities, such burying dung. However, they also expend a significant amount of energy searching for dung in flight, so it could be that dung beetle energy use may not be directly related to dung removal, but is more divided into searching for dung, burial of dung (for offspring) and individual physiological requirements.

Secondly, it is possible that I found no relationship between adult metabolic rate and dung removal due to the holometabolous development stages of beetles (Schmolz & Lamprecht, 1999). There are further complications when it comes to energy use for taxa like dung beetles, because adults primarily remove dung to provide food for their offspring, rather than to meet their own metabolic demands as they themselves feed on the liquid fraction of the dung (Simmons & Ridsdill-Smith, 2011). This is especially true for species that exhibit parental care, where the offspring receive food resources from one or both parents, including *Onthophagus taurus,* a species where both male and female devotes a considerable proportion of time providing care to produce only a single brood mass, a very unique evolutionary strategy to ensure the success of their offspring (Hunt & Simmons, 2002).

This is a different story for other taxa that carry out decomposition process. For example, the decomposition of alder leaf litter by detritivores was found to be independent of the richness and evenness of consumer types, and instead, it was driven by the metabolic requirements of consumers, which were linked to their body size (Reiss et al., 2011). Additionally, Reiss et al., (2011) showed that the organisms body size and energetic demand was directly linked to the resource use, suggesting that the complexities of dung beetle life histories could be a reason for masking effects of body size or metabolic rate on dung removal. Therefore, the relationship between adult dung beetle metabolic rate and dung removal may not be a reliable predictor of dung removal.

3.4.3 Conclusions

In summary, I set out to identify the biotic mechanisms that best explain variation in the ecosystem functioning of dung beetle communities by investigating their community structure, functional traits, and community energy use. I discovered that the best predictor of dung removal was nesting behaviour (measured as tibial robustness). Overall, this study demonstrates that functional traits of dung beetles must be tailored to the question being asked, and the choice of functional traits can be selected to align with the specific research questions. The findings emphasize the significance of incorporating several quantitative predictors, especially behavioral traits, to enhance the accuracy of predicting the effects of dung beetles on ecosystem functioning.

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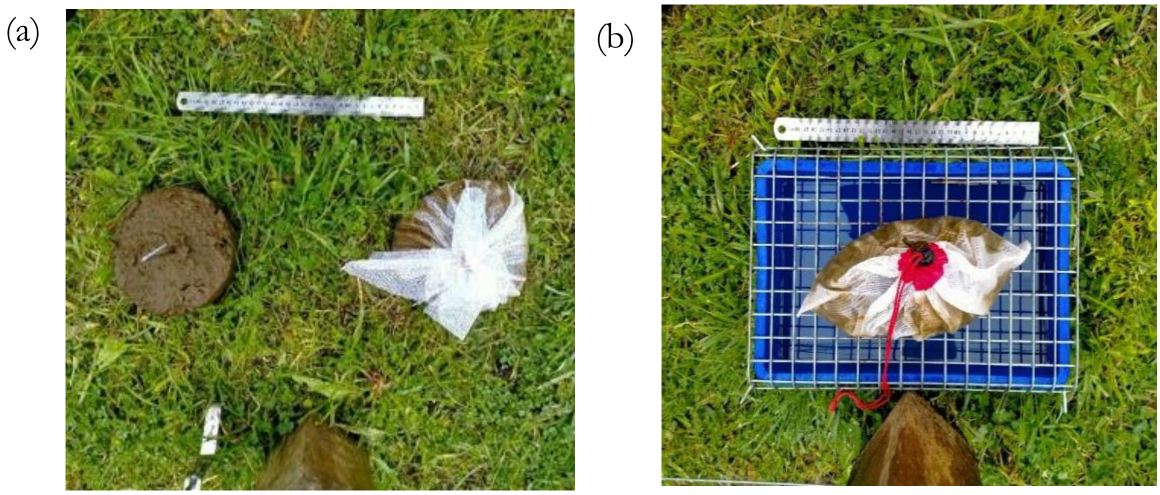
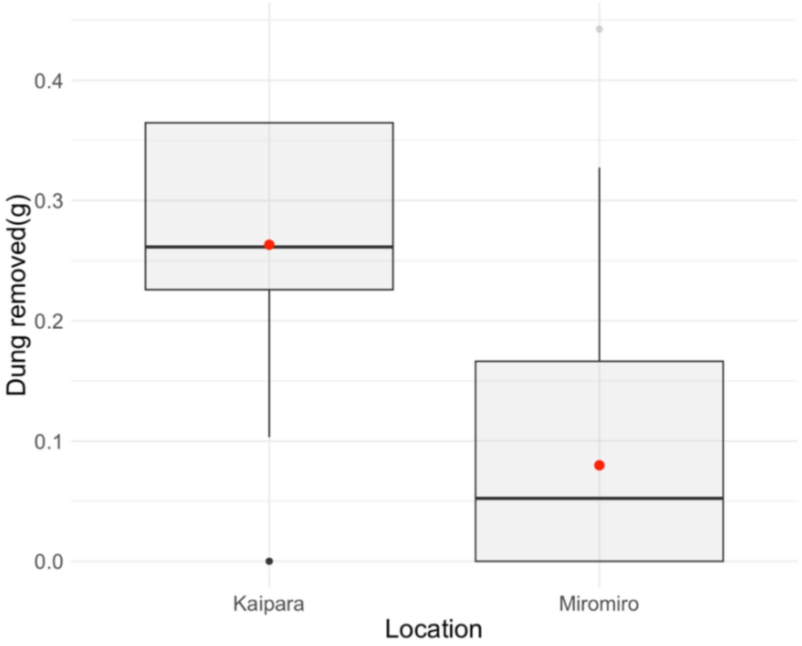
Appendices for chapter three

Appendix 3.1 The experimental set up for dung removal and dung beetle pitfall trapping is shown in photo (a) the dung removal trial; and photo (b) shows the dung beetle pitfall trapping set up to quantify the dung beetle community.



Appendix 3.2 Box plot showing the comparison of dung removal at the two locations: Kaipara and Miromiro farms. There was a greater amount of dung removal observed at the Kaipara farm (mean = 0.206 g) than the Miromiro farm (mean = 0.092 g).



Appendix 3.3 Summary of fixed effects for community structure model output:

logit_dung_scale ~ dominant_species + rich.scale + abun.scale + (1 | location)

Predictor Variable	Estimate	Std. Error	df	t value	p value	CI (95%)
C.incertus	2.36044	1.34416	22	1.756	0.093	(-0.44 – 5.16)
O.binodis	0.18944	1.54554	22	0.123	0.904	(-3.03 – 3.41)
O.taurus	1.63523	1.20304	22	1.359	0.188	(-0.87 – 4.14)
O.granulatus	1.15094	0.69881	22	1.647	0.114	(-0.31 – 2.61)
Even	1.17546	0.91887	22	1.279	0.214	(-0.74 – 3.09)
Richness	-0.06419	0.37115	22	-0.173	0.864	(-0.84 – 0.71)
Abundance	0.34156	0.33635	22	1.015	0.321	(-0.36 – 1.04)

Appendix 3.4 The average values for individual dung beetle species functional traits

	Fresh Bodymass (g)	Reproductive Capacity	Nesting Behaviour	Activity Period	Metabolism (J hr^{-1})
Geotrupes spiniger	875.0	0.88	0.131	0.0241	1.880
Copris incertus	271.0	1.68	0.114	0.0324	0.795
Onthophagus binodis	98.7	2.00	0.185	0.0148	0.375
Onthophagus taurus	69.9	2.04	0.164	0.0137	0.291
Bubas bison	69.5	2.09	0.195	0.0114	0.291
Digitonthophagus gazella	60.1	1.90	0.184	0.0173	0.259
Onthophagus granulatus	26.8	1.67	0.126	0.0171	0.144

Appendix 3.5 Summary of fixed effects for functional traits and CEU model output: logit_dung_scale ~ fresh.bodymass + reproductive.capacity + nesting.behaviour + activity.period + total.metabolism + (1 | location)

Predictor Variable	Estimate	Std. Error	Df	t value	p value	CI (95%)
Fresh body mass	-0.001	0.001	23.594	-0.962	0.346	(-0.00 – 0.00)
Reproductive capacity	-0.782	0.484	23.402	-1.616	0.119	(-1.78 – 0.22)
Nesting behaviour	**13.905**	**5.851**	**23.871**	**2.377**	**0.026**	**(1.77 – 26.04)**
Activity period	43.957	39.840	23.039	1.103	0.281	(-38.67 – 126.58)
Total metabolism	-0.011	0.017	23.059	-0.651	0.521	(-0.05 – 0.02)

Chapter Four. DUNG BEETLES DRIVE DIRECT AND INDIRECT CHANGES IN ECOSYSTEM MULTIFUNCTIONALITY

Abstract

Dung beetles are known to affect ecosystem functioning through biotic and abiotic mechanisms, but there is still limited understanding of the interrelationships among multiple ecosystem functions that occur simultaneously. Ecosystem multifunctionality (EMF) metrics may provide information about dung beetle effects on the simultaneous provisioning of multiple ecosystem functions, but this may come at the cost of over-simplifying complex systems and obscuring important information for managing ecosystem functioning in the context of global change. Using a mesocosm experiment in a pasture ecosystem in Aotearoa New Zealand, I tested for the effects of adding a single or multiple species, over time, on ecosystem multifunctionality. I quantified nine dung beetle mediated ecosystem functions, which have potential cascading direct and indirect effects on ecosystem multifunctionality: dung removal, total soil carbon, total soil nitrogen, Olsen phosphorus, soil microbial activity, nitrate, ammonium, anaerobically mineralisable nitrogen, and pasture biomass production.

I compared three methods to determine the most effective approach for evaluating the simultaneous delivery of multiple ecosystem functions, including (i) modelling the responses of each ecosystem function individually, (ii) calculating EMF metrics such as the averaging, threshold, and Hill numbers approach to test the effects of dung beetles on ecosystem multifunctionality, and (iii) using structural equation modelling (SEM) to test the direct and indirect effects of dung beetles on all simultaneously occurring ecosystem functions. Although dung beetle additions were only found to have a significant direct effect on one ecosystem function (dung removal), dung beetles significantly enhanced four of the calculated EMF metric values. Additionally, the structural equation model revealed that dung beetles had an indirect positive effect on both total N and anaerobically mineralizable N, via a positive direct effect on dung removal. These results underscore the importance of reporting both individual ecosystem functions and EMF metrics, and using causal inference methods such as SEM to improve our understanding of the effects of dung beetles on ecosystem multifunctionality. This knowledge can contribute to the development of sustainable nature-based solutions for regenerative agriculture and the promotion of improved ecosystem-function and ecosystem-service multifunctionality.

