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Ecological relationships between coprophagous insects and livestock production: a review

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Review Article

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Abstract

The ecological function played by the coprophagous insects is an important issue in livestock production contexts. The role of this fauna, specially dung beetles, provides benefits to both rangelands and production performance. This interaction has been studied and reported in many scientific articles, in very different places and with diverse production contexts. However, a comprehensive review of the relationship between coprophagous insects and livestock production is still lacking. We reviewed the research studies on this topic during the past five decades, with a focus in Scarabaeidae taxon and livestock production, in order to identify further research priorities. We analysed 435 research articles. The main results were: (I) studies were mostly located in temperate broadleaf forest biome, whereas arid environments were less studied; (II) *Production practices impacts* category was the most studied, for which the effects produced by antiparasitic products on the coprophagous insects ($n = 93$; 21% of total revised articles) was the topics with major number of articles. Followed was *Biology* category ($n = 69$; 16%), then in *Ecosystem function* category the most frequent studies were on dung removal ($n = 40$; 9%), whereas in the *Ecosystem Services* category the most frequent studies were on biological control ($n = 28$; 6%); (III) Australia, Mexico, Brazil, and United States were the countries with most research articles. We identified some knowledge gaps on relevant ecological functions of this fauna, in relation to benefits to livestock production. There is a need for future research on nutrient cycling, bioturbation, effects on primary production and vegetation diversity.

Introduction

The relation between coprophagous insects and livestock production has gained increased scientific attention in the last decade. This fauna performs a key role in the ecosystem mainly as nutrient cyclers and bioturbation (mixing of sediment particles by living organisms). When coprophagous insects feed and use dung as a nesting resource, it produces a modification of chemical and physical characteristics of the soil, improving its nutritional condition (Piccini *et al*., 2017a; Maldonado *et al*., 2019). The effects of coprophagous insects on primary production have an important interest in agronomic scenarios, since it is important not only at soil level but also when it participates in secondary seed dispersal and germination, to increase the likelihood of plant establishment. Other ecological factors of the coprophagous insects are more simply related to the benefits in livestock production, such as dung removal from the pastoral field. The accumulation of dung generates losses in the forage availability and increases pest flies and endoparasites (Bornemissza, 1960, 1970).

The benefits of coprophagous insects in livestock production were more deeply studied with different introduction of dung beetles' programmes, which had the goal to reduce the accumulation of cattle dung and control pest flies. The most important programmes were from the United States and Australia, promoted by United States Department of Agriculture's Agricultural Research Service(USDA/ARS) and Commonwealth Scientific and Industrial Research Organization (CSIRO), respectively (Pokhrel *et al*., 2021). The first successful introduction was in the Hawaiian Islands in 1923, mostly to control horn fly pest, *Haematobia irritans irritans* Linnaeus 1758, which breed in cattle dung (Fullaway, 1921; Waterhouse, 1974). In Australia, livestock were introduced in the XIX century, and the native coprophagous fauna did not use exotic mammal dung as a resource, so the accumulation of dung started to become a problem (Hughes, 1975; MacQueen and Beirne, 1975a).

The coprophagous insects and its ecological role are well documented, several reviews ($n = 34$) were published to resume studies on practices and improvements in livestock production. Some of these reviews focus on specific topics such as description of coprophagous diversity (Tiainen *et al*., 2020), biological control (Whartom and Norris, 1980; Szewc *et al*., 2021), other ecosystem services (such as nutrient cycling, bioturbation, secondary seed dispersal)

(Dymock, 1993; Nichols *et al.*, 2008; Doube, 2018), or the use of this fauna as land use indicators (Nichols *et al.*, 2007; Alvarado *et al.*, 2018). There are also many studies that review the effects of antiparasitic veterinary products on coprophagous insects (Strong, 1992; Rodriguez-Vivas *et al.*, 2021). However, a comprehensive review of the relationship between coprophagous insects and livestock production is still lacking. The following questions guided this review: (a) which kind of relationship between coprophagous insects and livestock production were studied in agronomic contexts?, (b) which ecological functions of coprophagous insects have been mostly studied in livestock production contexts and where? (c) why are these topics relevant in the relationship between coprophagous insects and livestock? (d) which kind of missing key issues are identified and why should they be prioritised in future research?

