















REVIEW

A trait-based framework for dung beetle functional ecology

Indradatta deCastro-Arrazola^{1,2}  | Nigel R. Andrew³  | Matty P. Berg^{4,5}  |
Alva Curtsdotter³  | Jean-Pierre Lumaret⁶  | Rosa Menéndez⁷  | Marco Moretti⁸  |
Beatrice Nervo⁹  | Elizabeth S. Nichols¹⁰  | Francisco Sánchez-Piñero²  |
Ana M. C. Santos^{11,12}  | Kimberly S. Sheldon¹³  | Eleanor M. Slade¹⁴  |
Joaquín Hortal^{15,16,17} 

¹Germans Cabot Franciscans 48, Bunyola, Spain; ²Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, Granada, Spain; ³Insect Ecology Lab, Natural History Museum, University of New England, Armidale, New South Wales, Australia; ⁴Department of Ecological Science, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands; ⁵Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands; ⁶Université Paul Valéry Montpellier 3, Montpellier, France; ⁷Lancaster Environment Centre, Lancaster University, Lancaster, UK; ⁸Biodiversity and Conservation Biology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland; ⁹Department of Life Sciences and Systems Biology, University of Torino, Torino, Italy; ¹⁰Department of Ecology, University of São Paulo, São Paulo, Brazil; ¹¹Terrestrial Ecology Group (TEG-UAM), Departamento de Ecología, Universidad Autónoma de Madrid, Madrid, Spain; ¹²Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain; ¹³Department of Ecology & Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, United States; ¹⁴Asian School of the Environment, Nanyang Technological University, Singapore, Singapore; ¹⁵Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain; ¹⁶Departamento de Ecología, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, Brazil and ¹⁷cE3c – Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências da Universidade de Lisboa, Lisbon, Portugal

Correspondence

Indradatta de Castro-Arrazola and Joaquín Hortal
Email: indradatta@riseup.net and jhortal@mncn.csic.es

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Abstract

1. Traits are key for understanding the environmental responses and ecological roles of organisms. Trait approaches to functional ecology are well established for plants, whereas consistent frameworks for animal groups are less developed. Here we suggest a framework for the study of the functional ecology of animals from a trait-based response–effect approach, using dung beetles as model system. Dung beetles are a key group of decomposers that are important for many ecosystem processes. The lack of a trait-based framework tailored to this group has limited the use of traits in dung beetle functional ecology.
2. We review which dung beetle traits respond to the environment and affect ecosystem processes, covering the wide range of spatial, temporal and biological scales at which they are involved. Dung beetles show trait-based responses to variation in temperature, water, soil properties, trophic resources, light, vegetation structure, competition, predation and parasitism. Dung beetles' influence on ecosystem processes includes trait-mediated effects on nutrient cycling, bioturbation, plant growth, seed dispersal, other dung-based organisms and parasite transmission, as well as some cases of pollination and predation.
3. We identify 66 dung beetle traits that are either response or effect traits, or both, pertaining to six main categories: morphology, feeding, reproduction, physiology, activity and movement. Several traits pertain to more than one category, in

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particular dung relocation behaviour during nesting or feeding. We also identify 136 trait–response and 77 trait–effect relationships in dung beetles.

4. No response to environmental stressors nor effect over ecological processes were related with traits of a single category. This highlights the interrelationship between the traits shaping body-plans, the multi-functionality of traits, and their role linking responses to the environment and effects on the ecosystem.
5. Despite current developments in dung beetle functional ecology, many knowledge gaps remain, and there are biases towards certain traits, functions, taxonomic groups and regions. Our framework provides the foundations for the thorough development of trait-based dung beetle ecology. It also serves as an example framework for other taxa.

KEYWORDS

ecosystem engineers, ecosystem processes, effect traits, multifunctionality, response traits, Scarabaeoidea, trait–function relationships

1 | INTRODUCTION

Trait-based ecology is advancing our understanding of species' responses to the environment, and their effects on ecosystem processes and services. Traits are morphological, physiological, phenological or behavioural features measurable at the individual level that relate to the organism's fitness and impact on ecosystem processes (Brousseau et al., 2018; Violle et al., 2007). Thus, trait-based frameworks seek to understand the consequences of environmental change by studying the linkage between traits and individual performance to determine how species respond to changes and, in turn, affect ecosystem processes (Gladstone-Gallagher et al., 2019; Lavorel et al., 2013; Lavorel & Garnier, 2002). Indeed, trait-based approaches provide a deeper understanding on the relationship between biodiversity and ecosystem functioning than species-based perspectives, allowing us to delve into the mechanisms and compare patterns across regions and taxa (McGill et al., 2006; Moretti et al., 2017). Based on the success of plant functional ecology, animal researchers have started portraying, measuring and applying traits in research questions (see Moretti et al., 2017). However, there remain knowledge gaps about which traits are more directly related to individual fitness (i.e. response traits) or impact ecosystem functioning (i.e. effect traits), and how to measure them in a standardized way.

This is the case of dung beetles, a group where the use of traits has received considerable attention (see Wong et al., 2019), but lacking an explicit framework for selecting key response and effect traits. Dung beetles (Coleoptera, Scarabaeoidea) are primarily coprophages; they use the excrement of mammalian herbivores as a resource in either or both adult and larval stages, although some species present other trophic preferences (see Holter & Scholtz, 2007). Besides participating in dung decomposition, they distribute dung horizontally and vertically across soils and landscapes, playing a crucial role in the recycling of nutrients and stimulation of plant productivity (Finn & Gittings, 2003; Nichols et al., 2008). Dung beetles

are also ecosystem engineers through the major effects that their burrowing and tunnelling activity have on soil physical structure and chemical composition (Jones et al., 1997). They also mix the organic matter from the dung with mineral soil, enhancing decomposition and nutrient mineralization, and reducing greenhouse gas emissions (Slade, Riutta, et al., 2016; Verdú et al., 2020). Moreover, they perform seed dispersal, dung fly and livestock parasite suppression and pest control, serve as trophic resources for insectivores, and some species are even pollinators or predators (Hanski & Cambefort, 1991; Nichols et al., 2008; Young, 2015).

The value of trait-based approaches for dung beetle ecology has long been recognized through their characterization in functional groups according to the way they utilize dung to feed and nest (Bornemissza, 1969; Halffter & Matthews, 1966). Dung beetles are grouped into five main functional groups: *paracoprids* (or tunnellers) dig tunnels under the dung pat where they relocate dung masses; *telecoprids* (or rollers) construct a brood ball, roll it away from the dung pat, and bury it; *endocoprids* (dwellers) nest and feed inside the dung pat or right beneath it in the dung–soil interface; *non-nesters* (also dwellers) feed on dung but do not make nests or nest elsewhere (e.g. on roots); and *kleptocoprids* (i.e. brood parasites) nest in the brood balls created by other species (Fountain-Jones et al., 2015; González-Megías & Sánchez-Piñero, 2003; Tonelli, 2021; see also Bornemissza, 1969; Halffter & Edmonds, 1982; Halffter & Matthews, 1966). These functional groups have been repeatedly correlated to variations in ecosystem functions such as dung removal (e.g. Tonelli et al., 2020), but they include large intraspecific and interspecific variations in different traits of functional significance (deCastro-Arrazola et al., 2020; Raine, Gray, et al., 2018). Body size relates to the efficiency in dung removal, so the combination of body size with nesting/feeding behaviour is commonly used to describe the ecological functionality of dung beetle communities (Doube, 1990). Other functional classifications have included competitive ability for

dung and space (Finn & Gittings, 2003; Krell et al., 2003), segregation of diel activity (e.g. Slade et al., 2007) or trophic behaviour (Larsen et al., 2008).