Key words

Ecosystem Function, Ecosystem Multifunctionality (EMF), PiecewiseSEM, Introduced Species, Dung Beetles, Scarabaeinae, EMF Metrics, Causal Inference, Mesocosm Experiment, biological control, regenerative agriculture, Nature-Based Solutions (NbS)

4.1 Introduction

Sustainable management of anthropogenic landscapes, such as agricultural pastures, can be achieved through the implementation of nature-based solutions (Seddon, 2022a). An example of such solutions is the introduction of species which are known to facilitate the simultaneous delivery of multiple ecosystem functions, enhancing the long-term delivery of ecosystem services (Grelet & Lang, 2021; Keesstra et al., 2018). Quantifying individual ecosystem functions and ecosystem multifunctionality (EMF), which is defined as the simultaneous delivery of multiple ecosystem functions (Hector & Bagchi, 2007) can therefore be a valuable tool for monitoring ecosystem health. Furthermore, such measurements can also offer valuable evidence to inform decision-making related to management strategies designed to protect ecosystem functions and services within production landscapes. While there are established metrics to quantify EMF (Garland et al., 2021), there remains a lack of quantitative comparisons with methods that can capture the complexities of effects resulting from introduced species, such as dung beetles (Giling et al., 2019).

Dung beetles (Coleoptera: Scarabaeoidea) have been shown to have positive net effects on pasture ecosystem functions through biotic and abiotic pathways, such as dung removal, bioturbation, and nutrient cycling (Bertone et al., 2006; Beynon et al., 2012b; Doube, 2018). Dung burial by dung beetles can lead to increased nutrient availability in soils, such as carbon (C), nitrogen (N), and phosphorus (P), which can lead to cascading direct or indirect effects on primary productivity (Bertone et al., 2006; Hea et al., 2005). They can also influence carbon and microbial activity pathways (Menéndez et al., 2016) and benefit microbial resource availability, such as nitrate N, ammonium N and anaerobically mineralisable N which has cascading effects on other ecological processes, such as plant growth (Yoshitake et al., 2014). While these different stages of cascading effects of dung beetles on multiple ecosystem functions have been identified, until now they have not been modelled together in a single framework to describe the direct and indirect effects of dung beetles on ecosystem multifunctionality.

Ecosystem multifunctionality can be quantified using EMF metrics (Byrnes et al., 2014), which involves measuring multiple individual ecosystem functions and converting them into a standardised unit scale (Garland et al., 2021). For example, the averaging approach calculates an average score across each measured ecosystem function, whereas the single threshold approach calculates the number of functions delivered above a predefined threshold percentage (Byrnes et al., 2014; Gamfeldt et al., 2008; Oliver et al., 2015). Metrics such as these provide a convenient, simplified overview of the ecosystem multifunctionality. However, even simple systems are dynamic and complex, revealing the limitations of EMF metrics, as they are reductionist in nature and can mask changes in specific functions (Hines, 2019). Thus, it can be argued that both the advantages and disadvantages of these different EMF metrics are the same: attempting to capture the complexity of ecosystems in a single value.

Like much of the world's landscapes, anthropogenic pressures in Aotearoa New Zealand have led to the conversion of native forests into simplified agroecosystems, primarily supporting introduced livestock with high stocking densities (Matisoo-Smith, 2017). These practices have resulted in large-scale environmental degradation and pollution problems across the country (Collins et al., 2007). Dung beetle introductions were proposed as a solution to mitigate these adverse effects (Dymock, 1993; Forgie et al., 2018), as they facilitate the physical removal of dung and accelerate decomposition processes which have cascading effects on other ecosystem functions (Aarons et al., 2009).

Previous research on dung beetle effects on ecosystem multifunctionality have reported the relationship between dung beetle species richness and environmental perturbations (such as anthelmintic exposure effects) on continuous threshold metrics (Manning, Beynon, et al., 2017; Manning, Slade, et al., 2017), while other studies test dung beetle effects on individual functions and discuss EMF without quantifying associated EMF metrics (Piccini et al., 2018; Slade et al., 2017; Slade & Roslin, 2016). Using a mesocosm experiment, Nervo et al., (2017) tested dung beetle mediated ecosystem multifunctionality in Alpine Pastures using stable isotope analysis. They tracked multiple interrelated ecosystem functions responsible for the cycling of dung-derived nitrogen in the soil and vegetation, showing dung beetle effects on ecosystem multifunctionality, but did not report corresponding EMF metrics. To my knowledge, this is the first comparison of how multiple interrelated ecosystem functions respond to the introduction of dung beetles to pasture ecosystems, alongside metrics of ecosystem multifunctionality.

In a framework proposed by Giling et al., (2019), they emphasize the importance of developing a suite of evidence-based *a priori* hypotheses to gain deeper insights into the interdependencies that govern multifunctionality within ecosystems. This framework focuses on the quantification of possible direct and indirect cascading effects through the measurement of individual functions and the use of SEM, a causal inference method that can disentangle the individual functions that contribute to overall ecosystem multifunctionality. This approach, therefore, can provide a mechanistic understanding of shifts in multiple ecosystem functions following environmental changes, such as the introduction of novel dung beetle species.

In this study, I use introduced dung beetle species in Aotearoa New Zealand as a model system to evaluate how the intentional introduction of multiple dung beetle species to agricultural pasture ecosystems will influence ecosystem multifunctionality over time. I compare single functions, EMF metrics, and the causal inference method, structural equation modelling. In doing so, I test the hypotheses that the introduction of multiple dung beetle species over time will (i) improve single ecosystem functions, namely dung removal, associated physicochemical soil processes, and pasture growth; (ii) these enhanced individual functions will lead to overall increases in EMF values (i.e. metrics of EMF); and (3) using structural equation modelling will provide a mechanistic understanding of EMF trends, through dung removal having direct and indirect flow-on effects on multiple interconnected soil processes and pasture biomass production.

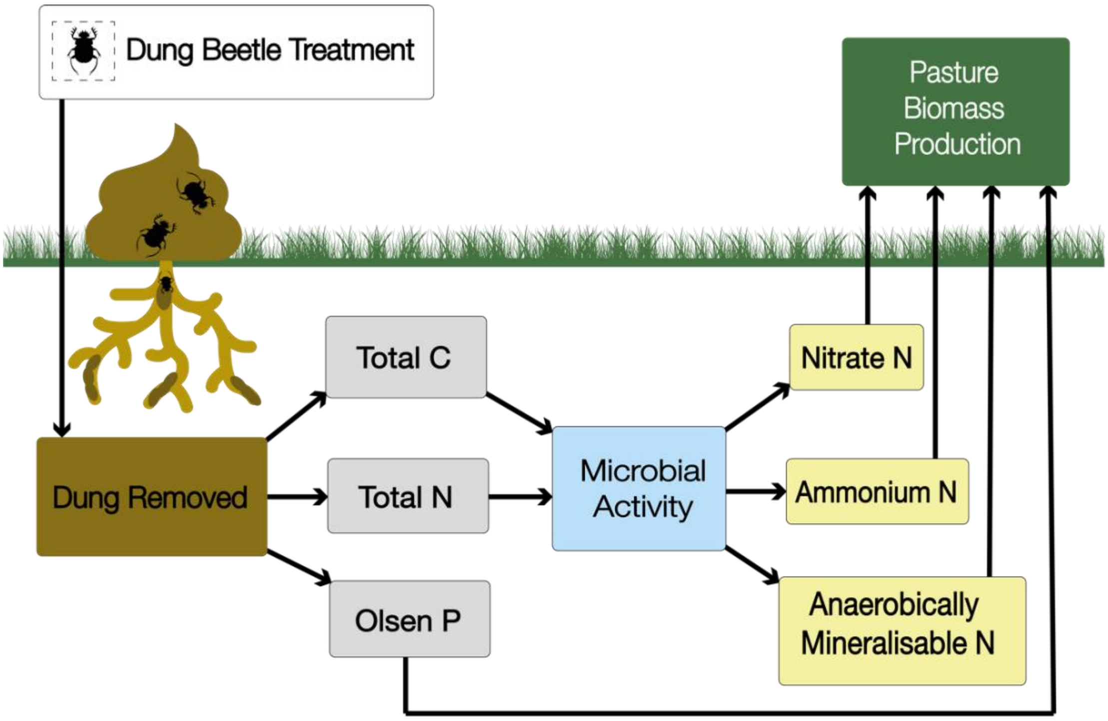


Figure 4.1 Hypothetical model showing how dung beetles are expected to directly and indirectly affect ecosystem multifunctionality in pasture ecosystems. I predict that dung beetles will increase dung removal through burial and bioturbation (brown box), leading to an increase in a suite of physiochemical soil properties including macro-nutrients such as total C, total N, and Olsen P (grey boxes). In turn, I expect Olsen P to directly enhance pasture biomass production (green box), and total C and total N to increase soil microbial activity (blue box), subsequently leading to the formation of three further plant-available forms of inorganic N (yellow boxes), which then ultimately enhances primary productivity (green box).

4.3 Methods

4.3.1 Study site

To test the effects of introduced dung beetles on ecosystem multifunctionality in pasture systems, I carried out a mesocosm experiment on a dry stock farm in Otorohanga, Aotearoa | New Zealand (S38°12’4220 E175°6’2020). The mean annual temperature of the site was 13.2°C, with an average annual precipitation of 1495 mm per year (McCarthy et al., 2021). The soil at the site was classified as allophanic, which is known to have very high soil organic matter stocks (Barrat, 1981).

4.3.2 Experimental design

To evaluate the effects of adding single and multiple dung beetle species on ecosystem multifunctionality in pasture ecosystems, I conducted a temporally replicated experiment that occurred in two consecutive years, with trials lasting 6 months each: February 2020 – September 2020 (year 1) and March 2021 – September 2021 (year 2). I added *Onthophagus binodis* to beetle treatments in year 1 and *Onitis alexis* to beetle treatments in year 2 of the experiment (Appendix). To test the pathways outlined in my *a priori* hypotheses (Figure 4.1) I established treatments including: (1) ‘No_beetles’ treatments (n = 10) where only dung was added to the experimental plots in each of year 1 and year 2, serving as a control group with no dung beetles added; (2) ‘One_beetle’ treatments (n = 20) where one species of dung beetle (and dung) was added at the start of year 1, and only dung was added in year 2, or vice versa, where the second species of dung beetle (and dung) was added at the start of year 2, and only dung was added in year 1. This allowed for testing the effect of a single species of dung beetle in either year 1 or year 2; and (3)‘Two_beetles’ treatments (n = 10) where one species of dung beetle (and dung) was added at the start of year 1, and a second species of dung beetle (and dung) was added at the start of year 2. This treatment allowed for testing the effects of two different dung beetle species added sequentially in year 1 and year 2.

Overall, the treatments allowed for testing the influence of temporal diversity of dung beetle species over a 1.5-year period, including a control group with no dung beetles, a single species treatment, and a two-species treatment with dung beetles added in different years. In treatments containing beetles, 1g total dry mass of dung beetles was added to each of the beetle-treatment mesocosms. The average dry weight of a single *O. binodis* beetle was measured at 27 mg and *O. alexis* was 95 mg. To facilitate dung burial success, I ensured that 30 individual *O. binodis* beetles and 10 individual *O. alexis* with an equal sex ratio of approximately 50:50 during year 1 and year

2, respectively. I established two controls to test for the effects of the mesocosm structure, including (1) 'mesocosm_control' treatments (n = 3) which did not receive any dung or dung beetles set up within the mesocosms; and (2) 'open_control' treatments (n = 3) which also did not receive any dung or dung beetles in an adjacent area of pasture that is equivalent in size to the mesocosms, but without the steel enclosures (See Appendix). All dung beetles were sourced from a commercial mass-rearing facility (Dung Beetle Innovations ™) (Dung Beetle Innovations, 2019).