The objective of this review was to identify the research focus during the past decades with respect to the relationship between coprophagous insects, specially dung beetles, and livestock production, in order to recognise information gaps and further research priorities aimed at understanding how this interaction is evolving in agroecosystems. Our core attention was posed on the most studied topics and their temporal evolution, as well as the geographic and the environmental contexts.

Methods

We performed a bibliographic search in the Scopus database on 13 July 2022. It was oriented by two broad dimensions, which defined the keywords used for the search: (a) entomological, and (b) agricultural. Hence, the combination of words used to search scientific articles involving the interaction between coprophagous insects and livestock production were: *Scarabaeidae OR dung – beetle OR coprophagous OR cyclers AND grazing OR cattle OR livestock*. These words could appear both in the title and in the abstract. The search has two parts separated by 'AND' (i.e. referring to the two different dimensions), which implies that at least one word of each part has to be present. Inside each part, 'OR' indicates that at least one of those words must be displayed, respectively. The first part of the search was oriented to the coprophagous insects and focused on the modification in soil as an ecological function, which is one of the key functions of this fauna. This role is mainly studied on dung beetles, which are consider ecosystem engineers (Nichols *et al.*, 2008; Barragán *et al.*, 2022), so we decided to include specifically the term *Scarabaeidae* and *dung-beetles*, besides *cyclers*. The second part of the search covers the keywords related to livestock production, which includes both extensive and intensive systems (i.e. feed-lots), whereas grazing focalised pastoral systems. Cattle were included because it is the most studied and produced domestic animal. The result was 621 scientific articles. After a systematic revision of all of them, we discarded the articles that described communities or specific biological topics about the coprophagous insects but merely mentioned their role in animal production. Then, we only included in the analysis the articles with some feature of animal production in the material and methods section and those where livestock production was the main context of the investigation, which also included a coprophagous insects research topic. Hence, the review process was done over 435 articles, and the analysed information was: (i) the publication year; (ii) the country and region where the research was done; (iii) the type of biome; and (iv) the main focus of the article' contribution to the coprophagous insects and livestock production relationship. For this last description, the articles were grouped under broad categories that were proposed to better organise and describe the information studied in each research work. These categories were developed using a bottom-up and ex-post procedure, each research article was analysed critically, and the categorisation was modified and adapted during the whole process. First, we evaluated their contribution to the revision topic, identifying the research themes. As a second step, we organised the diversity of themes in five broad categories, based on their contribution similarities to coarser research topics. In this classification there were articles with research contributions in more than one of the proposed categories. In these cases, they were grouped under the category of their main objective. Some of them were more concerned with the study of biological characteristics of the coprophagous insects related with livestock production, but others to the diversity description of this fauna in production contexts. A third group of research articles were more focused on the ecological functions that coprophagous insects perform in the productive systems, and a fourth in the ecosystem services that these functions provide to farmers. A fifth group included research articles concerned about the effects of veterinary antiparasitic products on the coprophagous insects, and the habitat changes by human land use. These categories were named: (1) Biology, (2) Diversity, (3) Ecological Functions, (4) Ecosystem Services, and (5) Production Practices Impact. Within each category, the articles were arranged in sub categories to better describe the heterogeneity of studied topics. This information was summarised in the following sections, whereas the articles organised by themes can be found in the Annex.

Results

Trend of scientific production

The first research article found was published in the year 1969, and until 1990 the number of articles was under five per year (fig. 1). The main trigger for most of the first publications was the Australian Dung Beetle Project (1964-to date), the CSIRO's programme for the introduction of dung beetles. The first years of this project were dedicated to searching for possible dung beetle species to import from Africa, southern Europe and Asia. The research articles published during that time were mainly from the Australian Dung Beetles Project team (65% until 1990). They were related to surveying the establishment of these introduced species and their effects for biological control (Annex Section 1.A.I–II).