Beyond functional classifications, several traits have been related to dung beetle responses and effects (reviewed in Halffter & Edmonds, 1982; Scholtz et al., 2009; Simmons & Ridsdill-Smith, 2011). Comparatively little systematic research on dung beetle trait ecology has been done so far (but see e.g. Griffiths, Louzada, et al., 2016; Radtke & Williamson, 2005; Raine, Gray, et al., 2018). Thus, there is a dearth of knowledge on which traits are associated with dung beetle responses to environmental stress, how intraspecific variation links to fitness, and the effects of shifts in species composition on ecosystem processes. This is particularly important as dung beetles show consistent species responses to habitat transformation, mammalian defaunation and changes in climate and weather (e.g. Calatayud et al., 2021; Fuzessy et al., 2021). However, the increasing use of dung beetle traits has not been backed up by a conceptual framework for their standardized measurement and analysis as it has for plants or other animal groups (e.g. Moretti et al., 2017; Pérez-Harguindeguy et al., 2013; see Schneider et al., 2019 for a review). Establishing a theoretically robust dung beetle functional ecology requires (i) recognizing the limitations of traits as simplifications of natural variation in the performance of individuals and (ii) contextualizing their use within a comprehensive functional ecology that relates traits with individual responses to environmental gradients and effects on ecosystem functions.

Here we develop a framework for the study of the functional ecology of animals from a trait-based response–effect approach, using dung beetles as a model system. We review the main trait-based dung beetle responses to the environment and effects on ecosystem functions, outlining the measurable traits that are either known or hypothesized to be related to them. Then, we identify the potential trait-mediated linkages between responses and effects following a multi-trait approach, and discuss their implications for setting up a hypothesis-driven dung beetle functional ecology. The framework will help researchers to select specific traits according to particular research questions, identify research knowledge gaps and serve as a starting point for a collaborative research program to study the ecological significance of dung beetle traits. More broadly, we aim to provide an example of how to develop such trait-based research programs for other animal groups.

2 | TRAIT RESPONSES TO THE ENVIRONMENT

Dung beetles respond to both abiotic conditions, such as temperature or moisture, and biotic interactions, such as presence of predators or competitors (Figure 1). We identify the traits involved in these responses, outlining the main relationships between traits and environment (see Supplementary Table S1), and identifying gaps

in the knowledge necessary to predict dung beetle community responses to global change.

2.1 | Temperature

Dung beetle species differ in their thermal limits and associated physiological traits, such as thermal tolerance to extreme hot or cold conditions (Birkett et al., 2018; Gaston & Chown, 1999; Sheldon & Tewksbury, 2014). Therefore, they respond to ambient temperature in various ways along geographical and altitudinal gradients (Calatayud et al., 2021; Williamson et al., 2022). This affects activity time (Cuesta & Lobo, 2019a; Gotcha et al., 2021), reproduction (Holley & Andrew, 2019), habitat selection (Giménez Gómez et al., 2020, 2022), community composition (Gaston & Chown, 1999; Nyamukondiwa et al., 2018) and geographical distributions (Lobo et al., 2002; Sheldon & Tewksbury, 2014). Extreme soil temperatures are avoided by flying to cooler places (Caveney et al., 1995), walking to other (micro)habitats (Menéndez & Gutiérrez, 2004), using their balls as temporal thermal refuges (Smolka et al., 2012), digging deeper into the soil (Macagno et al., 2016; Mamantov & Sheldon, 2021) or nesting deeper in the soil to protect eggs/larvae from superficial heat (Kirkpatrick & Sheldon, 2022; Snell-Rood et al., 2016)—which could lead to a reduced brood ball size and number (Mamantov & Sheldon, 2021), abandoning the reproductive attempt (Holley & Andrew, 2019), or community-level shifts in the dominant nesting strategy along altitudinal gradients (Chamberlain et al., 2015). As well as increased thermal tolerances (e.g. critical thermal maxima) increased body size and decreased pilosity have been found to be associated with higher temperatures (Williamson et al., 2022). Furthermore, many species can heat themselves through the rapid movement of wing muscles (Giménez Gómez et al., 2020) or adopt different behaviours during flight to dissipate heat (Verdú & Lobo, 2008). This allows them to segregate their activity along temporal and spatial gradients of temperature through different thermoregulatory strategies (Verdú et al., 2022). The current rise in average annual temperature due to climate change has indeed resulted in phenological shifts, anticipated egg laying (Wu & Sun, 2012), faster larval development rate (Macagno et al., 2018) and geographic range shifts (Menéndez et al., 2014), but more information on the upper thermal limits of dung beetles (i.e. when they stop reproducing; Holley & Andrew, 2020) is needed to forecast their responses to climate change.

2.2 | Water

Insects respond to spatial and temporal variations in air, soil and moisture (Block, 1996; Sømme, 1986). Dung desiccation may affect reproduction success through impediments on larval feeding (especially in dwellers). Dung beetles respond quickly to variations in water availability by dispersing to appropriate locations

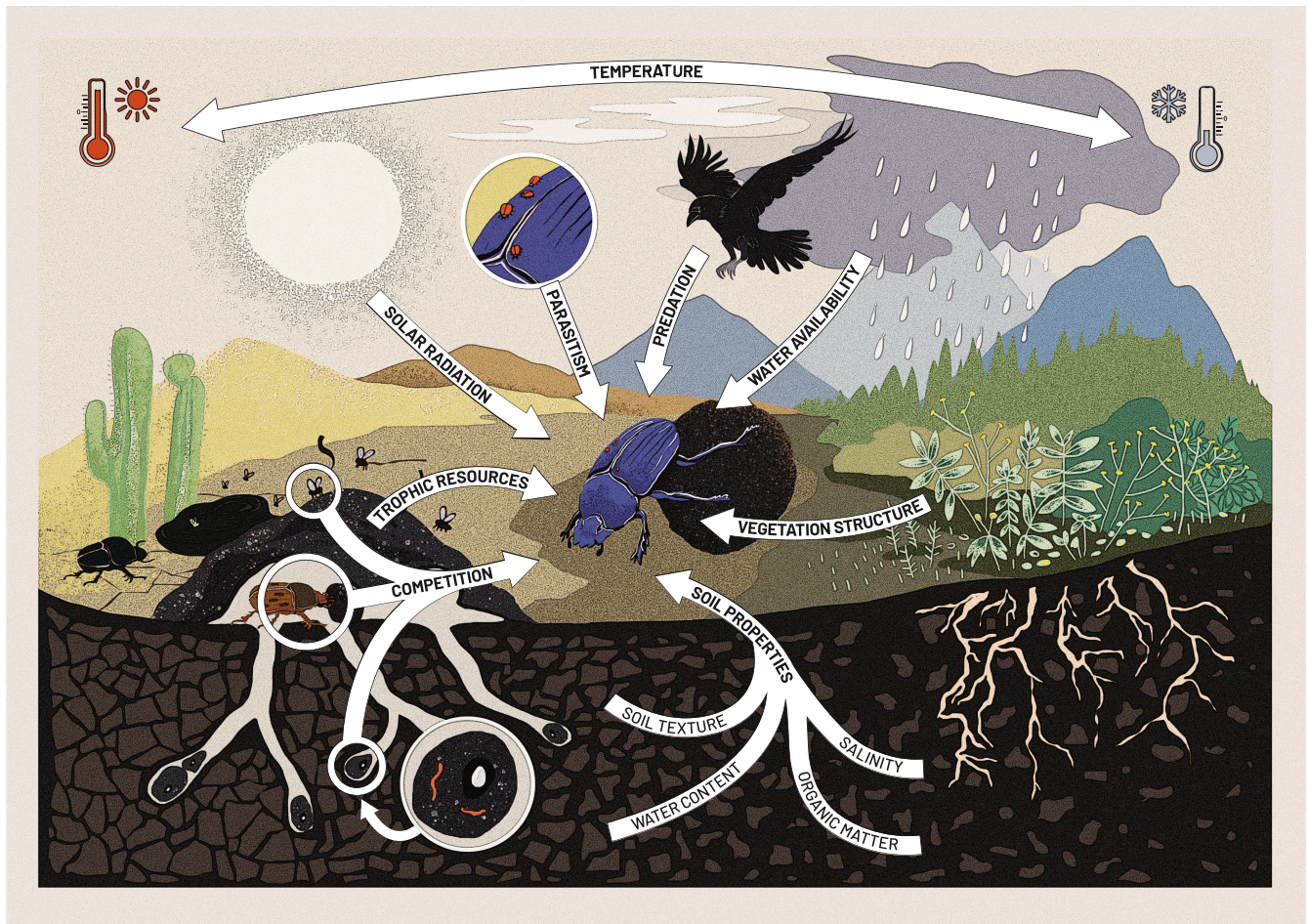


FIGURE 1 Dung beetle responses to the abiotic and biotic environment. Arrow titles in bold identify the main types of stressors or filters to which dung beetle traits respond, depicted as subsections in this review. Arrow titles in regular font identify some specific stressors.