Mesocosm design

Experimental mesocosms were installed at the study site on flat land 100 m from tall woody vegetation to avoid shade effects. We built 43 square mesocosms measuring 590 mm length × 590 mm width × 20 mm height (Appendix 4.1) from 1.5 mm thick stainless steel to avoid rust and chemical reactions in the soil once placed in the ground. We partially buried each mesocosm in the soil at a depth of 100 mm, leaving 120 mm above the ground and with a 0.5 m gap between each replicate mesocosm or open control. An insect-grade mesh was secured over the mesocosms, preventing added dung beetles from escaping and unwanted insects (e.g. blowflies and other dung beetles) from entering. To prevent cattle from grazing the experimental area and immediate surrounds, we placed a fence around the mesocosm array measuring 60 m long × 4 m wide × 1.5 m high, creating a protective buffer zone (Appendix).

Dung source

Fresh cattle dung from the study site was collected and frozen at -20 °C to kill any macroinvertebrates present in the dung before the start of each year. Frozen dung was thawed at ambient temperature for 24 hours and homogenized ensuring that the dung quality with treatments containing dung were comparable. Anthelmintics are used for internal parasite control and decreases the emergence of dung beetles from the dung, negatively affecting associated decomposition processes (Manning et al., 2017; Manning et al., 2018). The use of antibiotics also causes a decrease in microbial communities in cattle dung, eventually affecting the symbiosis between dung beetles and their own gut microbiota, reducing the individual fitness of beetles (Hammer et al., 2016). To ensure that this did not influence my results, the cattle at the study site had not received pharmaceutical treatment for the past three years.

4.3.3 Measuring ecosystem functions

Following the hypotheses outlined in the *a priori* model (Figure 4.1), I measured nine ecosystem functions related to dung beetle activity including (1) proportion of dung removed from pasture surface; (2) total soil C; (3) total soil N; (4) Olsen P; (5) microbial activity; (6) nitrate N; (7) ammonium N; (8) anaerobically mineralisable N; and (9) mean pasture biomass production.

Dung removal

Each mesocosm received 1 kg homogenised dung in each of year 1 and 2, placed on a 25 cm^2 square of plastic trellis with mesh size 3 cm^2 on the pasture surface to ensure the easy removal of the remaining dung from the pasture surface (Appendix). At the same time, three sub samples of homogenised dung were dried at 70 °C for a minimum of 24 hours and weighed to calculate the average dry biomass of the dung input into each treatment. All mesocosms were covered with insect-grade mesh for 28 days after the addition of dung beetles to the appropriate treatment mesocosms. After 28 days, the remaining dung was collected by lifting the trellis from the pasture surface and then fully drying samples in an oven at 70 °C for a minimum of 24 hours or until there was no further weight change due to moisture. The proportion of dung removed from the pasture surface was then calculated by dividing the total dry mass of dung remaining on the pasture surface by the total dry mass of dung input.

Physiochemical properties

Soil was sampled to 1 cm depth using a 2.5 cm diameter stainless steel soil corer (three mixed subsamples per mesocosm subquadrate) and samples were kept cool at ca. 4 °C to ensure the reliability of tests conducted on field fresh fraction of samples. To characterise background levels of soil properties, I took pre-treatment soil samples immediately prior to the start of year 1 and year 2. Post-treatment soil cores were taken 6 months after treatment additions (Appendix 4.3). In preparation for quantifying total C, total N, and Olsen P, samples were air-dried in a forced air convection dryer at 35 °C and crushed to pass through a 2 mm sieve. Tests for nitrate-N, ammonium N and anaerobically mineralisable N were all conducted on field-fresh samples. Analyses were done at Hill Laboratories (Hamilton, NZ). Total C (%) and total N (%) were determined by a near-infrared spectroscopy (NIRS) calibration based on the Dumas combustion method (Hill Laboratories Technical Note, 2020). The organic fraction of P that is plant-available (mg L^{-1}) was quantified using the Olsen P method, which is a 30-minute bicarbonate extraction at pH 8.5 followed by Molybdenum Blue colorimetry (Olsen & Sommers, 2015). Nitrate N was quantified from a field-fresh fraction of each sample using a 0.1 M potassium chloride (KCl) extraction followed by a Cadmium (Cd) reduction and NED (N-(1-Naphthyl) ethylenediamine) colorimetry and reported as a dry weight (mg kg^{-1}) (Hill Laboratories Technical Note, 2020). Ammonium N was also quantified from a field-fresh fraction of each sample using a 0.1 M KCl extraction using Berthelot's reagent, a solution which turns blue in the presence of ammonia that is then analysed through colorimetry and reported as a dry weight (mg kg^{-1}) (Hill Laboratories Technical Note, 2020). To quantify anaerobically mineralisable N (AMN), soil samples were incubated at 40 °C in anaerobic conditions for seven days followed by a 2M KCL extraction and Berthelot colorimetry to determine any free ammonium N. The readily mineralisable N fraction is then added to this to produce a μg g^{-1} value for each sample (Hill Laboratories Technical Note, 2020). The analyses of pre-treatment baseline measurements of physicochemical variables showed that there were no significant differences between baseline values between treatments, bar one effect of total N in control treatments, before starting the long-term experiment (Appendix 4.3).

Microbial activity

Soil samples were processed at the University of Waikato soil lab. To prevent non-soil-related respiration, I removed any obvious vegetation from field-fresh soil samples during sieving soil through a 4 mm soil sieve. A 10 g subsample of homogenised soil was then placed in a 350 ml preserving jar and sealed. I also prepared three empty 350 ml jars as blanks. Samples were incubated for seven days at 18 °C, after which I extracted 1.0 ml gas from the headspace and evolved CO_2 analysed using a LI-7000 infrared gas analyser. Microbial respiration was expressed as μg CO_2 g^{-1}soil hr^{-1} (Robinson et al., 2017).

Pasture biomass

I measured biomass production in each mesocosm by cutting pasture > 5 cm above ground every 28 days after treatment addition totalling six pasture samples. To obtain biomass (g) I dried samples in an oven at 60 °C for 48 hours. I then calculated an average biomass production across six months per mesocosm for year 1 and year 2.

4.3.4 Data preparation

To test for the effects of one and two species of dung beetle on ecosystem functioning and multifunctionality, I calculated aggregate values for all ecosystem functions. Firstly, the total accumulated dung removed across both year 1 and 2 was calculated as a measure of dung removal. Secondly, the change in physicochemical variables from baseline values was determined and averaged across year 1 and year 2. Thirdly, the average microbial respiration across year 1 and year 2 was calculated as a measure of microbial activity. Finally, the accumulative pasture growth across both years was quantified as a measure of pasture growth.

4.3.5 Calculating ecosystem multifunctionality metrics

Quantifying EMF metrics can be employed to characterise the simultaneous provisioning of multiple ecosystem functions and services (Byrnes et al., 2014; Hector & Bagchi, 2007; Lefcheck et al., 2015). I calculated three different EMF metrics; the averaging approach, the single threshold approach, and the Hill numbers approach. These metrics were calculated using the nine ecosystem functions previously measured. I used the 'multifunc' package in R (Byrnes et al. 2014) to standardize the values of the nine ecosystem functions in each mesocosm and calculated the 'meanFunction' which produced the metric for the averaging approach. For the single threshold approach, I calculated the number of ecosystem functions that were provided versus the number of ecosystem functions that were not provided at four different thresholds of 20%, 40%, 60%, and 80% using the 'getFuncMaxed' function with 'proportion = FALSE' (Byrnes et al. 2014). For the Hill numbers approach, I used the 'getMF_eff()' function with the Shannon case setting, with the order q = 1 and the argument 'standardized = TRUE' to return a value for the product of the average standardized function and the Hill numbers of functions for each mesocosm replicate (Byrnes et al., 2022).

4.3.6 Statistical analyses

To determine whether treatments with no, one and two dung beetle species affected individual ecosystem functions, I first compared the means of each of the nine measured ecosystem functions using analysis of variance (ANOVA) models. I then tested the effects of treatments on (1) the averaging approach, (2) the single threshold approach, and (3) the Hill numbers approach EMF metrics. For the averaging and the Hill numbers approach, I used ANOVA models and for the individual thresholds approach I used generalised linear models (GLM) to examine the binomial outcome of "successes" vs "fails" of ecosystem functions provided at thresholds of 20%, 40%, 60%, and 80%. Post hoc pairwise comparisons of no beetles and one beetle, no beetles and two beetles, and one beetle and two beetles were conducted using the Tukey method in the 'emmeans' package (V. 1.8.3).

I used structural equation modelling (SEM) to investigate the effects of dung beetle treatments on the direct and indirect pathways of multiple ecosystem functions using the 'piecewiseSEM' package in R (Lefcheck, 2016). I treated dung beetle treatments (no beetles, one beetle and two beetles) as a continuous predictor variable, using a coding of 0, 1, and 2, to facilitate the construction and presentation of the SEM. I logit transformed dung removed (a continuous proportion), and log transformed total C, total N, Olsen P, nitrate N, and ammonium N to ensure that models met the assumptions of normally distributed residuals and homogeneous of variance. Raw values were used for remaining response variables.

I created nine linear models representing each pathway in the hypothetical a priori model (Figure 4.1) with mesocosm code as a random effect. A directed separation test (the d-sep test; Shipley, 2009) was then used to test for any missing paths in the model, based on Fisher's C-test statistic calculated as:

$$C = \sum_{i=1}^{k} . \ln(p_i) \tag{4.1}$$

where pi is the probability that a given response and predictor variable pair in the model are independent of each other (i.e. an independence claim (Shipley, 2009)). C is then compared to a Chi square ($\mathcal{X}^2$) distribution with $2K$ degrees of freedom (where K is the number of independence claims in the model). A p-value < 0.05 from the $\mathcal{X}^2$ distribution suggests that the data are significantly different from what would be expected under the specified causal model. A p > 0.05 indicates that the hypothesised causal model adequately describes the data. I created two global models (SEMs) and compared them using the Akaike information criterion (AIC) using the formula:

$$AIC = C + 2K \tag{4.2}$$

where C is the Fisher's C test statistic and K is the total number of parameters in the global model. The maximal model included all possible paths in the hypothetical model that still yielded p > 0.05, and was compared to a simplified model where non-significant paths were removed from the structural equations until there was no further improvement in the global model AIC. The maximal SEM model (Appendix 4.9, AIC = 1761.05, p = 0.727) was refined to produce a simplified SEM model (Appendix 4.8, AIC = 1752.65, p = 0.711) that better fit the data. All analyses were conducted in R (R Core Team, 2022).

4.4 Results

4.4.1 Effects of dung beetles on individual ecosystem processes

I found a significantly greater dung removal with the addition and increasing temporal diversity of dung beetles ($F = 15.508_{2,37}$, $p < 0.001$, Appendix) and post-hoc pairwise comparisons of dung removal against the dung-only treatment showed the greatest increase in dung removal in treatments that received two species over the course of the experiment (estimate = - 0.117 , $p < 0.01$) compared with treatments containing only one species in either year one or year two (estimate = - 0.302 , $p < 0.05$) (Figure 4.2a). However, I did not detect any significant effects of temporal dung beetle diversity on all remaining ecosystem functions (Figure 4.2b - i, Appendix 4.6).