In the '90s decade the interest in the subject grew, and so did the number of published scientific researches. One fourth of the published articles during the 1990–2000 period still were from Australia, whereas 10% of the articles were from Pretoria, South Africa, where an overseas operation centre for the Australian Project was functioning (Bornemissza, 1979) (Annex Section 1.B.I–II).

In the following years the number of published articles increased, reaching a big outbreak in 2007, which doubled the mean scientific production of the previous decade, including research from different countries (Annex Section 1.C) and 34 review articles (Annex Section 1.D). As from 2010 it has been continuously growing at an average rate of 15 articles per year.

Main categories

The revised research articles were separated according to five main categories related with their broad research topic contribution (fig. 2).

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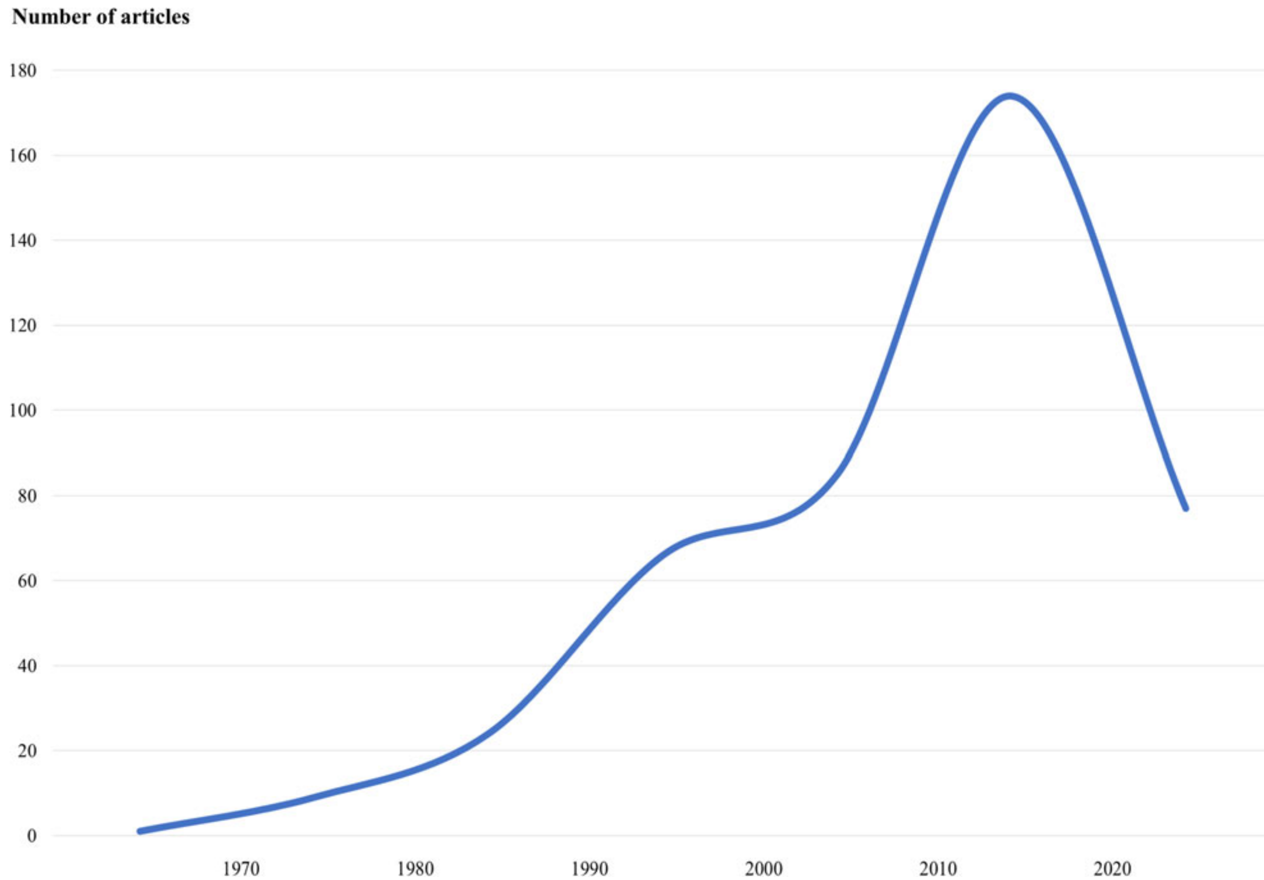

Figure 1. Number of research articles per year between 1969 and 2021. The year 2022 is not included because there are only 7 months of data.