(Sowig, 1995), via behavioural traits like time invested in reproduction or the structure of the burrows they build (Rougon & Rougon, 1983; Sowig, 1996), or by adjusting their seasonal phenology (deCastro-Arrazola et al., 2018; Liberal et al., 2011). At longer time-scales, variation in soil humidity can cause changes in morphological and reproductive traits (Duncan, 2002; Hammond, 1976; Rougon & Rougon, 1983; Verdú & Galante, 2004), and even in ontogenetic development (Vessby, 2001). In general, larger body sizes allow a higher desiccation resistance (Nervo, Roggero, Chamberlain, Caprio, et al., 2021), although physiological responses to desiccation vary at the species and individual levels, with females often being more resistant than males within a species (Nervo, Roggero, Chamberlain, Rolando, et al., 2021). Physiological traits also respond to water gradients along with behavioural responses, reducing water loss rate and/or tolerating water loss in dryer conditions (Duncan & Byrne, 2000; Nervo, Roggero, Chamberlain, Caprio, et al., 2021), or increasing their tolerance to the hypoxic conditions in the wet dung pats of humid environments (Holter, 1991; Whipple et al., 2013). Wet dung can sometimes reach up to 90% water content, requiring particular adaptations in mouthparts' morphology to squeeze fluids out of the

food (Holter, 2004; Tonelli et al., 2021). Given recent increases in drought and flooding events, more information is needed on dung beetle tolerance to these extreme conditions.

2.3 | Soil properties

The physical properties of the soil, such as texture, structure and compactness—which are related to types of soil particles (clay, silt and sand), can affect its water content (see previous section), but also dung beetle underground movements. Some dry sandy soils are too loose for tunnelling (Barkhouse & Ridsdill-Smith, 1986), while digging in loamy soils is time consuming (Sowig, 1995). Thus, variation in soil physical conditions generate responses in traits related to digging ability—such as prothorax volume and metatibia shape and size, as well as in nesting behaviour (see Macagno et al., 2016). Soil conditions may influence time investment in nest construction for burrowing species (paracoprids and telecoprids), thus affecting several traits of the extended phenotype of dung beetles (see Royauté et al., 2018), including burrow depth, burrow ramification, burrow distance from the dung pat or soil relocation (Brussaard &

Runia, 1984; Silva et al., 2015). These traits may also respond to soil chemical properties such as pH and organic matter content (influencing soil structure and cation exchange capacity), salinity (tightly related to soil humidity), nutrient availability and microbial activity (Brady & Weil, 2001). Tolerance to soil acidity and salinity affect dung beetle performance, and therefore their nesting and burrowing behaviour (Simons et al., 2018).

2.4 | Trophic resources

The characteristics, quantity, quality and types of trophic resources (i.e. dung, carrion, fungi or plant detritus) vary widely through time in many environments, hence driving spatial and temporal changes in dung beetle diet (e.g. Barton et al., 2011; Raine & Slade, 2019). This promotes responses in traits involved in modifying yearly and diel activity (e.g. thermoregulation; Ybarrondo & Heinrich, 1996), as well as in locating and reaching the resource (olfactory traits, Dormont et al., 2010; Tribe & Burger, 2011; eye size, Raine, Mikich, et al., 2018; movement and dispersal traits, Raine, Gray, et al., 2018). Both quantity and quality of dung are important for larval development (Shafiei et al., 2001; Sullivan et al., 2016), size of adults, and male horn allometry (Emlen, 1997). Although most dung beetles and their larvae are fairly generalist in their feeding habits (Frank et al., 2018; Raine & Slade, 2019), some show trophic preferences even within species (Raine et al., 2019), via mouthpart adaptations to shift from filtering to triturating mouthparts and modifications in their nesting and burrowing behaviour (Tonelli et al., 2021; Verdú & Galante, 2004). These behavioural responses may cause changes in traits linked to dung relocation, such as leg length (elongated for ball rolling), and body size (related to resource quantity). However, little is known about resource selection for nesting, although DNA metabarcoding has revealed diet shifts during different life stages in a South African beetle (Kerley et al., 2018). Furthermore, reproductive activity responds to the presence of pesticides and ivermectins in the dung, which affect community structure and ecosystem functioning (González-Tokman et al., 2017; Tonelli et al., 2020; Verdú et al., 2018).

2.5 | Light

Dung beetles respond to variations in near-infrared, visible light, UV and light intensity (Dacke et al., 2021; el Jundi et al., 2015). UV radiation can damage internal tissues causing mortality (Beresford et al., 2013) or inhibiting development (Faruki et al., 2005). Exoskeleton ultrastructure (i.e. arrangement of chitin layers) responds to these radiations. It determines heating rate via absorption of different light wavelengths (Cuesta & Lobo, 2019b), facilitating activity in cold environments (Amore et al., 2017), but also produces different colours and/or iridescence (Alves et al., 2018; Carrascal et al., 2017), which can diminish deleterious UV effects (Shi et al., 2015) or affect species interactions (Bothwell et al., 1994; Rousseaux et al., 1998).

Body areas that fluoresce under UV light have a function in sexual selection (Vulinec, 1997), but can also attract predators (Bennett & Cuthill, 1993; Young, 2015) or protect against them (Alves et al., 2018; Hernandez, 2002). Within the visible light spectrum, polarized and non-polarized natural and artificial light serve as orientation cues for foraging dung beetles (Dacke et al., 2003). These behavioural responses are associated with morphological changes in eye size and the lower/upper ratio of the eye divided by the canthus (Byrne & Dacke, 2011; Raine, Gray, et al., 2018). Higher sight resolution allows for a safer landing directly on dung pats, thus reducing predation risk (Byrne et al., 2009). Higher sight sensitivity allows for obstacle avoidance while moving under reduced light conditions. Structural responses to reduced light include increasing focal lengths and eye aperture (McIntyre & Caveney, 1998; Warrant & McIntyre, 1993) and larger rhabdoms (Dacke et al., 2003). These responses to light may be highly conserved among related species (Alves et al., 2018).

2.6 | Vegetation structure

Vegetation structure is a major driver of the diversity and composition of dung beetle communities (Gardner et al., 2008; Nichols et al., 2007), as it produces variations in many environmental stressors (e.g. microclimate conditions, resource availability and soil conditions). The more extreme conditions and microclimatic variations of open habitats may promote a higher diversity of physiological traits (Giménez Gómez et al., 2022), whereas the structural complexity of vegetation affects movement, social signalling and perching behaviours and their associated morphological traits (e.g. body size, eye size, wing size). The complex vegetation of dense forests favours shorter flights and higher manoeuvrability, and thus lower wing aspect ratio and larger eyes (Bai et al., 2012), although variations in wing morphology may be a response to constraints associated with foraging on the ephemeral and patchy resources typically found in forests (Ospina-Garcés et al., 2018). Dung beetle colour may also respond to vegetation structure through evolutionary pressures related to social signalling (Vulinec, 1997), with iridescence potentially favouring co-specific detection (male advertisement and female mate choice) in habitats with higher vegetation complexity as a result of varied light conditions (see Douglas et al., 2007). Furthermore, some tropical dung beetles use specific plants for perching, a behaviour associated with resource detection (Gill, 1991; Howden et al., 1991) and pre-flight body-heat increase (Young, 1984), which has been related to body size and feeding guilds (Noriega et al., 2020).