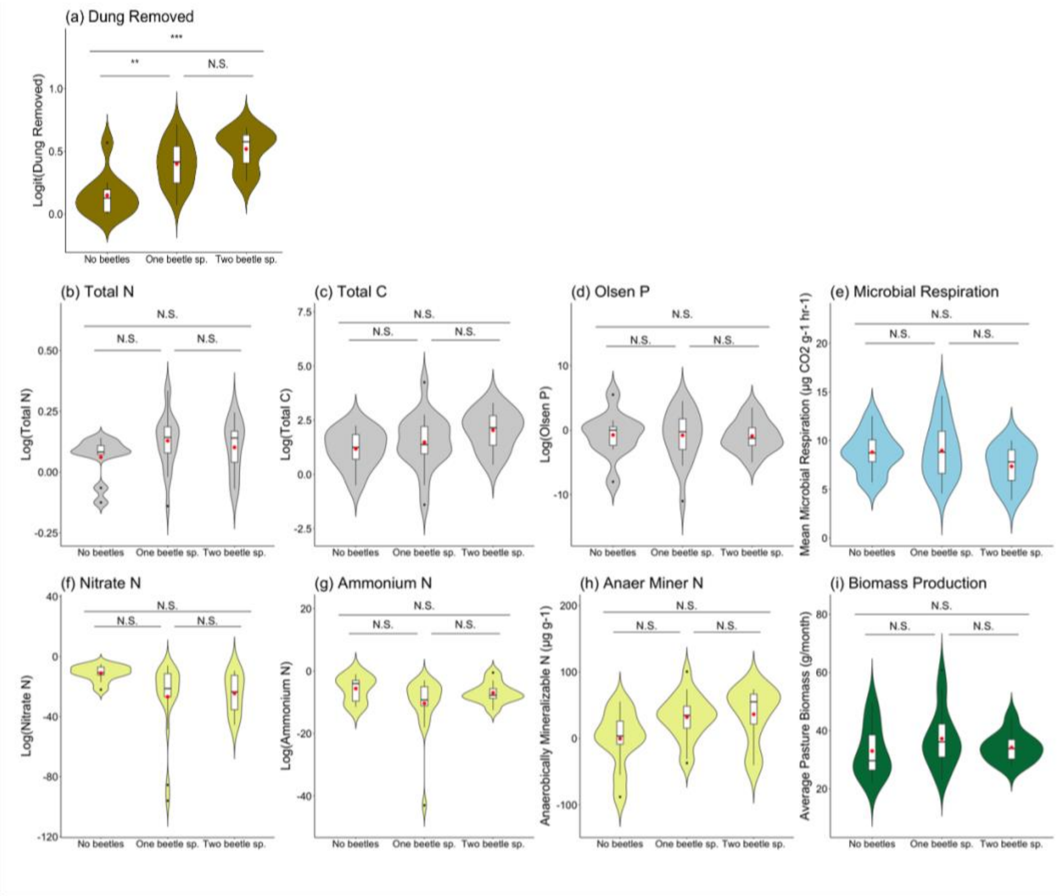


Figure 4.2 The influence of introduced dung beetles (with one or two species added over time) on (a) accumulative proportion of dung removed; (b) total N; (c) total C; (d) Olsen P; (e) average microbial respiration; (f) nitrate N; (g) ammonium N; (h) anaerobically mineralisable N; and (i) accumulated pasture biomass production. Box plots show the median and quartiles with whiskers, and outliers are shown by black points. The shaded area around the box plots shows the density data (estimated by the kernel probability density of the data). The red point shows the average of each ecosystem function. Pairwise comparisons indicate significance levels of ecosystem functions delivered (value adjustment: Tukey method for comparing a family of 3 estimates) $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*) and non-significant (N.S.).

4.4.2 Improved ecosystem multifunctionality metrics

When testing the effects of dung beetle temporal diversity on ecosystem multifunctionality from six different metrics,Ifound that the presence of dung beetles generally enhanced EMF. Specifically,Ifound a generally increasing EMF value with increasing dung beetle temporal diversity on all EMF metrics (Table 4.1).

Table 4.1 ANOVA and summary outputs for the effects of treatment on ecosystem multifunctionality (EMF) metrics. Significance is indicated as **$p < 0.05$** and $p > 0.05$.

EMF metrics		Estimate	Standard Error	t-value	p-value
Averaging	***One beetle***	0.07135	0.03143	2.27	**0.0291**
	Two beetles	0.08234	0.03629	2.269	**0.0292**
20% threshold	***One beetle***	1.1701	0.5439	2.151	**0.0315**
	Two beetles	2.2914	1.0652	2.151	**0.0315**
40% threshold	***One beetle***	0.5063	0.3364	1.505	0.132
	Two beetles	0.5536	0.4036	1.372	0.17
60% threshold	***One beetle***	0.7419	0.263	2.821	**0.00478**
	Two beetles	0.5837	0.3018	1.934	**0.05311**
80% threshold	***One beetle***	0.1967	0.317	0.621	0.535
	Two beetles	0.3747	0.3553	1.054	0.292
Hill numbers	***One beetle***	0.08895	0.03817	2.33	**0.0253**
	Two beetles	0.10758	0.04407	2.441	**0.0196**

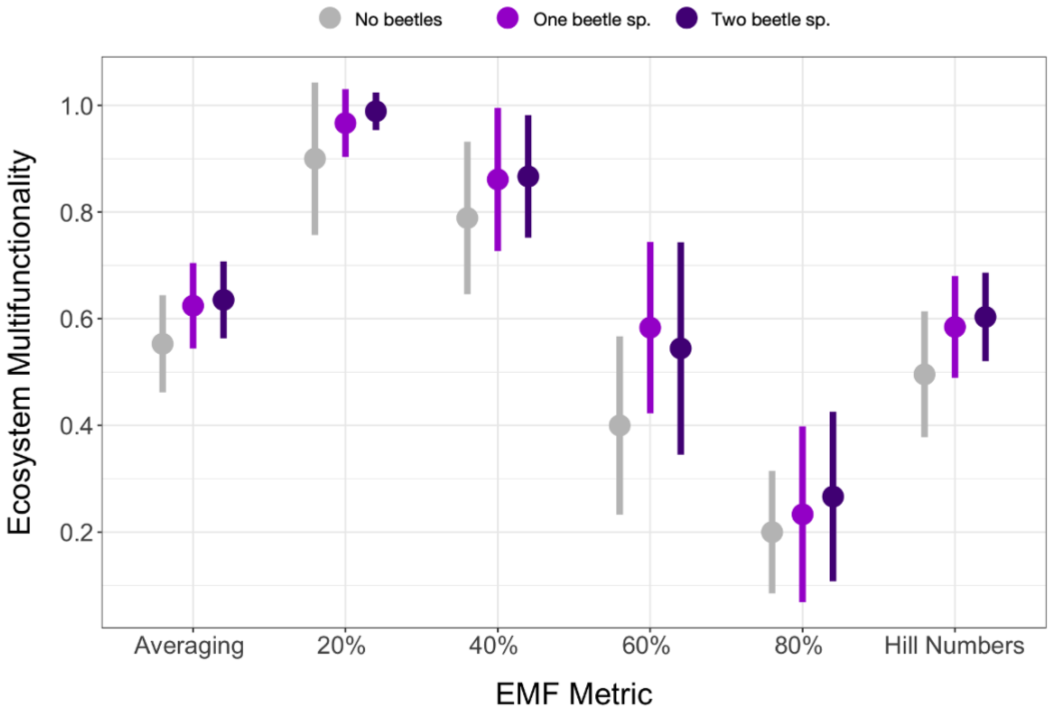


Figure 4.3 The mean (± standard deviation) values of ecosystem multifunctionality for treatments with no beetles, one beetle species (either in year one or year two), and two beetle species (across year one and two), based on six EMF metrics: the averaging approach, threshold approach (set to: 20%, 40%, 60%, 80% thresholds) and Hill numbers approach.

4.4.3 Ecosystem multifunctionality through direct and indirect pathways

Our structural equation model revealed that while dung beetle temporal diversity directly enhanced only dung removal, this resulted in cascading effects on other related ecosystem functions (Figure 4.4). In particular, the model revealed that dung beetles had a significant impact on ecosystem multifunctionality through three direct and indirect positive effects, with one isolated relationship between microbial activity on ammonium N that was not significantly associated with the dung beetle treatments (Figure 4.4 and Table 4.2). For example, there was a direct positive effect of dung beetles on dung removal (standardized effect size = 0.6346, $p < 0.001$), and dung removal subsequently had a significant flow-on effect on total N (standardized effect size = 0.3779, $p < 0.05$) which enhanced anaerobically mineralisable N (standardized effect size = 0.0.7192, $p < 0.001$). While there was a direct positive effect of microbial activity on ammonium N (standardized effect size = 0.4049, $p < 0.001$), this was not directly detected through a significant flow-on effect of dung beetle treatment (Figure 4.4). Contrary to expectations, there was no indirect effects of dung beetle temporal diversity on pasture biomass production (Figure 4.4).

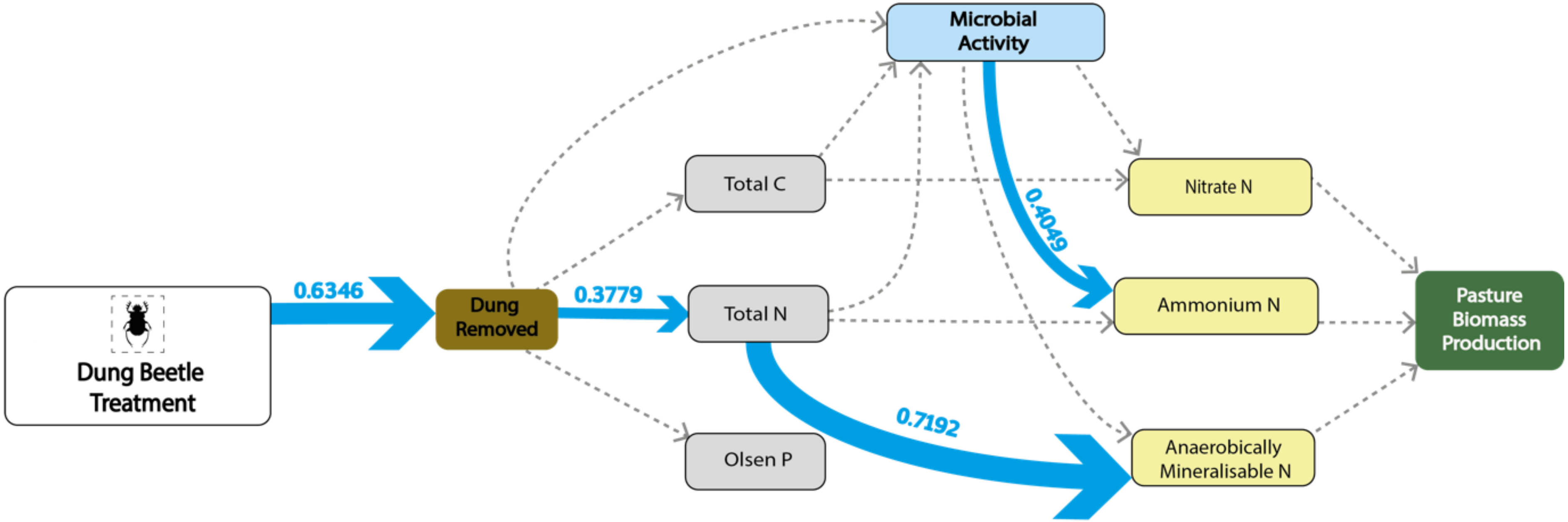


Figure 4.4 Simplified SEM (Fisher's C = 30.872, p = 0.711, df = 36) revised from results from the maximal SEM. Model shows significant positive effects with solid blue arrows, significant negative effects with solid red arrows and dashed arrows indicating non-significant effects. The width of the arrows are proportional to their standardised effect sizes (only shown for significant effects).