Biology

This category has 16% of total research articles ($n = 69$, Annex Section 2). The studies focused primarily on the biological aspects of the coprophagous insects in the livestock production context but did not have any special variable related to production. In this category, the research articles were separated in three main subcategories: (I) Specific attributes, (II) Habitat preferences, and (III) Food preferences.

Specific attributes of the coprophagous insects were studied with the purpose of knowing different aspects of its nature for the application in a production system. For example the research articles studied vital cycles, reproduction, genetic patterns (Shymanovich *et al*., 2020), or ecological traits such as behaviour patterns, interspecific relationship, heterotrophic succession (Forgie, 2009) (see Annex Section 2.A).

Other studies focus on the aspects of the habitat preferences, analysing distribution related with the specific attributes (Verdú and Galante, 2002). These traits are also used in palaeontology or anthropology researches, where the presence of coprophagous insects in the study sites is used as a *Pasture Biome Indicator* (Smith *et al*., 2014) by the long historical relation between domestic and native herbivores and this fauna (Annex Section 2.B).

Food preferences was also an issue well represented in this bibliographic search There were two main streams or groups of the research articles that fall into this category. On the one hand, research studies focused on the mechanisms by which coprophagous insects chose, or not, a specific dung type. These articles evaluated the attraction produced by chemical clues like odour, C/N ratio, and moisture, and visual clues like the size of the dung pad. On the other hand, studies of the assemblage preferences on dung from different herbivores, relating this to the production system (e.g. cattle versus sheep dung), with changes in the resource (e.g. domestic livestock versus wild ungulates or rabbit dung), and also the study of the impact of habitat modifications in the dung preferences of the assemblages (e.g. native versus exotic grasslands, woody versus pastures) (Annex Section 2.C).

The majority of the research articles described in this section were performed on dung beetles specifically, but 10 articles focused on other coprophagous groups. In specific attributes subcategory there were five articles on both dung beetles and flies, another two specific on flies and only one on termites. One article described the heterotrophic succession between dung beetles and flies (Sladecek *et al*., 2021). And there were also two articles about flies food preferences. In Habitat preferences subcategory, dung beetles were the only studied coprophagous insect.

Diversity

This category has 16% of total research articles ($n = 68$, Annex Section 3). Most of these research articles are focused on describing the coprophagous insects communities in particular sites or local scales ($n = 30$, Annex Section 3.A–C). To perform these surveys two strategies were developed: on the one hand, some studies took into account the number of species (richness) and their abundance, named *Taxonomic Diversity* (e.g. Wagner *et al*., 2021). On the other hand, other studies considered ecological characteristics to classify the different groups, such as nesting