2.7 | Competition

Mammal faeces are ephemeral and patchily distributed, making competition for resources a major driver of dung beetle diversification and community structure (Halfpeter & Edmonds, 1982; Hanski & Cambefort, 1991). The ability to reach fresh excrement is determined

by dispersal ability (related to wing morphology and wing load) and olfactory capacity (e.g. antennal development area). Competition for nesting space and mating partners drive trait selection and promote phenotypic and niche divergence (Simmons & Ridsdill-Smith, 2011). Dung exploitation strategies have selected for diverse traits, such as elongated body shape (associated with poor burrowing capabilities), dorsal surface area of head and prothorax (Halffter & Edmonds, 1982; Hernández et al., 2011), and the size and shape of front and hind tibiae (deCastro-Arrazola et al., 2020). Competition for nesting inside the dung pat triggers variations in eggs (size, number, survival), larvae (body size, development time, survival), and female oviposition rates (Finn & Gittings, 2003). In paracoprids, horns help to defend burrows and attract females, and horn size and shape correlate with the quality of the immune system and physiological differences between individuals (Knell, 2011). Finally, kleptocoprids (i.e. brood parasites) show a special type of interference competition in which a species parasitizes both food resources and parental care provided by adult beetles of the same or a different species for their larvae (González-Megías & Sánchez-Piñero, 2003; Moczek & Cochrane, 2006). Dung beetles also compete with other dung feeders, in particular flies, that hatch earlier and have shorter development times than non-nester larvae (Hirschberger & Degro, 1996). Several strategies have been hypothesized for dung beetles to avoid nest infection by kleptocoprids and kleptoparasites, including divergence in seasonal and diel activity—leading to asynchrony of host and parasite species, and avoidance of microhabitats with higher parasitization probability (González-Megías & Sánchez-Piñero, 2004). Once infection occurs, sensorial traits (i.e. related to olfactory, visual, vibration cues) would potentially be key for detecting brood parasites, which may trigger responses like nest abandonment, increasing clutch size to dilute parasite impact or increasing the number of nests while reducing clutch sizes in a risk-spreading strategy (González-Megías, 1999; González-Megías & Sánchez-Piñero, 2004).

2.8 | Predation

Dung beetles are predated by vertebrates and invertebrates, sometimes in large quantities (Young, 2015). Although the effect of predation has been seldom studied (Horgan & Berrow, 2004; Wu et al., 2011), the high diversity of dung beetle predators has resulted in the evolution of a variety of anti-predatory mechanisms (Halffter & Edmonds, 1982; Halffter & Matthews, 1966), including cryptic and aposematic coloration (comprising both Müllerian and Batesian mimicry); defensive secretions (Burger et al., 1995); stridulatory organs producing sound that elicits a startle or aposematic response (Bailey, 1991); flight ability and changes in diel activity involving modifications of other traits such as endothermy (Kojima & Kato, 2017; Mena, 2001); and behavioural mechanisms such as thanatosis (Goljan, 1953). Additionally, predation on larvae may have driven the evolution of nesting strategies (Kingston & Coe, 1977; Scholtz et al., 2009).

2.9 | Parasitism

Dung beetles are attacked by a variety of ecto- and endoparasites. Ectoparasitic mites reduce longevity, especially of large beetles (Kotiaho & Simmons, 2001), and may affect mate selection (Buzatto et al., 2019). Mechanisms to prevent or reduce ectoparasites include behavioural (such as brushing or kicking parasites), morphological (cuticle thickness and hairiness) and physiological and chemical (defensive secretions) traits (Price et al., 2011). The semiochemicals of dung beetles' cuticles provide the parasites with an advantage over the host (i.e. keiromonal), and favour the host-finding behaviour of phoretic mites (Niogret et al., 2006). Endoparasites may also reduce dung beetle survival and reproductive success; parasitic nematodes reduce burrow depth and dung removal and consumption in several Scarabaeinae species (Boze et al., 2012). Defensive responses against endoparasites include toxicity of digestive fluids, impermeability of the peritrophic membrane, encapsulation of parasites or pathogens within tissues and brood mass reduction (Reaney & Knell, 2010; Servín-Pastor et al., 2020; Speight et al., 2008; Verdú et al., 2013). Dung beetle body mass and maximum diameter of particles ingested may respond to the pressure of infection intensity by endoparasitic helminths (Nichols & Gómez, 2014).

3 | EFFECTS OF TRAITS ON ECOSYSTEM FUNCTIONS

Dung beetles affect ecosystem functions (Figure 2; Nichols et al., 2008), and effect traits have been studied both in the field (e.g. Andresen, 2002; Braga et al., 2013; Slade, Riutta, et al., 2016) and in laboratory and field mesocosms (e.g. Beynon et al., 2012; deCastro-Arrazola et al., 2020; Nervo et al., 2014). In this section, we review how dung beetle traits may determine the delivery of ecosystem functions, outlining the main relationships between traits and functions (see all relationships in Supplementary Table S2, and additional bibliography at Supplementary Table S4), and identifying knowledge gaps that need to be addressed to predict changes in ecosystem functioning due to global change.

3.1 | Nutrient cycling

Dung beetles play an essential role in recycling through the removal, relocation and burial of mammalian dung, the instigation of micro-organisms, and via chemical changes in the upper soil layers (Nichols et al., 2008). They incorporate phosphorus into the soil and plants through their dung burial activities (Haynes & Williams, 1993; Maldonado et al., 2019; Rowarth et al., 1985). Differences in feeding and reproductive behaviour, body size and morphology can influence the rates of dung burial. Paracoprids play a greater role in dung removal compared to telecoprids and dwellers (Nervo et al., 2017; Slade et al., 2007), although telecoprids may relocate dung to microhabitats that are less accessible



FIGURE 2 Dung beetle effects on ecosystem functioning. Arrow titles in bold identify the main types of trait-driven effects of dung beetles on the ecosystems, depicted as subsections in this review. Arrow titles in regular font identify some specific effects.

by mammals, removing large proportions of dung in some contexts such as Mediterranean Region (see, e.g., Milotić et al., 2019; Verdú et al., 2018). Next to body size (e.g. Kaartinen et al., 2013; Nervo et al., 2014), several morphological traits (i.e. head area and width, pronotum length and width, prothorax height and volume and size of both fore and hind tibiae) have been positively related with dung removal, while others cause reductions in this function (longer lengths of head, protibia and metatibia; deCastro-Arrazola et al., 2020). A smaller set of traits has been positively related to dung burial (i.e. prothorax height and volume and protibia surface area), while total body length appears to negatively affect it (probably due to its association with the elongated Aphodiinae body-plan; deCastro-Arrazola et al., 2020). Protibia area is the only trait known to relate to burrow depth (Macagno et al., 2016). Several non-morphological traits, such as thermal tolerance, yearly and daily activity period, dung colonization stage, and interactions between individuals and sex within species may also indirectly affect dung removal (Giller & Doube, 1989; Nervo et al., 2022; Piccini et al., 2020), reducing nitrogen loss from dung pats (Gillard, 1967), since nutrient content decreases with dung aging (Holter, 2016).

Dung beetles also impact nutrient cycling through direct effects on microbial community composition (Slade, Roslin,

et al., 2016; Tixier et al., 2015), and indirectly by promoting aerobic conditions in both dung pat and soil (e.g. Maldonado et al., 2019; Manning et al., 2016; Yokohama et al., 1991). Dung relocation strategy determines where nitrogen mineralization and nitrification takes place: inside the dung pat or at the dung–soil interface (dwellers) or below the surface (tunnellers and rollers; Evans et al., 2019; Nervo et al., 2017), potentially reducing ammonia volatilization (Ma et al., 2006; Sugimoto et al., 1992). Dung beetles play a key role in regulating greenhouse gas emissions from cattle dung (Iwasa et al., 2015; Penttilä et al., 2013; Slade, Riutta, et al., 2016). Body size impacts the reduction of methane fluxes from dung pats; larger individuals excavate larger holes and galleries promoting aerobic processes, although these dynamics may vary with clutch size and female reproductive investment (Piccini et al., 2017). The importance of dung beetles in regulating these fluxes is evidenced by the strong impacts of treating cattle with ivermectins and antibiotics on greenhouse gas emissions from cattle faeces (Hammer et al., 2016; Verdú et al., 2020). Also, as the microbial activity that drives mineralization processes depends on temperature and water availability, dung beetle seasonal and daily activity may modulate their impact on nutrient cycling (Evans et al., 2019; Lee & Wall, 2006).