Table 4.2 Effects of the revised simplified model. The marginal R^2 values indicate the total proportion of variance explained by all significant predictors and their conditional variables in the significant mixed-effects models.

Response	**Predictor**	**Estimate**	**Standard Error**	**P-value**	**Standard Estimate**	**Marginal R^2**
Dung removed	Dung beetle treatment	1.062	0.210	**0.000**	0.635	0.40
Total N	Dung removed	0.029	0.011	**0.016**	0.378	0.14
Total C	Dung removed	0.259	0.163	0.121	0.249	0.06
Olsen P	Dung removed	0.132	0.325	0.686	0.066	0.00
Microbial respiration	Total N	-0.519	5.411	0.924	-0.019	0.02
Microbial respiration	Total C	0.059	0.379	0.877	0.029	
Microbial respiration	Dung removed	-0.277	0.381	0.472	-1.302	
Nitrate N	Microbial respiration	-0.088	0.676	0.898	-0.021	0.08
Nitrate N	Total N	-32.832	18.865	0.090	-0.276	
Ammonium N	Microbial respiration	0.549	0.204	**0.011**	0.405	0.16
Ammonium N	Total N	0.279	5.691	0.961	0.007	
Anaerobically mineralisable N	Microbial respiration	2.404	1.787	0.187	0.152	0.53
Anaerobically mineralisable N	Total N	317.083	49.848	**0.000**	0.719	
Pasture biomass	Nitrate N	-0.161	0.140	0.259	-0.199	0.09
Pasture biomass	Ammonium N	0.473	0.418	0.266	0.186	
Pasture biomass	Anaerobically mineralisable N	-0.033	0.035	0.362	-0.149	
Pasture biomass	Olsen P	0.710	0.621	0.261	0.194	

4.5 Discussion

Overall, the results show that the introduction of dung beetles with varying temporal diversity had a positive effect on dung removal and ecosystem multifunctionality (Figure 4.2a, and Figure 4.4). In particular, species temporal diversity (whether there was one or two species added over the course of the experiment) played a significant role in determining the magnitude of this effect. In this experiment, I did not have any treatments where multiple dung beetle species were present simultaneously in each mesocosm. Rather, I observed that dung removal was greatest when two species were sequentially added over the year and a half experimental duration, compared to when only one species was added. In doing so, the results demonstrate the importance of temporal diversity for maintaining ecosystem multifunctionality in ecosystems where dung beetles are introduced.

4.5.1 Structural equation modelling can describe ecosystem multifunctionality

The results from the analysis of individual functions across treatments detected only one response out of nine possible ecosystem functions (dung removal) where dung removal was highest in the two species treatment (Figure 4.2a). Individual ecosystem functions in isolation, such as dung removal, do not accurately detect significant changes in other simultaneously occurring ecosystem functions in response to dung beetle species introductions. This is likely due to the fact that the effect of dung beetle additions alone cannot explain the observed variations in other ecosystem functions, making it difficult to establish a significant relationship between them (Figure 4.2b – i). However, the incorporation of multiple predictors that account for related environmental processes increased the precision of the estimates of the effect of the primary predictors on the outcome variable, as demonstrated in the SEM (Figure 4.4). This method can uncover a mechanistic understanding of ecosystem multifunctionality. For example, research by Grace et al., (2016) used SEM to find the mechanisms that connect productivity and plant species richness from 1,126 grassland plots spanning five continents, revealing substantially higher explanatory power than traditional bivariate analyses. Their results showed a strong and consistent positive effect of species richness on productivity, the significance of competition across various levels of productivity , and the importance of macroecological gradients in promoting local species richness, despite it being viewed as a competing hypothesis. Ecological studies assessing dung beetle effects on ecosystem functioning often use dung removal as a proxy indicator for other ecosystem processes (Carvalho et al., 2020). My result highlights the need to quantify a broader suite of ecosystem functions in order to capture the underlying mechanisms leading to ecosystem multifunctionality. As Grace et al., (2016) show, SEM can yield significant progress in understanding the underlying processes in ecological systems, and these findings can have implications for determining the role of environmental change on ecosystem functioning. The results of my SEM revealed the interconnections among multiple ecosystem functions in response to an environmental change (Giling et al., 2019), like dung beetle introductions.

Using SEM in ecosystem multifunctionality research has the capacity to show underlying mechanisms, rather than focusing solely on individual functions and EMF metrics. This is a beneficial method because it allows for the description of complex natural systems by resolving multivariate relationships among interrelated variables (Grace, 2006b). For example, dung beetles had a direct positive effect on dung removal, and there was a significant flow-on effect on total nitrogen, enhancing anaerobically mineralisable nitrogen, yet this was not detected through bivariate analyses. Timing of sampling could play a role in the extent to which I was able to detect certain physicochemical processes. For example Kazuhira et al., (1991) found that organic N in dung is converted to plant-available forms within five days regardless of dung beetle presence, however, dung beetles initiated ammonification processes on residual cow dung and dung balls after 15 days. Therefore, the timing of measurements should be carefully considered, as I may have missed possible effects because of my experimental design, where the interval between treatment additions and the final soil measurements may have been too long. I also found a direct positive effect of microbial activity on ammonium nitrogen, although this was not mediated through a significant flow-on effect of dung beetle treatment (Figure 4.4), which could again be due to the timing of the sampling since treatment addition. In addition to this, the two species of dung beetles, *O. binodis* and *O. alexis,* have also been observed to excavate horizontally, which means that the soil cores may not have captured the full extent of their contribution to soil processes.

4.5.2 Ecosystem multifunctionality metrics can obscure the story

My results showed that dung beetle temporal diversity enhanced ecosystem multifunctionality metrics, as evidenced by the significant increase in ecosystem multifunctionality across four out of six metrics in treatments where dung beetles were present in both years compared to no beetles present (Figure 4.3). This raises the question of whether calculating EMF metrics overinflates the importance of introduced dung beetle activity for the provisioning of ecosystem multifunctionality. I found that even when only a subset of functions, (dung removal, total N, and anaerobically mineralisable N), were significantly influenced by the dung beetle treatments (as seen in the SEM in Figure 4.4), the overall EMF metrics were significantly enhanced.

Furthermore, certain functions that were more responsive to the treatments (such as dung removal) led to a disproportionate influence on the overall EMF metric response despite other functions, such as pasture biomass production, being unaffected by the treatments (Figure 4.4). Therefore, the interconnected nature of the ecosystem functions I measured could have affected the EMF metric values. For example, Garland et al., (2021) discuss how ecosystem functions that are related to each other may affect the overall EMF metric, and state that future studies should consider the correlations between ecosystem functions when measuring EMF metrics. Due to this, and the unequal contribution of individual functions to the overall response, reporting EMF metrics may not be a suitable method for understanding ecosystem multifunctionality in dung beetle functional ecology research, and it is important to interpret EMF metric results with caution, as the contributions of individual functions may vary. This also raises concerns for the secondary use of EMF metric within other analyses, such as structural equation models. For example, Liu et al., (2019) show how earthworms enhance multifunctionality in soil ecosystems through indirect effects rather than direct effects, however, they include EMF metrics as a factor in their SEM. This may yield unreliable inferences which could have consequences to agroecosystem management.

4.5.3 Possible mechanisms of dung beetle mediated ecosystem multifunctionality

There are examples of dung beetles having negative effects of plant growth from the literature (Andresen & Urrea-Galeano, 2022), highlighting possible gaps in our understanding regarding the specific mechanisms through which dung beetles facilitate plant growth. The mechanisms through which I expected plant growth to occur in my a priori hypotheses (Figure 4.1) were not detected through structural equation modelling. While experimental design may be a factor contributing to this outcome, processes are complex, and indirect factors that are seldom considered could be playing a role, such as the presence of specific microbial communities across the life cycle of the dung beetle. For example, our understanding of the mechanisms underlying the influence of dung beetles on plant-soil interactions remains fragmented and incomplete, particularly as beetle larval stages are known to facilitate decomposition (Griffiths et al., 2021). In addition to this, there may be specific microbiological divers of these processes. Suárez-Moo et al. (2020) discovered that the composition of gut microbiota in Copris incertus differs across its life cycle, with variation in dominant bacterial genera at each stage. Furthermore, the variations in microbiota composition were observed to correlate with functional profiles of distinct genes associated with nitrogen fixation, uric acid metabolism, and plant cell wall degradation across all stages. Nitrogen fixation and plant cell wall degradation genes were particularly enriched in intermediate stages of the beetle life cycle, while uric acid metabolism genes showed enrichment in adult mothers (Suárez-Moo et al., 2020). In addition to this, insect frass is known to contain unique nutrients, biomolecules, and microorganisms that are plant biostimulants, promoting plant growth and increase their tolerance to abiotic stresses and resistance to pathogens and pests (Pereira et al., 2021; Poveda, 2021). There is currently no research on whether the dung of dung beetles have unique plant biostimulants, presenting an intriguing avenue for future investigations.

4.5.4 Conclusion

I hypothesised that dung beetles would positively affect the simultaneous delivery of multiple ecosystem functions over time through the cascading effects that occur after physically removing dung from the pasture surface (Figure 4.1). By comparing individual functions with established EMF metrics and structural equation modelling, my study highlights how multiple approaches lead to different inferences, and the importance of using the appropriate method to better understand the effects of dung beetle introductions on ecosystem multifunctionality. My findings indicate that both the bivariate tests of single functions and EMF metrics fail to capture the full picture. They either underestimate (Figure 4.2) or overestimated (Figure 4.3) effects of dung beetles on ecosystem multifunctionality, as is revealed by the SEM (Figure 4.4). Although EMF metrics may serve as a quick tool to identify potential effects on EMF, causal inference methods like SEM provide a more powerful approach for the assessment of ecosystem multifunctionality. Therefore, by detecting effects that simple tests of single functions cannot, there can be a more comprehensive and integrated understanding of the interplay among multiple functions in response to an environmental change, such as the introduction of dung beetles. This is important for the implementation of nature-based management, because it provides a more detailed understanding of the relationship between dung beetle introductions and ecosystem multifunctionality, which can help inform actions taken to protect the delivery of ecosystem functions and predict the consequences of environmental changes to the sustainability of agro-ecosystems.