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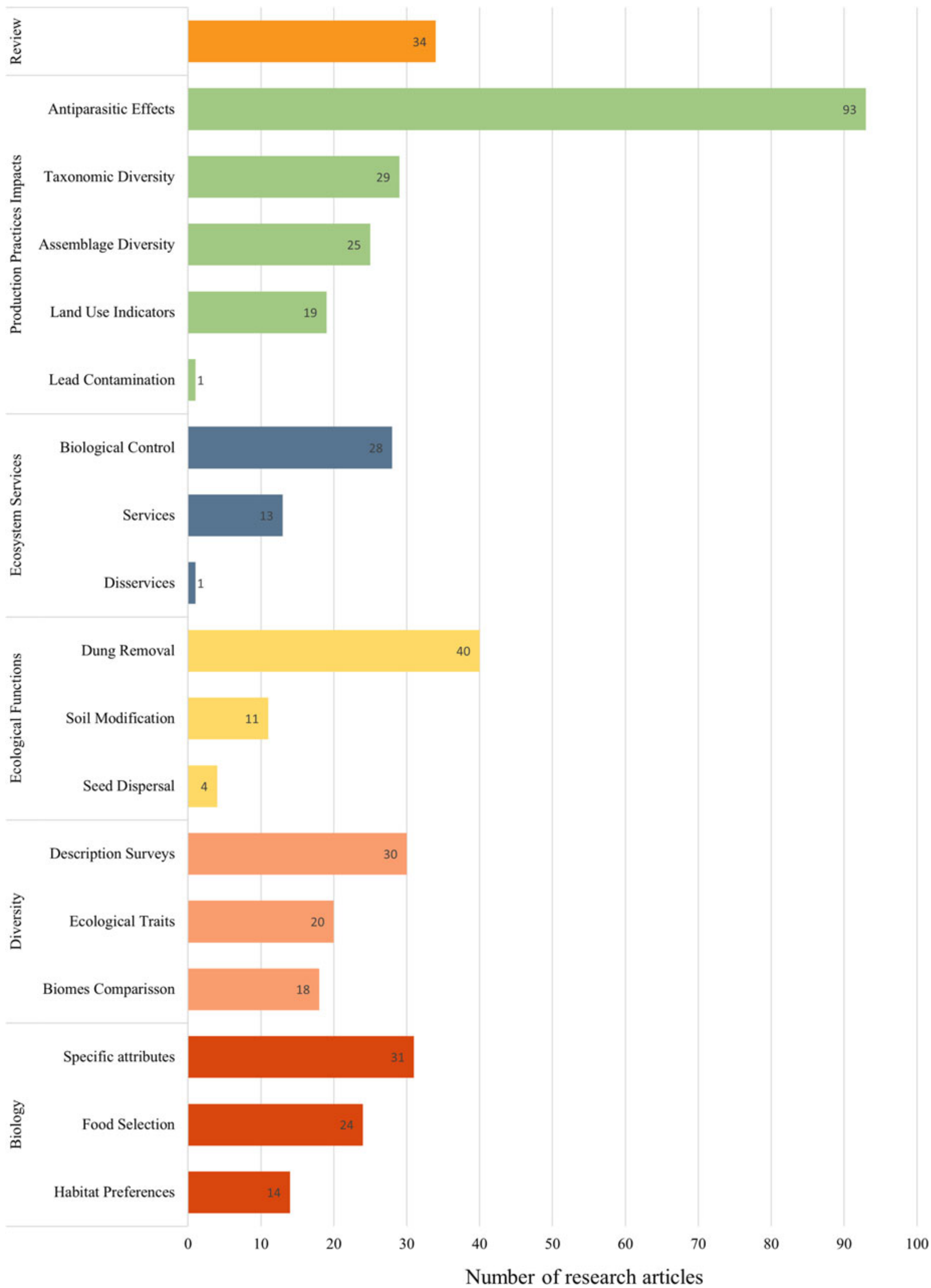

Figure 2. Number of research articles on each category and subcategory.

strategies or morphological similarities, named *Assemblage Diversity* (e.g. Sullivan *et al.*, 2016). There were also two articles focused on *Phylogenetic Diversity*.

In this category, some studies added some specific ecological traits to explain the diversity in the different evaluated sites: the biomass or the body size as related to the amount of dung they

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could bury (Annex Section 3.B.I–II), temporal and spatial distribution related with seasonal pattern and capacity of burying at different times of the year (Annex Section 3.B.III). There were also studies that included environmental descriptions, such as flora diversity or other arthropods assemblages from the same collecting sites (Annex Section 3.B.III–IV).

Coprophagous insects diversity has been also used to compare different biomes as a consequence of the specific community's habitat needs. The studies where woody and grassland habitats were compared, focus was usually on the shift in the assemblage mainly as an effect of the dominant vegetation cover. Different ecology gradients that change the biomes' characteristics were also compared using the evaluation of coprophagous assemblages in each site, such as in the case of altitudinal or precipitation gradients (Annex Section 3.C.I–III).