3.2 | Bioturbation and plant growth

Dung beetles play a key role in bioturbation (i.e. the displacement and mixing of sediment particles). Their burrowing activity enhances soil aeration (Manning et al., 2016), increases water infiltration, soil porosity and water retention (Keller et al., 2022), decreases soil erosion (Brown et al., 2010; Forgie et al., 2018), and increases soil nutrient content (Slade et al., 2017). These structural and compositional changes of top soil layers alleviate the impact of drought on plants and maintain plant productivity under climate warming (Johnson et al., 2016; Slade & Roslin, 2016). Burrowing enhances soil fauna, fungi and microbial activity (Manning et al., 2016; Slade, Roslin, et al., 2016), and maintain nutrient cycling, affecting all three main aspects of plant performance: survival, growth and reproduction (e.g. Bang et al., 2005; Bornemissza & Williams, 1970; Manning et al., 2017; Rougon & Rougon, 1983; Slade et al., 2017). Although the role of dung beetles on bioturbation has been little studied from a trait-effect perspective, it is most likely related with traits involved in burrowing either for feeding or reproduction (Simmons & Ridsdill-Smith, 2011; Slade & Roslin, 2016). This includes behavioural traits, such as reproductive strategy, where the effects of paracoprids and telecoprids probably have larger impacts at deeper soil layers than endocoprids, whose crucial contribution to bioturbation occurs at the dung-soil interphase (Slade & Roslin, 2016). Indeed, depth, length and ramification of burrows (which can be considered traits as part of the extended phenotype of dung beetles) determine bioturbation delivery (Mittal, 1993). So does parity, as more reproductive events per female result in higher net bioturbation. Bioturbation may also be affected by morphological traits such as adult and larval body size, or digging-related traits such as prothorax volume and metatibia shape and size, which in turn respond to soil properties (see Section 2). Furthermore, physiological traits such as thermal performance and metabolic rates may also influence soil movement rates (Macagno et al., 2018), and many of the dung beetle traits that respond to temperature (see Section 2.1) might have an indirect effect on bioturbation.

3.3 | Seed dispersal

Many mammals ingest considerable quantities of seeds while feeding, that are afterwards expelled in the dung (Janzen, 1984). Dung beetles unintentionally are secondary seed dispersers, relocating seeds vertically and/or horizontally away from the original dung deposition (Nichols et al., 2008). Seeds may benefit from these indirect actions in several ways, including relocation to more suitable microhabitats (Griffiths et al., 2015; Pérez-Ramos et al., 2013) and avoidance of pathogens and predation in the original dung pat (Beaune et al., 2012). This will increase seedling emergence and survival (Lawson et al., 2012; but see D'hondt et al., 2008 and deCastro-Arrazola et al., 2020) and decrease competition of seedlings for space and resources (Griffiths, Bardgett, et al., 2016; Lawson et al., 2012). Moreover, burial activity brings soil from deep layers to the surface, potentially raising seeds

from the seed bank to more appropriate conditions for their germination (Santos-Heredia & Andresen, 2014; Urrea-Galeano, Andresen, Coates, Mora Ardila, & Ibarra-Manríquez, 2019). As seeds are dispersed during dung manipulation, dung relocation strategy is a key trait (Halffter & Edmonds, 1982). In general, dung beetles disperse fewer large than small seeds (Andresen & Feer, 2005; Griffiths, Bardgett, et al., 2016), as they actively clean the dung ball before relocation to remove 'contaminants', such as large seeds or small stones (Andresen & Levey, 2004). Also, large seeds are placed at shallower depths than small seeds (Braga et al., 2017; Griffiths, Bardgett, et al., 2016). All these traits are highly correlated with dung relocation strategy and morphological traits, such as body size, clypeus and protibia shape and size (associated with digging ability), and metatibia shape and size (related to ball size and rolling distance). Indeed, large paracoprids show high rates of seed burial (Andresen, 2002; Slade et al., 2007), although some of these seeds may end up being buried too deep, as larger beetles dig deeper burrows (Gregory et al., 2015), making germination more difficult (Andresen & Levey, 2004; Koike et al., 2012). Telecoprids, in contrast, may bury less seeds (Andresen & Feer, 2005; Vulinec, 2002) but relocate them to more suitable locations for both germination—due to shallow nests (Gregory et al., 2015), and seedling survival—away from the higher competition in the dung deposit (Lawson et al., 2012; but see Urrea-Galeano, Andresen, Coates, Mora Ardila, Diaz Rojas, et al., 2019; Urrea-Galeano et al., 2021).

3.4 | Influence on other dung-associated organisms

Dung beetle activity profoundly alters dung pat conditions (see Section 3.1) and dung availability (Hanski & Cambefort, 1991). These alterations affect other dung-associated organisms, such as flies, soil mesofauna and microbes (Nichols et al., 2008; Skidmore, 1991), promoting fungal growth (Yokohama et al., 1991) and the transfer of microbes across the soil-dung interface (see Section 3.1; Slade, Roslin, et al., 2016). Furthermore, tunnelling inside the dung pat may favour access to other groups, such as Staphylinid beetles or, after the dung is dry, to generalist saprophages and predators, such as Histerid beetles, predatory mites or spiders. However, little is known on the indirect effects of dung beetle activity on the assemblages of microorganisms and invertebrates associated with mammal faeces, beyond their role in controlling fly populations. The number of fly eggs and larvae in the dung are affected through various direct and indirect mechanisms during dung manipulation (Nichols et al., 2008), which are, in turn, determined by body size, dung exploitation strategy, aggregation and phenology. Dung beetles limit the survival and development of fly eggs and larvae through asymmetric competition (i.e. resource preemption, see Section 2.7; Nichols et al., 2008). They impair microclimatic dung conditions for fly development by removing, spreading, desiccating and burying dung (Nichols et al., 2008). This is especially true when dung beetles aggregate in large numbers (e.g. some Aphodiinae species from genera like *Melinopterus*, *Nimbus*, *Chilothorax* or *Anomius* in Europe). The timing of dung colonization may also determine the magnitude

of the effects on other dung-associated organisms. Dung beetles arrive within the first hours after dung deposition and remove part of the dung which directly damage fly eggs and early instar larvae, while late-colonizing species affect late instar fly larvae through resource competition (Ridsdill-Smith et al., 1987; Ridsdill-Smith & Hayles, 1990). Seasonal activity period can also exert indirect effects on flies depending on phenological (a)synchrony (Ridsdill-Smith & Hayles, 1990). Dung beetles also control fly populations indirectly through the transport of phoretic mites that predate on fly eggs and larvae. Transport of phoretic mites is mediated by body size (larger beetles transport higher mite loads), dung beetle aggregation in the dung pats (allowing mite dispersion) and phenology (Glida et al., 2003; Niogret et al., 2009).

3.5 | Parasite regulation

Dung beetles interact with a large diversity of mammal parasites with faecal-oral transmission through the consumption, manipulation and relocation of vertebrate faeces during feeding and reproduction (Bílý et al., 1978; Mutinga & Madel, 1981). Some dung beetles affect parasite survival and transmission through direct and indirect mechanical interference, while others maintain or amplify successful transmission via indirect mechanical facilitation, direct biological facilitation and direct transport facilitation (Nichols & Gómez, 2014). The outcome of dung beetle–parasite interactions is influenced by dung relocation strategy and body size. For example, direct mechanical interference occurs when parasite eggs are damaged during passage through the beetles' masticatory and gastrointestinal systems (Mathison & Ditrach, 1999; Ryan et al., 2011), which may be most common for large-bodied species capable of consuming larger food particles (Holter et al., 2002). Indirect mechanical interference occurs when dung beetles impair dung pat abiotic conditions for parasites (Mfitilodze & Hutchinson, 1988; Stromberg, 1997). Here, endocoprid activity appears to have a particularly strong impact on dung pat microclimate (see Section 3.4) and may be associated with both positive and negative influences on parasite emergence rates over time (Chirico et al., 2003; Sands & Wall, 2017).

Dung beetles may also facilitate parasite survival and transmission rates through indirect mechanical, and direct biological and transport mechanisms (Bílý et al., 1978). It has been repeatedly argued—however with little empirical evidence—that the shallow burial of infected faeces by small-bodied paracoprids and telecoprids may enhance parasite survival and development, by creating an oxygenated and buffered environment from both solar radiation and temperature extremes (Bryan, 1976; Chirico et al., 2003; Coldham, 2011; Houston et al., 1984). Dung beetles also frequently act as intermediate hosts for parasites with indirect life cycles, particularly those that include insectivorous, omnivorous or carnivorous final hosts (Anderson, 2000; Nichols & Gómez, 2014). When dung beetles are infected, the intensity and prevalence of such infection varies widely, with greater infection intensity biased towards larger-bodied species (Gregory et al., 2015). These differences in infection patterns likely stem from a combination

of exposure to infection (e.g. diet breadth and feeding volume) and infection susceptibility (i.e. immune function). Finally, dung beetles may positively contribute to parasite transmission success by transporting parasite eggs or larvae on beetle exoskeletons or within their gastrointestinal systems (Mushkambarova & Dobrynin, 1972). While empirical data on this relationship are scarce, larger-bodied beetles may also have a higher capacity for such transport activities (Boze et al., 2012; Mutinga & Madel, 1981).