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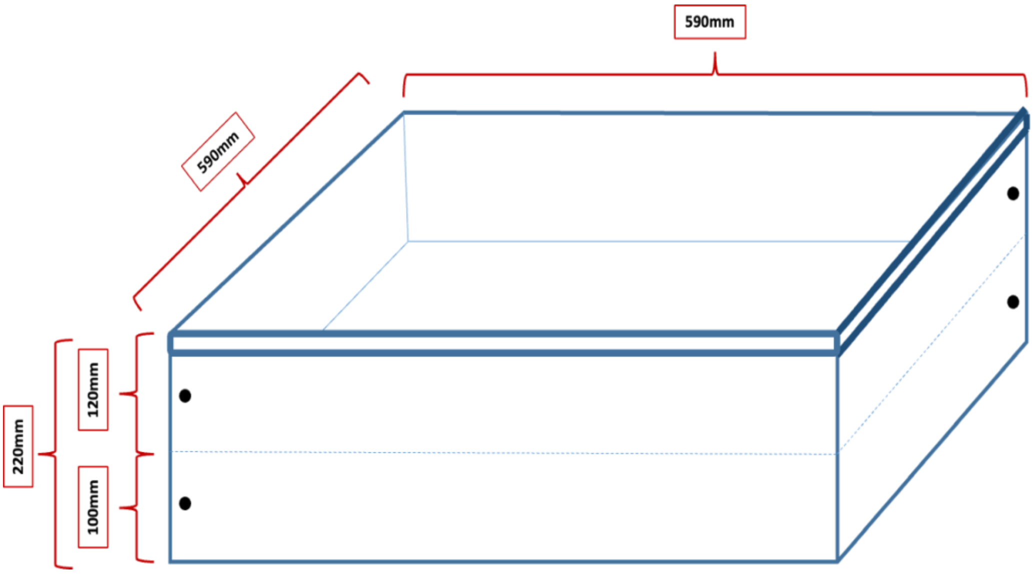
Appendices for chapter four

Appendix 4.1 Diagram of dimensions of a stainless steel mesocosm. Stainless steel was chosen because it is inert and would not react with the soil, which would negatively impact the soil properties.

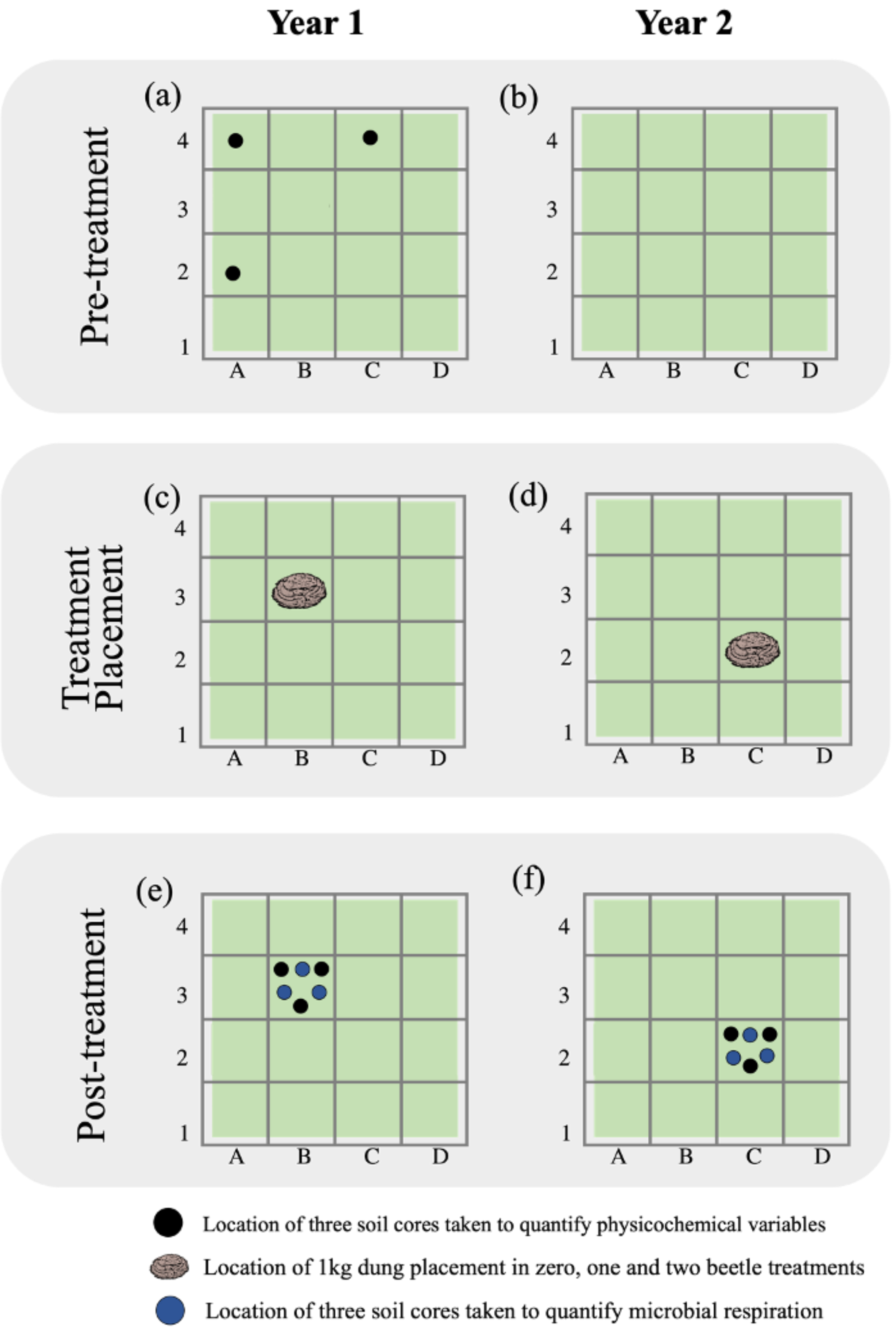


Appendix 4.2 Photo showing experimental mesocosms and an open control treatment (red stakes) installed along a 100 m array, with a fenced buffer zone to prevent grazing.

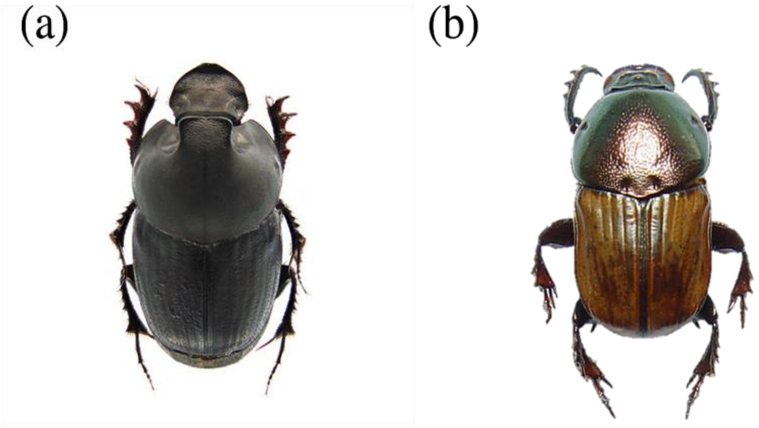
Appendix 4.3 ANOVA tables of baseline soil parameters between mesocosm treatments. I fitted regression models to test whether there was a difference between mesocosm treatments by sampling baseline soil variables.

	Soil Parameters	***Sum of Squares***	***df***	**Mean square**	**F**	**p-value**
(a)	***Total N***					
	Dung beetle treatments	0.125	4	0.031	1.784	0.148
	Residuals	0.825	47	0.018		
(b)	***Total C***					
	Dung beetle treatments	4.960	4	1.239	0.753	0.561
	Residuals	77.421	47	1.647		
(c)	***Olsen P***					
	Dung beetle treatments	284.280	4	71.069	2.354	0.067
	Residuals	1419.170	47	30.195		
(d)	***Nitrate-N***					
	Dung beetle treatments	7825.700	4	1956.420	3.837	**0.009**
	Residuals	23966.400	47	509.920		
(e)	***Ammonium-N***					
	Dung beetle treatments	336.210	4	84.052	1.652	0.177
	Residuals	2391.720	47	50.888		
(f)	***Anaerobically Mineralisable N***					
	Dung beetle treatments	10171.000	4	2542.800	2.279	0.075
	Residuals	52431.000	47	1115.500		

Appendix 4.4 Sampling locations within the mesocosm quadrat during year 1 (left) and year 2 (right). (a – b) soil core samples to characterise baseline soil variables; (c – d) locations of treatment placement; (e – f) soil core samples to identify effects of dung beetles on physicochemical ecosystem function variables after 6 months. The green area is the area of pasture biomass cut monthly over the course of the 6 months.



Appendix 4.5 The two species of introduced dung beetle used in the mesocosm experiment (a) Onthophagus binodis was added to treatments during year 1 and (b) Onitis alexis which was added to treatments during year 2. Photo credits: Dung beetle innovations.



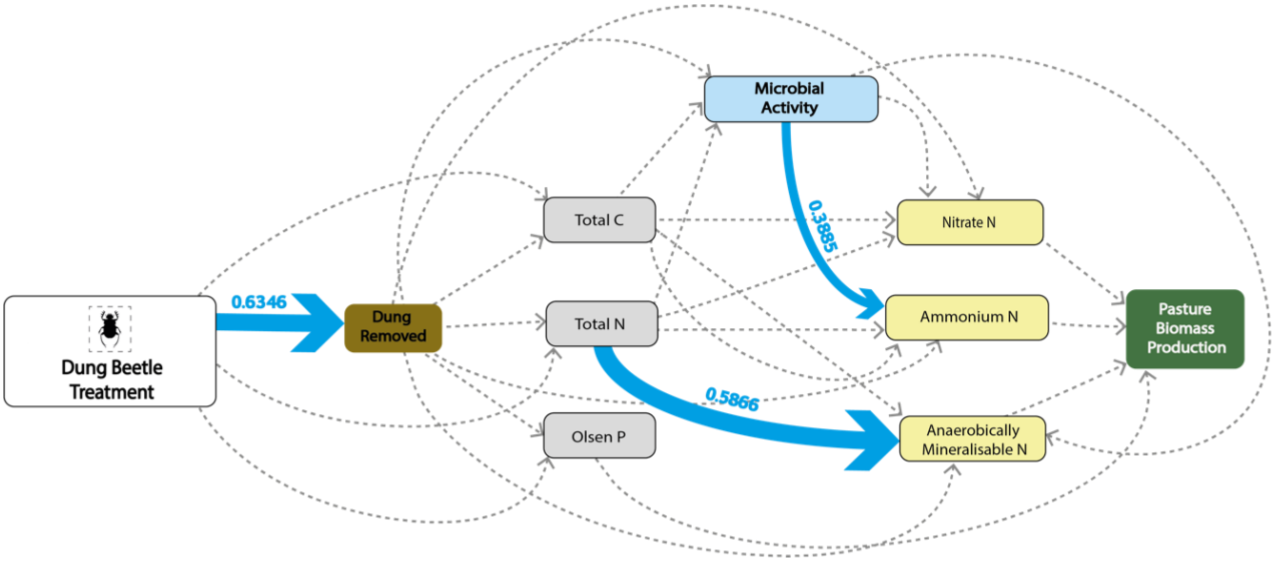
Appendix 4.6 ANOVA tables for linear models for nine ecosystem functions listed (a – i)