In this category, the number of research studies was all on dung beetles.

Ecological functions

In this category, we included the research articles where the main focus was the role that this fauna performs in the ecosystem, in the context of a livestock production system. Note that the previous two categories (Biology and Diversity), support the ecological functions here presented. Based on the research articles present in this review, we divided this category in three subcategories: (1) Dung Removal, (2) Soil Modifications, and (3) Seed Dispersal (fig. 2).

Dung removal: This subcategory of research articles is directly related to livestock production, and the programmes of dung beetles introduction aimed at managing the amount of dung accumulation in fields ($n = 40$, 9% of total articles; Annex Section 4.A). This accumulation occurs because in an animal production context the amount of dung deposited onto soil is much larger than in natural systems, where predators control the herbivores populations, and the ecological role of coprophagous insects that deals with it becomes more essential (Huerta *et al*., 2018).

The fragmentation, removal and burying of the dung is different depending on the coprophagous assemblage. For example, the nesting strategy in dung beetles is very related to dung removal rate. Three main broad nesting strategies are well documented: (i) tunneller species (paracoprid) bury the dung in vertical tunnels beneath or in the proximity of the dung patch; (ii) roller species (telecoprid) transport the dung away from the patch shaping a dung ball and rolling it, or just carrying pieces; and (iii) dwelling species (endocoprid) who build the nest inside the dung patch (Halffter and Edmonds, 1982). The greater the diversity of dung beetle species with different nesting habits, the faster the incorporation of dung in the soil, and the consequent nutrient cycling (e.g. Ortega-Martínez *et al*., 2016). The behavioural patterns of the decomposers and the way they use the dung as a resource (e.g. nesting strategies in the case of dung beetles) is one of the variables that significantly modified the dung removal rate. The individual sizes and the biomass of each group is also relevant, as we mention above, the biomass is also used to measure the abundance. Big individuals have the capacity to remove more dung, but little and numerous ones are also very important for this activity as they are more abundant. The coprophagous assemblages have seasonal differences, so the key species in dung removal sometimes differ throughout the year (Miranda-Flores *et al*., 2020). For example, termites are mentioned in the dryer season in some studies (Gould *et al*., 2001) or earthworms in wet areas (Gittings *et al*., 1994). There is also a heterotrophic succession that occurs in the dung patch. Diverse groups of invertebrates use the dung in the different decomposition stages, and the abiotic factors (e.g. climatic conditions, type of soil) additionally modify the removal rate (Wassmer, 2020).

Soil modification: The dung removed is generally mixed and buried in soil, so this activity is directly related to soil modification. This subcategory included two main ecological functions: *Bioturbation* and *Nutrient Cycling*. Both are associated with the same biological activity, but they are studied with different methodologies. Soil modification subcategory represents only 2.6% of the total number of research articles in this review ($n = 11$, Annex Section 4.B).

The research articles that focused on physical effects on soil structure, such as water infiltration or soil aeration, were classified specifically as *Bioturbation* ($n = 4$; 1% of total articles; Annex Section 4.B.I). The importance of this ecological factor, and the very little information on it, was already emphasised in the review by Nichols *et al.* (2008); after more than a decade there is still very little research. These articles mention the problem of compaction of soil in grazing environments, and how tunnelling dung beetle species facilitate water infiltration from the surface to the deeper soil layers, increase soil porosity, and reduce surface water runoff. There are two articles included in this section, where the authors evaluated bioturbation and others ecological functions provided by the dung beetles when modifying the soil: seedling establishment (Leiva and Sobrino-Mengual, 2022), and seed dispersal (Arias-Álvarez *et al*., 2022).