3.6 | Other effects

Some dung beetle species can act as pollinators (Sakai & Inoue, 1999) or predators (ants, Silveira et al., 2006; millipedes, Larsen et al., 2009). Although these cases may be anecdotal at a global scale, both functions can have important ecosystem effects. Indeed, dung beetles are often obligate pollinators of decay-scented flowers (i.e. Araceae and Lowiaceae species; Sakai & Inoue, 1999). Like other insects, flight ability and traits related to pollen attachment to the body (e.g. cuticle hairiness) are likely to affect pollination efficiency of dung beetles. On the other hand, predator dung beetles can effectively control leaf ant populations (Araújo et al., 2015). Species with predatory behaviour show clypeus shape modifications enabling the killing of prey (Larsen et al., 2009; Silveira et al., 2006). For both pollination and predation, spatiotemporal activity overlap with the resource (i.e. flower or prey) and detection ability (i.e. through detection of volatiles emitted by the resource) are likely to be important (e.g. Schmitt et al., 2004).

4 | INTERACTIONS BETWEEN TRAITS, ENVIRONMENTAL RESPONSES AND EFFECTS ON ECOSYSTEMS

Functional traits are not isolated, but part of an organism's body plan and physiology, where the same traits can be involved in both responses to the environment and effects on ecosystem processes (Lavorel et al., 2013; Lavorel & Garnier, 2002). This results in numerous interactions between functional traits and ecosystem processes, as response traits might either be linked to effect traits, or be the same trait (Piccini et al., 2018). Linkages between response and effect traits are key to understanding the cascading effects of community trait shifts in response to environmental stressors and the corresponding effect on ecosystem processes and services (Hébert et al., 2017; Moretti et al., 2013). Thus, any comprehensive approach to trait-based ecology must address the interactions among traits together with their associated effects and responses. With this aim, we compiled a list of response and effect traits and identified the links of each one of them to several environmental stressors and effects on ecosystem processes.

We identified 66 dung beetle traits, and assigned them to six main categories: morphology, feeding, reproduction, activity, physiology and movement (Table 1). For practical reasons, we have

TABLE 1 Relationships between dung beetle traits (middle column), responses to environmental stressors and filters (left columns) and effects on ecosystem functions (right columns). All stressors and functions correspond to sections of the main text, and are ordered according to their place in this review. The left columns identify the main types of stressors (environmental factors and/or evolutionary drivers) which dung beetles respond to, and ecosystem functions are the main types of effects of those traits on the ecosystem. Life aspect corresponds to the main categories of traits (related to activity, feeding, etc.), where traits that correspond to different aspects or ways of measuring the same structure or behaviour are grouped in a line, separated by commas. *Influence on other organisms* corresponds to the section entitled *influence on other dung-associated organisms, Perc.* for traits related with *Perception*, and *O.* for *Other* types of traits. All numbers correspond to either column or line counts, that is, the number of traits related to each stressor or function and the number of stressors or function linked to each trait, respectively (e.g. we identified 19 traits responding to temperature or 3 effects of phenology on ecosystem functions). Further information on these trait–response and trait–effect relationships can be found in supplementary Tables S1 and S2, and a fully searchable version of this table is provided as Supplementary Table S3

	Environmental stressors				Traits				Ecosystem functions										
	Temperature	Water	Soil properties	Trophic resources	Light	Vegetation structure	Competition	Predation	Parasitism	Life aspect	Trait	Nutrient cycling	Bioturbation/plant growth	Seed dispersal	Influence on other organisms	Parasite regulation	Pollination	Predation	
	136	19	16	13	5	7	33	10	14	14	Activity	19	13	9	7	12	9	8	77
1											Breeding period								0
7	✓	✓			✓		✓	✓	✓		Daily activity period	✓					✓		2
3	✓				✓		✓				Larval development time								0
6	✓	✓			✓		✓	✓	✓		Phenology	✓			✓		✓		3
2					✓		✓	✓			Feeding	✓		✓		✓		✓	4
1		✓									Feeding mode				✓				2
2					✓		✓	✓			Larval resource use	✓	✓						2
2					✓		✓	✓			Mouthparts morphology				✓			✓	3
1								✓	✓		Maximum ingestible particle size				✓			✓	1
8	✓	✓	✓		✓		✓	✓	✓		Morphology	✓	✓	✓	✓	✓	✓	✓	7
1	✓										Aerial sacs								0
3	✓				✓			✓			Body coloration								0
1							✓				Body fat								0
2	✓							✓			Body hairiness				✓		✓		3
1				✓							Clypeus area		✓						1
0											Clypeus shape			✓				✓	2
4	✓				✓			✓			Cuticle properties					✓			2
4					✓		✓	✓			Eye size and shape								0
5	✓				✓		✓	✓			Glossiness / iridescence								0
1							✓				Horn size								0
2				✓			✓	✓			Larval body mass	✓	✓						2
1					✓		✓				Metatibia length			✓					1
2					✓		✓				Metatibia shape	✓	✓						2
1							✓		✓		Peritrophic membrane								0
1					✓		✓				Prothorax volume	✓	✓						2
1							✓				Prothorax area	✓		✓					2
2							✓				Prothorax shape								1
1									✓		Stridulatory organs								0
1		✓									Subelytral cavity								0

TABLE 1 (Continued)

Environmental stressors			Traits				Ecosystem functions										
Temperature	Water	Soil properties	Trophic resources	Light	Vegetation structure	Competition	Predation	Parasitism	Life aspect	Trait	Nutrient cycling	Bioturbation/plant growth	Seed dispersal	Influence on other organisms	Parasite regulation	Pollination	Predation
1						✓			Movement	Antipredatory behaviour							0
2			✓		✓					Flight capacity					✓		3
1				✓						Perching behaviour							0
1				✓						Wing aspect ratio							0
2			✓		✓					Wing load					✓		3
4	✓		✓		✓				Perc.	Fused elytra					✓		3
3			✓		✓					Antennae size							0
3			✓		✓					Olfactory ability	✓				✓		3
1		✓						Physiology		Acid tolerance							0
0										Active metabolic rate	✓		✓				2
1	✓									Basal metabolic rate							0
2						✓		✓		Defensive secretions							0
1		✓								Desiccation resistance							0
1								✓		Digestive fluids							0
2		✓								Hypoxia tolerance							0
1								✓		Kairomones							0
1								✓		Parasite encapsulation							0
2	✓									Respiratory rate							0
1		✓								Salinity tolerance							0
1	✓									Thermal performance							0
1	✓									Thermal resistance							0
5		✓	✓		✓	✓	✓			Adult resource relocation strategy	✓	✓	✓	✓			4
2			✓		✓	✓	✓		Reproduction	Brood mass size	✓		✓	✓			3
3					✓	✓	✓			Burrow branching	✓	✓	✓				3
4	✓				✓	✓	✓			Burrow depth	✓	✓	✓				4
2	✓				✓					Burrow length	✓	✓	✓				2
3	✓				✓					Clutch size	✓						1
3		✓	✓		✓					Egg size							0
3		✓	✓		✓					Kleptoparasitism							0
1					✓					Oviposition rate							0
5	✓				✓	✓	✓			Parental care of the brood masses	✓			✓			2
1	✓				✓					Parity	✓	✓					2
1					✓					Number of ovary and ovarioles							0
1					✓					Size/weight of testes							0
1					✓					Sperm motility							0
1					✓					Spermathecal size/structure							0
1						✓			O.	Brushing, kicking behaviour							0

excluded all larval morphological traits except body size from our review, although some of them might perform the same role as they do in adults. Dung handling during feeding and reproductive behaviours are often very similar, so they are included in both categories. There are, however, many traits specific to feeding, related to mode of feeding, diet and ingested particle size (Holter, 2016; Holter & Scholtz, 2007). In the same way, many reproductive traits are not related to feeding, such as clutch size and egg size, or parts of the extended phenotype, such as burrow ramification, covering burrow walls with dung or presence of antimicrobial substances in brood masses (Bellés & Favila, 1983; Cortez et al., 2015). The category 'activity' aims to group traits describing the timing and phenology of dung beetle activity at different time-scales: within a day, during the dung desiccation process and within a year (Doube, 1990; Gittings & Giller, 1997; Silva et al., 2019).