	Ecosystem Function	***nDf***	***dDf***	**F**	**p-value**
(a)	***Dung removed***				
	Dung beetle treatment	**2**	**37**	**15.508**	**<0.0001**
(b)	***Total N***				
	Dung beetle treatment	2	37	2.412	0.104
(c)	***Total C***				
	Dung beetle treatment	2	37	0.667	0.519
(d)	***Olsen P***				
	Dung beetle treatment	2	37	0.118	0.889
(e)	***Microbial respiration***				
	Dung beetle treatment	2	37	1.470	0.243
(f)	***Nitrate N***				
	Dung beetle treatment	2	37	1.818	0.177
(g)	***Ammonium N***				
	Dung beetle treatment	2	37	1.123	0.336
(h)	***Anaerobically Mineralisable N***				
	Dung beetle treatment	2	37	2.968	0.064
(i)	***Pasture biomass production***				
	Dung beetle treatment	2	37	0.900	0.415

Appendix 4.7 Dung beetles improve ecosystem multifunctionality metrics

Based on *a priori* information (Figure 4.1), I obtained an initial maximal model showing four significant effects of dung beetle treatment treatments on ecosystem multifunctionality (see Appendix 4.8 and Appendix 4.9 for full model outputs). There was a significant direct positive effect of accumulated dung removal from the pasture surface with increasing dung beetle treatment (standardized effect size = 0.6170, $p < 0.0001$). There was a significant direct positive effect of dung removal on anaerobically mineralisable N (standardized effect size = 0.2745, $p < 0.05$). There was a significant direct positive effect of total N on anaerobically mineralisable N (standardized effect size = 0.6260, $p < 0.0001$). There was a significant direct positive effect of microbial activity on ammonium N (standardized effect size = 0.3781, $p < 0.05$). There were no significant effects detected in the model output independence claims suggesting that the claims could be considered independent.

Appendix 4.8 Initial maximal SEM (Fisher's C = 29.122, p = 0.511, df = 30) showing significant positive effects with solid blue arrows and dashed arrows indicating non-significant effects. The width of the arrows are proportional to their standardised effect sizes (only shown for significant effects).



Appendix 4.9 Effects of the initial maximal model. The marginal R^2 values indicate the total proportion of variance explained by all significant predictors and their conditional variables in the significant mixed-effects model

Response	**Predictor**	**Estimate**	**Standard Error**	**P-value**	**Standard Estimate**	**Marginal R^2**
Dung removed	Dung beetle treatment	1.0618	0.2098	**0.0000**	0.6346	0.40
Total N	Dung removed	0.0294	0.015	**0.0572**	0.3866	0.14
Total N	Dung beetle treatment	-0.0017	0.0251	**0.9449**	-0.0137	
Total C	Dung removed	0.2306	0.214	0.2881	0.2219	0.06
Total C	Dung beetle treatment	0.0751	0.358	0.8349	0.0432	
Olsen P	Dung removed	0.0944	0.4256	0.8258	0.0470	0.00
Olsen P	Dung beetle treatment	0.0998	0.7122	0.8893	0.0297	
Microbial respiration	Total N	-0.5188	5.4111	0.9242	-0.0186	0.00
Microbial respiration	Total C	0.0590	0.3789	0.8772	0.0289	
Microbial respiration	Dung removed	-0.2766	0.3808	0.4723	-0.1302	
Nitrate N	Microbial respiration	-0.1128	0.6876	0.8707	-0.264	0.11
Nitrate N	Total C	-1.5875	1.5637	0.3170	-0.1819	
Nitrate N	Total N	-19.8509	22.3257	0.3800	-0.1666	
Nitrate N	Dung removed	-0.6769	1.5823	0.6714	-0.0746	
Ammonium N	Microbial respiration	0.5262	0.2042	**0.0143**	0.3885	0.22
Ammonium N	Total C	0.6730	0.4644	0.1561	0.2431	
Ammonium N	Total N	-2.1076	6.6301	0.7525	-0.0558	
Ammonium N	Dung removed	-0.3511	0.4699	0.4600	-0.1220	
Anaerobically mineralisable N	Microbial respiration	2.7879	1.7321	0.1165	0.1764	0.59
Anaerobically mineralisable N	Total C	3.3203	3.9392	0.4050	0.1028	
Anaerobically mineralisable N	Total N	258.5994	56.2439	**0.0001**	0.5866	
Anaerobically mineralisable N	Dung removed	7.8299	3.9861	0.0575	0.2333	
Pasture biomass	Nitrate N	-0.1607	0.1399	0.2586	-0.1989	0.09
Pasture biomass	Ammonium N	0.4733	0.4182	0.2655	0.1857	
Pasture biomass	Anaerobically mineralisable N	-0.0326	0.0353	0.3616	-0.1493	
Pasture biomass	Olsen P	0.7101	0.6212	0.2607	0.1943	

Chapter Five. SYNTHESIS

5.1 Synopsis

This thesis is a collection of research studying the role of dung beetles on ecosystem functioning, exploring their effects from a global perspective to Aotearoa NZ pastures. First, I set the scene for the research topic in chapter one by describing the natural history of dung beetles and how the use of dung as a resource has stimulated the evolution of unique nesting behaviours through the process of niche partitioning. (Halffter & Edmonds, 1982). I highlight that these diverse nesting behaviours, in turn, make significant contributions to ecosystem functioning (Tonelli, 2021). I then describe the biotic mechanisms that may influence dung beetle-mediated ecosystem functions, including community characteristics such as biodiversity, as well as functional traits (deCastro-Arrazola et al., 2022). Next, I provide a foundational background on ecosystem function research starting with the biodiversity-ecosystem functioning literature and expanding to further biotic drivers of ecosystem functioning, including functional traits. I then emphasise the importance of considering the simultaneous provision of multiple ecosystem functions, also known as ecosystem multifunctionality, and how this may inform ecosystem service multifunctionality (Manning, Van Der Plas, et al., 2018b). I then introduce the concept of nature-based solutions and provide a brief overview on the key criteria that need to be met in order for an approach to be considered a nature-based solution (Seddon, 2022b).

In chapter two, I significantly broaden our understanding of dung beetle-mediated ecosystem functions at a global scale, a topic that was previously qualitatively reviewed by Nichols et al., (2008). By quantitatively synthesising data from published studies regarding dung beetle-mediated ecosystem functions on a global level, I shed light on the gaps in our understanding of certain ecosystem functions, particularly the over-representation of dung removal as an ecosystem function, and how little we know about dung beetle mediated trophic regulation and primary productivity. I then narrow the focus to investigate the relationship between various biotic drivers of ecosystem functioning in chapter three. I quantify community structure and community-weighted measures of functional traits including community weighted mean behaviour and total community energy use (Brandl et al., 2022; Reiss et al., 2009), a trait not yet studied in the dung beetle ecology literature. My results showed that indices of behavioral traits, particularly nesting behaviour, serve as an effective predictor of dung removal in introduced dung beetle communities in Aotearoa NZ pastures.

Chapter four continues to zoom in, this time investigating the relationship between temporal dung beetle diversity and ecosystem multifunctionality (Manning, Van Der Plas, et al., 2018). I use a controlled mesocosm experiment to quantify nine biotic and abiotic ecosystem functions and use structural equation modelling to disentangle the direct and indirect mechanisms by which dung beetles enhance ecosystem multifunctionality (Giling et al., 2019). I discover that this causal inference method, when compared to other approaches such as bivariate analysis and the calculation of ecosystem multifunctionality metrics (Byrnes et al., 2014), better captures and describes the multifunctionality derived from the activities of dung beetles.

In all chapters, I have used quantitative methods to ensure the reproducibility of all conducted experiments. Having emphasised the significant role of dung beetles in ecosystem functioning, I put forward the proposition that they hold promising potential as a nature-based solution to foster sustainable agricultural landscapes in Aotearoa NZ. In the subsequent discussion, my objective is to consolidate the knowledge obtained from these chapters. I will assess the future implications of the role and significance of dung beetles in ecosystem functioning, and draw upon concepts such as ecological intensification (Kleijn et al., 2019) and multitrophic diversification (Gossner et al., 2016) to foster the advancement of nature based management of sustainable agro-ecosystems (Allen et al., 2022).

5.2 Discussion

In December 2022, the United Nations Convention on Biological Diversity incorporated nature-based solutions into its decision texts within the framework of the Kunming-Montreal Global Biodiversity Framework (CBD, 2022) emphasising the importance of using nature-based solutions and ecosystem-based approaches for addressing biodiversity challenges:

> "*TARGET 11: Restore, maintain and enhance nature's contributions to people, including ecosystem functions and services, such as regulation of air, water, and climate, soil health, pollination and reduction of disease risk, as well as protection from natural hazards and disasters, through nature-based solutions and/or ecosystem-based approaches for the benefit of all people and nature.*"

Dung beetles are often used in biodiversity studies, but we do not have a full understanding of their ecological consequences. Yet, despite the significant attention given to the benefits of dung beetles on ecosystem functioning (Nichols et al., 2008), and the pressing need to restore ecosystem functioning in all ecosystems (CBD, 2022), there has been no studies that provide a quantitative synthesis of the ecological processes mediated by dung beetles at a global level, which was my aim in chapter two. It was evident from the results of the meta-analysis that our understanding of dung beetle mediated ecosystem functioning was geographically biased, and contrary to my predictions there was greater ecosystem functions delivered at temperate latitudes. This has implications for targeting of ecosystem protection, as I mentioned in Chapter one, historically, this has been prioritised in areas with high levels of biodiversity (Myers et al., 2000; Reid, 1998). The outcome of the meta-analysis demonstrates that this should not be the case, because in addition to this, while Frank et al., (2018) found a highly generalist use of dung resources along the latitudinal gradient, the magnitude of the effects across seasonal variations and subsequent ecological consequences are not clear. In chapter four, my mesocosm experiment demonstrated that facilitating dung beetle beta diversity has positive benefits for ecosystem multifunctionality. The seasonal variations in temperate zones exhibit high levels of beta diversity and under global change scenarios this is predicted to lead to multi-trophic homogenisation which has detrimental impacts on the processes that occur within ecosystems (Gossner et al., 2016). The role of spatial homogenisation of community composition and the potential interaction between diversity at different scales in maintaining ecosystem functioning has been studied across grasslands, and homogenisation across space negatively affected ecosystem functioning and services (Hautier et al., 2018). Therefore, knowledge gained from the meta-analysis (chapter two) and the mesocosm experiment (chapter four) can help target future research into dung beetle temporal diversity, which can aid in the development of ways in which we can maintain ecosystem multifunctionality at both local and landscape scales.