Our review identified a high number of linkages between traits and functions or processes, totalling 136 trait–response and 77 trait–effect relationships (Table 1). A full description of the links between traits and either stressors or effects is given in Supplementary Tables S1 and S2, respectively. The responses to stressors, either environmental factors or evolutionary drivers, are inextricably related with the effects of dung beetles on ecosystem functions, as almost all responses and effects are mediated by traits of at least five of the six categories we considered (Figure 3). Nonetheless, availability of trophic resources, environmental moisture and air temperature stand out as the most important environmental stressors, acting as environmental filters for community assembly and inducing trait-based responses in dung beetles (e.g. Nichols et al., 2013; Raine, Gray, et al., 2018; Silva & Hernández, 2015; Stanbrook et al., 2021) (Table S1). The large number of traits that can be involved in the responses to these three key stressors are likely to be under strong selection, thus leading to a complex intertwined organismic response, which poses the challenge of separating trait responses to each one of the stressors.

With regard to effects, dung burial may be the behavioural activity with the highest ecological impact, as it directly affects key ecosystem processes such as decomposition, seed dispersal, several aspects of soil structure, composition, aeration and control of populations of other dung-associated organisms (e.g. deCastro-Arrazola et al., 2020; Griffiths et al., 2015; Nichols & Gardner, 2011; Table S2). It follows that such digging behaviour thus makes dung beetles important ecosystem engineers, playing a significant role in soil structure and fertility (Keller et al., 2022; Nichols et al., 2008). Indeed, the variations in all traits related to burrow construction and soil and dung manipulation play a key role in the most important effects of dung beetles on ecosystem functioning.

5 | ADVANCING TRAIT-BASED DUNG BEETLE FUNCTIONAL ECOLOGY

Ecology comprises a wide scope of spatial, temporal and organizational scales; from very localized to planetary, from static patterns of diversity to macroevolutionary ecology and from trait heritability

along lineages to regional species pools. A comprehensive framework for the study of dung beetle traits is critical for these scales. Our current knowledge of dung beetles includes good baselines for behaviour (e.g. Halffter & Edmonds, 1982), population and community (e.g. Hanski & Cambefort, 1991), evolution (e.g. Scholtz et al., 2009), physiology, ontogeny, development and sexual selection (see Simmons & Ridsdill-Smith, 2011), and, thus, provides a solid foundation for developing a trait-based approach to their functional ecology. However, there are large gaps in our knowledge of many traits and their functional significance. Furthermore, there are some consistent biases, as most dung beetle ecological research has focused on: (i) a few traits (e.g. nesting behaviour and body size); (ii) a few processes (e.g. dung removal, dung burial and seed dispersal); (iii) mainly the Scarabaeinae (except for Europe, where Aphodiinae and Geotrupidae have also been widely studied); (iv) largely Europe, tropical and subtropical America and South Africa; and (v) adults. In addition, it is important to remark that the relationships between traits, responses and processes reviewed here have been mostly hypothesized or assumed rather than corroborated with solid data. Indeed, knowledge of many of the trait–ecosystem process relationships discussed in our review is based on limited field data and correlative studies (Noriega et al., 2018). Beyond the extensive studies on sexual selection and parental care for a few species (e.g. Emlen et al., 2005; Macagno et al., 2018), only a handful of works have established direct trait–function relationships across species through experimental work (deCastro-Arrazola et al., 2020; Macagno et al., 2016; Nervo et al., 2014; Slade et al., 2007; compare with the 128 references cited in Supplementary Table S4).

Importantly, studies on global change effects on dung beetle communities have seldom addressed response traits (Giménez Gómez et al., 2022; Williamson et al., 2022). As a result, there is limited understanding of trait-mediated responses in relation to the impact of abiotic and biotic stressors, including resource competition, predation, temperature and humidity at all life stages. Besides other global change stressors, this is particularly important in the case of stressors derived from different agricultural practices, such as pasture abandonment (Tonelli et al., 2018) or land use intensification (Braga et al., 2013), but also cattle intensification (Tonelli et al., 2018) and use of antiparasitic treatments (González-Tokman et al., 2017; Verdú et al., 2018, 2020), and in general the implantation of either conventional or agroecological management practices (Hutton & Giller, 2003; Piccini et al., 2019). Therefore, further experimental work is needed to provide solid evidence of mechanistic cause–effect relationships, using response and effect traits (Noriega et al., 2018; Wong et al., 2019). However, the study of trait–process relationships is challenging and we suggest some important issues that need to be taken into consideration.

The classification of different traits into trait categories is subject to the limitations of categorizing complex natural variation within and across species. Many traits may also belong to two or more categories: for example, dung relocation behaviour is part of both the feeding and reproductive trait categories. Furthermore, some traits from a particular category may even be used as proxies