Moreover, although numerous individual studies have quantified the effects of dung beetle nesting strategy on ecosystem functions (Batilani-Filho & Hernandez, 2017; Cheng et al., 2022; Piccini et al., 2020), there is a lack of overall synthesis regarding the relative contribution of nesting behaviour types to the extent of function delivery. This aspect is of particular interest to investigate further, as dung beetle introduction programs have frequently emphasised that paracoprid behaviour is the most effective strategy for dung removal and other essential ecosystem functions, such as pest and parasite control (Doube et al., 2014). Unlike individual studies, a meta-analysis approach considers the collective evidence beyond environmental variables or specific species (Koricheva et al., 2013). Through this approach, I discovered that mixed nesting behaviour assemblages enhance ecosystem functions, highlighting importance of complementarity, harking back to the evolution of coprophagy as I discuss in chapter one, where diverse nesting strategies evolved to make use of the entire dung pad (Halffter & Edmonds, 1982). Therefore, it is no surprise that the magnitude and direction of the delivery of specific functions may vary in under differing nesting behaviours, as the evolutionary history of species and their interactions can influence the relationship between biodiversity and ecosystem functioning (Eisenhauer et al., 2019). Hence, it is plausible that dung beetle introduction programs should strive to introduce a diverse range of nesting behaviours within novel assemblages. This approach could increase the chances of the facilitation of a wide array of ecosystem functions and maximise waste removal from the pasture surface.

Based on the meta-analysis presented in chapter two, dung beetles do not appear to have adverse impacts on ecosystem functioning in both agricultural and wild landscapes. Furthermore, I found no significant difference between introduced or wild dung beetle species in ecosystem function delivery which is an important finding for introduction programs as it is evidence that they can deliver ecosystem function in agro-ecosystems. While there was a slight reduction in plant growth enhancement values in studies quantifying introduced dung beetles, this could be attributed to the method of measurement used. The meta-analysis in chapter two also showed that mixed nesting behaviours have a positive influence on primary productivity, however, the proportion of effect sizes demonstrating plant growth enhancement in the presence of dung beetles accounted for less than 10% of the ecosystem functions. This finding is in line with a review of the current knowledge on how dung beetles affect tropical forest plants, where authors underscore that further research is needed to understand the mechanisms driving plant growth in both tropical and temperate zones (Andresen & Urrea-Galeano, 2022) especially because the current evidence is limited and comes from controlled experiments only (Badenhorst et al., 2018; Hea et al., 2005). However, research on the effects of invertebrate decomposers on plants in general often focuses on isolated aspects of plant growth rather than comprehensively exploring the combined effects of enzymatic degradation of plant material, modification of soil structure by soil fauna, and subsequent implications for soil properties, microbial communities, and plant outcomes (Griffiths et al., 2021). Interestingly, in the mesocosm experiment in chapter four, I found that temporal dung beetle diversity did not significantly enhance plant growth, even though the structural equation modelling revealed underlying mechanisms of microbial activity on enhanced ammonium N levels which should facilitate primary productivity. While excess ammonium may have affected dung beetle mediated plant biomass production (Liu & Von Wirén, 2017), the underlying mechanisms are still not clear. Especially because the literature also discusses possible negative effects of dung beetles on plant growth (Andresen & Urrea-Galeano, 2022) highlighting that we simply do not know the specific mechanisms by which dung beetles facilitate plant growth.

In the third chapter of my research, I focused on comparing different approaches to predict ecosystem functioning, specifically dung removal, carried out by introduced dung beetle communities in Aotearoa NZ pastures. I aimed to investigate the relationship between various biotic drivers, including community structure and functional traits, as well as the previously unexplored aspect of community energy use. While community structure and community energy use did not predict dung removal rates, the community weighted mean nesting behaviour index was significant. This highlighted the value of taking a more targeted approach to the selection and use of functional traits in predicting ecosystem functioning, and a reminder of the mechanisms that lead to the functions of interest. For example, dung removal occurs through nesting behaviour, that nesting behaviour is a function of the legs. Therefore, a measure of leg robustness is an appropriate trait to select to predict the extent to which a community can deliver dung removal. Furthermore, different traits can be selected for different questions, for example the eye morphology of dung beetles in South Africa show a highly refined temporal partitioning strategy, with differences in peak of activity even within the diurnal, crepuscular, and nocturnal guilds, independent of nesting behaviour and taxonomic classification (Tocco et al., 2021). Nocturnal species have bigger eyes than crepuscular and diurnal species, and corneal structure is influenced by the activity period of the species (Tocco et al., 2021). Although the authors do not directly address the implications for ecosystem function, understanding the dynamics of dung beetles well-defined "shift work" schedule and eye morphology can enhance our understanding of their relative contribution to ecosystem functioning over time. While I only discuss the effect traits that are responsible for driving changes in ecosystem functioning, this method is equally capable of determining response traits, which are traits are influenced by external factors such as resource availability, climate, or habitat conditions (deCastro-Arrazola et al., 2022). Investigating the response traits could shed light on whether morphological traits exhibit responses to environmental changes such as warming temperatures under climate change. Future research endeavours can establish a catalogue of standardised behavioural traits that can be quantified using morphological measurements, providing a means to predict specific aspects of ecosystem functioning (Giménez Gómez et al., 2022).

5.3 Future research

Trophic regulation in the dung beetle ecology literature often refers to secondary seed dispersal, plant growth enhancement and pest parasite control (Nichols et al., 2008). However, in my study I defined trophic regulation as any measure of above or below ground biodiversity benefits resulting from dung beetle activity. Technically, the effect sizes found from the secondary seed dispersal, plant growth enhancement and pest parasite control categories could have been repeated in the trophic regulation category, but the decision to treat these categories separately has exposed a gap in our understanding of the biodiversity benefits that dung beetles may offer. As a result, the trophic regulation category was represented by a handful of effect sizes measuring the feeding activity of soil organisms using bait lamina strips, which are indicators of functioning soils and healthy belowground soil organism communities. It is important to ensure we understand the trophic regulation mediated by dung beetles, because interactions spanning multiple trophic levels and ecosystem compartments establish connections between different ecosystem types, and ensure the stability of trophic dynamics, the flow of matter and energy (Barnes et al., 2018). This has consequences for the provision of ecosystem functions and services. Slade et al., (2016) investigated microbial diversity in both the dung and the soil in the presence of dung beetles and found that the microbial community composition was associated with differences in substrate usage, showing the importance of considering the interactions between macroscopic and microscopic organisms in ecosystem processes. With this hindsight, the mesocosm experiment in chapter four could have also investigated the belowground biodiversity through bait lamina strips and taking soil cores of belowground soil organisms, which could have been included in the SEM. However, sampling for this may have been challenging due to the volume of soil required to do the physicochemical analyses as well as belowground soil community identification. In future studies, it could also be valuable to sample the above ground flying insect communities that are associated with the dung, which can be achieved by setting yellow sticky traps positioned adjacent to the dung (Gill & O'neal, 2015). This approach may capture the effects of different aspects of trophic regulation, leading to a more thorough understanding of the consequences of dung beetle trophic links.

The meta-analysis had variation in the approaches used to measure diverse ecosystem functions (for which I did not collect data). This raises the question of whether standardising measurements should be considered. Standard methods for dung beetles biodiversity studies exist (Larsen & Forsyth, 2005) however, there are no frameworks for a standardised methods that allow for comparative evaluation of biodiversity ecosystem functioning studies across biomes. Standardised biodiversity survey methods exist for insect groups, such as suction trapping for aphids and light trapping for moths, which have enabled us to establish the temporal changes in populations and communities over time (Bell et al., 2020). Like dung beetles, termites are also an ecologically important species and much knowledge of termite assemblages in tropical ecosystems was obtained through the standardised transect method (Jones & Eggleton, 2000) with updated recommendations to tailor these methods to ensure they are biome-specific sampling methods to enhance knowledge of termite diversity and influence on ecosystem functioning (Davies et al., 2021). By adopting and using a standardised field protocol, future studies can contribute to a more robust understanding of global trends in dung beetle effects on ecosystem functioning, as well as a foundation for assessing functional traits, allowing for meaningful comparisons across different regions and habitats in future meta-analyses.

The work by Raine et al., (2018) was inspirational in the development of my hypotheses in chapter three. If dung beetle morphological measures can be used to quantify an index of a behavioural trait to predict the natural history of a cryptic species, then can it be used to predict ecosystem functioning? The results not only showed that the community weighed mean value for nesting behaviour was significant in predicting dung removal, but it also circled back to the initial functional guilds of the dung beetles: their nesting behaviour (Halffter & Edmonds, 1982). If a standardised survey method for dung beetle effects on ecosystem function were established, it would enable the calculation of community weighted trait measures across different biomes, and potentially be used to forecast ecosystem function delivery under different environmental scenarios.

Ecological intensification is a concept that aims to harness ecosystem services to sustain agricultural production while minimizing adverse effects on the environment. It is a nature-based alternative to high-input agriculture (Kleijn et al., 2019). In chapter four, despite hypothesised mechanisms, structural equation modelling did not detect the expected plant growth processes, nonetheless, this raises numerous intriguing avenues for speculation worth exploring. For example, is the presence of specific microbial communities throughout the dung beetle life cycle that can facilitate to nitrogen fixation, uric acid metabolism, and plant cell wall degradation (Suárez-Moo et al., 2020) and whether there are unique plant biostimulants associated with dung beetle activity (Pereira et al., 2021). On the other hand, the reporting consistency of plant growth enhancement in dung beetle studies is brought into question. Given that it is frequently mentioned in the literature, one would expect it to be commonly measured. However, there is a high likelihood that this particular ecosystem function may suffer from the "file drawer" problem, where studies with non-significant or contradictory results are less likely to be published (Koricheva et al., 2013). This has consequences for nature-based agroecosystem management, as knowledge of the magnitude and direction of dung beetle mediated plant growth enhancement can facilitate the investigation into the underlying mechanisms leading to this result. This in turn will enable a more tailored approach to optimal management to facilitate sustainable agroecosystems (Allen et al., 2022).

5.4 Conclusion

In conclusion, the findings presented here emphasise the important role of dung beetles on ecosystem functioning. It has contributed to filling knowledge gaps of global trends of dung beetle mediated ecosystem functions, the predictive capacity of community weighed values of functional traits, and the role of dung beetles in facilitating ecosystem multifunctionality in

Aotearoa NZ pastures. Furthermore, it has raised novel avenues for research, particularly related to specific ecosystem functions including plant growth enhancement and trophic regulation (chapter two), the use of targeted community weighted trait indices to predict ecosystem functioning (chapter three) and the importance of facilitating temporal diversity in ecosystem multifunctionality in introduced communities (chapter four).

Based on the research conducted across these chapters, I sought to determine whether dung beetles are a viable nature-based solution for Aotearoa NZ's agricultural pastures. Considering the collective findings, it is evident that dung beetles have a significant potential as a nature-based solution, through the ecological intensification and trophic diversification of pasture food-webs. Their nesting behaviour has the potential to be used in models to forecast future rates of dung removal, and they enhance ecosystem functioning by dung removal and improved nutrient cycling through direct and indirect pathways and contribute to overall ecosystem multifunctionality.

Overall, this thesis has highlighted the benefits of dung beetles on ecosystem functioning, from global trends to Aotearoa NZ pastures. For a nature-based solution to be classified as such, it is necessary to showcase its positive impact on biodiversity (Seddon et al., 2020). My assertion is that the introduction of dung beetles is ecological intensification, and can be considered a form of "re-wilding" for agricultural ecosystems, effectively bringing in biodiversity. Similar to how degraded secondary forest systems require intentional human planting, agricultural pastures calls for the deliberate release of beneficial insects such as dung beetles to recreate functional, self-sustaining ecosystems.

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