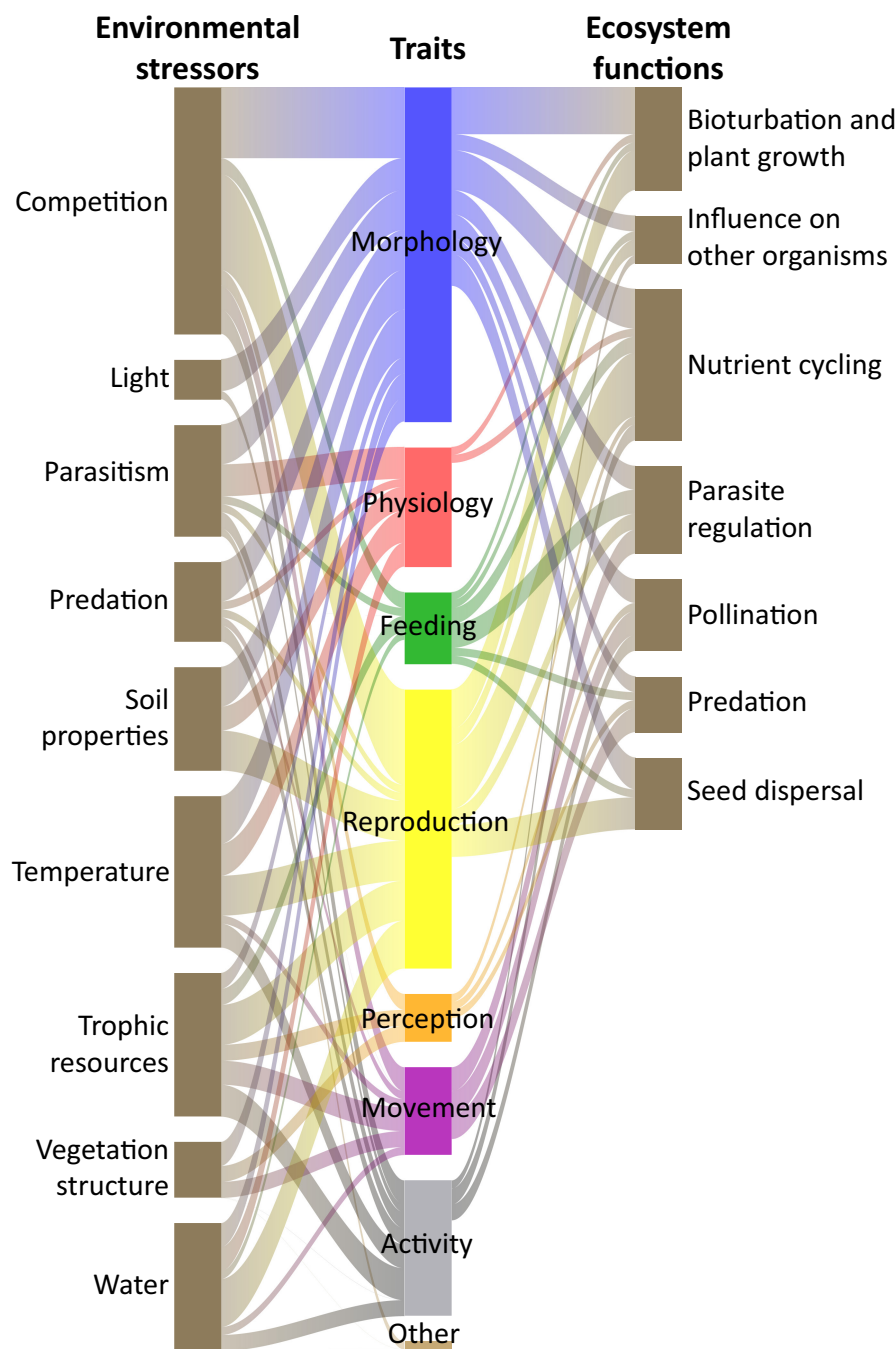


FIGURE 3 Relationships between dung beetle traits, responses to environmental factors and effects on ecosystem functions. Coloured bars identify the main types of traits, the environmental factors and/or evolutionary drivers to which they respond, and the ecosystem functions they perform (central, left and right columns, respectively). Bar heights indicate the number of traits within each category, and the width of the links between bars indicates the number of trait-response (to environmental factors) and trait-effect (on ecosystem functions) relationships identified during this review (see Table 1 and Supplementary Tables S1–S3).

for traits in other categories; for example, morphological traits, such as fused elytra, can be used as a proxy for physiological traits related to thermoregulation (see Gallego et al., 2018). As discussed above, traits are integrated aspects of an individual that perform an array of biological processes with a finite number of structures and behaviours. It follows that most, if not all, traits perform and participate in several ecosystem processes, so the delivery of ecosystem functions by individuals results from the synergy and trade-off between several traits (Violle et al., 2007). A good example is prothorax volume, a single morphological trait that acts as a proxy for muscle volume (in the morphology category), which determines walking and flying ability (in movement category), and is also involved in dung and soil manipulation and

during burial (from feeding and reproduction categories), as well as in temperature regulation via heat production (within the physiological category) (deCastro-Arrazola et al., 2020; Edmonds, 1972; Verdú et al., 2012).

Disentangling the trait-mediated responses of a particular individual from the trait-based effects on ecosystem processes of that same individual may be difficult. The response of an individual to an environmental variable is an organism-wide response involving several traits, which may lead to trade-offs or synergies in its responses to different environmental stressors, and eventually in its effects on the ecosystem. As an example, a heat wave can trigger a response in multiple physiological, morphological or phenological traits, and even in their feeding and reproductive habits.

Individuals can adapt their metabolism (Carter & Sheldon, 2020; Fleming et al., 2021), enhance heat loss due to evaporative cooling under extreme conditions (e.g. Nervo, Roggero, Isaia, Chamberlain, et al., 2021), become crepuscular or nocturnal to avoid the hottest time of the day, change their phenology to avoid the hottest days of the season (Galante et al., 1991; Mena et al., 1989), or dig deeper to avoid extreme surface temperatures. This has consequences for the ecosystem processes affected by individuals, such as soil aeration and the depth at which they bury the seeds embedded in the excrement.

Furthermore, a specific trait may simultaneously increase both desirable and undesirable ecosystem processes, providing ecosystem services and disservices. A good example are the traits involved in dung beetle–parasite interactions. Feeding mode and ingested particle size determine which parasites enter the host, while burrow depth and, more importantly, antimicrobials in brood masses may inhibit parasite use of individuals as hosts and/or vectors. Individual suitability as either host or vector can be also determined by body size and certain characteristics of the external surfaces, such as hairiness or the presence of particular chemicals used to recognize sexual partners or by phoretic organisms. Furthermore, colonization moment determines the possibility of interacting with the right infective phase of parasites, while movement traits are key features for the potential role of beetle individuals as vectors. This indicates the complexity of the functional responses induced by environmental and biotic stressors and the subsequent effect they infer on the environment (Slade et al., 2017, 2019). The development of experiments for measuring trait responses to environmental stressors (both biotic and abiotic), and effects on the ecosystems, should feed upon the trait–process relationships identified in this review, based on standardized measurements of traits (Moretti et al., 2017). It follows that a first step would be to develop a handbook of measurement protocols particularly tailored for dung beetles, ideally as a collaborative process involving the community of dung beetle (functional) ecologists. After this handbook is ready, the next step is to compile databases of functionally relevant traits, building on the example of Buse et al. (2018), but gathering individual measurements rather than averages and ratios of trait values per species.

6 | CONCLUDING REMARKS

Functional ecology, regardless of spatial, temporal or organizational scale, should be based on a good understanding of the biological meaning of all the variables that are relevant for the studied taxa and system. The trait-based framework developed here establishes the foundations to answer key ecological questions for dung beetles, providing a robust template for studying the important role they play in many terrestrial systems, including how variations in climate, soil or vegetation, via response traits, may affect their key role as ecosystem engineers, via effect traits. However, working on functional ecology should ideally involve measuring functions (either responses

to environmental stressors, effects on ecosystems, or both), which is incredibly challenging in many cases. Many of the trait–environment relationships we identified are lacking quantitative experimental data, so we highlighted where the main knowledge gaps for future research lie (deCastro-Arrazola et al., 2020; Wong et al., 2019). The limited and sparse development of functional ecology and the challenges outlined in this review are not exclusive to dung beetles—a particularly well-known group, but can be extended to most animal groups (see Moretti et al., 2017). Therefore, we encourage experts in other taxa to design-specific frameworks that account for the responses and ecological roles of their study organisms. Studies performed within the conceptual umbrella of these frameworks will aid to the development of a solid trait-based ecology. Attention should be paid to the fact that, although the use of traits as proxies for functions can simplify studies, the traits that are measured must have clear links to the functions or the responses to the environment that are being investigated. Therefore, a first step should be to conduct a review such as the one presented here, eventually identifying large gaps in the knowledge of the response to particular stressors or the delivery of some effects. In these cases, further empirical work may be needed to identify and characterize potential functions and the traits related to them. This may require a standardization of trait measurements (Moretti et al., 2017), ensuring that the observations of trait variations coming from different studies can be readily compared. Once such knowledge is available, the links between traits, stressors, ecosystem effects and their interactions should be tested experimentally to identify cause–effect relationships (Noriega et al., 2018). We believe that adopting this kind of thorough and comprehensive approach will help bridge the current gap between the functional ecology of plants and animals, increasing our understanding of the roles that many animal groups play in ecosystem functioning and biogeochemical cycles.

AUTHOR CONTRIBUTIONS

Indradatta deCastro-Arrazola and Joaquín Hortal conceived the idea, with Francisco Sánchez-Piñero and Marco Moretti; Indradatta deCastro-Arrazola reviewed the literature, with extensive contribution of all authors; all authors discussed and synthesized known evidence; Indradatta deCastro-Arrazola developed the tables, with contribution of all authors; Indradatta deCastro-Arrazola, Beatrice Nervo, Ana M. C. Santos and Joaquín Hortal outlined the figures, with contribution of all authors; Indradatta deCastro-Arrazola and Joaquín Hortal led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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ORCID

Indradatta deCastro-Arrazola  <https://orcid.org/0000-0001-6558-5730>

Nigel R. Andrew  <https://orcid.org/0000-0002-2850-2307>

Matty P. Berg  <https://orcid.org/0000-0001-8442-8503>

Alva Curtsdotter  <https://orcid.org/0000-0001-6870-7924>

Jean-Pierre Lumaret  <https://orcid.org/0000-0003-2926-3974>

Rosa Menéndez  <https://orcid.org/0000-0001-9997-5809>

Marco Moretti  <https://orcid.org/0000-0002-5845-3198>

Beatrice Nervo  <https://orcid.org/0000-0002-0512-9079>

Elizabeth S. Nichols  <https://orcid.org/0000-0002-4960-6842>

Francisco Sánchez-Piñero  <https://orcid.org/0000-0002-9852-8318>

Ana M. C. Santos  <https://orcid.org/0000-0002-9197-792X>

Kimberly S. Sheldon  <https://orcid.org/0000-0002-3215-2223>

Eleanor M. Slade  <https://orcid.org/0000-0002-6108-1196>

Joaquín Hortal  <https://orcid.org/0000-0002-8370-8877>

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