The second ecological factor that relates coprophagous fauna and soil in livestock production context is *Nutrient Cycling* ($n = 7$; 1,6% of total articles; Annex Section 4.B.II). In the bibliography, this process is directly related to improvement of soil nutrition, since relocating dung underground accelerates the incorporation of organic matter, prevent the loss of nitrogen by volatilisation through ammonia, and increase the labile nitrogen available for plants (Nichols *et al*., 2008). But there were very few studies where these affirmations were verified in a livestock production context. The research articles on this section have chemistry measures of the nutrients in soil after the treatment with dung beetles removing and burying dung. The authors compared the dung beetles nesting strategies and their efficiency in nutrient cycling (Maldonado *et al*., 2019; Cheng *et al*., 2022). Others included primary production and plant growth measures in soils modified by dung beetles (Yoshihara and Sato, 2015; Barragán *et al*., 2022).

All the research articles in this specific ecological function are focused on dung beetles.

Seed dispersal: *Seed dispersal* subcategory has a small number of articles ($n = 4$; 1% of total articles; Annex Section 4.C). They addressed this role mainly to the roller dung beetles which transport the dung away from the patch and mention the small tunnellers as germination facilitators. In this subcategory, dung beetles were the only taxon studied in the revised articles.

Ecosystem services

This category summarises the research articles that study the services that coprophagous insects performed in the productive ecosystems (fig. 2). Most of them are related with dung removal ecology function, and the modification of dung when it is processed and buried. Hence, in this category there were mainly research articles on dung beetles ($n = 42$; 10% of total articles, Annex Section 5).

Biological control: This ecosystem service is the most studied inside this category, representing 67% of the articles related with

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ecosystem services and 6% of total articles in this review ($n = 28$, Annex Section 5.A). It was one of the first research themes in the relationship between coprophagous insects and livestock production (Bryan, 1973; Fincher, 1973, 1975). Fly pest infestations on livestock reduce its productivity and decrease quality, which represents economic losses to farmers (Nichols *et al.*, 2008). The population of flies was decreased by competition for the resource dung, for feeding and breeding, and, as the dung was manipulated by dung beetles, the flies' eggs and larvae were broken or damaged. Dung beetles were the most studied coprophagous fauna as biological control of pest flies, and in this search there is only one article that mentioned Staphylinidae predatory beetles, besides dung beetles, as biological control agents (Koller *et al.*, 2002) (Annex Section 5.A.I). The effect produced by dung removal has also been studied in the survival of gastrointestinal parasites such as nematodes and helminths. In the majority of these research studies the results exhibited the great potential of dung beetles for biological control of these parasites (Sands and Wall, 2017) (Annex Section 5.A.II).

Other Services: Besides biological control as the most studied ecosystem service, in the research articles on this review there was one research article that related dung beetles diversity and several ecosystem services such as dung removal and bioturbation. The authors made a comparison of single-species treatments to a three-species mixture and its performance to deliver these ecosystem services, and showed the importance of diversity to support them (Manning *et al.*, 2016). Other important issue that appear in these research articles is *soil carbon sequestration* as an ecosystem service that coprophagous insects provide to the productive ecosystems (Gilroy *et al.*, 2014; Williams *et al.*, 2017).

Regarding the *Effects on Greenhouse Gas Emission* there were some special research articles that were included in this subcategory ($n = 10$; 2% of total articles; Annex Section 5.B.III). The results presented in these studies were contradictory because some authors affirmed that the presence of coprophagous insects in dung pads increases the emission of CO_2, CH_4, and N_2O, but others stated that this fauna reduced emissions (Piccini *et al.*, 2017b).

There was one article that was classified as an ecosystem disservice, where the possible role of dung beetles in the transmission of cysticercosis in cattle was discussed (Lonc, 1980).

Production practices impacts

This category gathers the research articles related with the effects of livestock production on the coprophagous insects. The productive ecosystems have particular practices that change some of the ecosystem functions that this fauna performed in natural environments. The use of veterinary products on animals, and how this practice affects the coprophagous insects is one of the most studied topics. The modification in the diversity of the coprophagous communities due to land use is another important issue that appears in the research articles (fig. 2).

Antiparasitic effects on coprophagous insects: The most studied category was the effect produced by antiparasitic veterinary products on the coprophagous insects ($n = 93$; 21% of total articles; Annex Section 6.A). Keystone research in this topic was based on laboratory experiments showing the lethality produced in flies and in dung beetles that feed on dung from cattle treated with an avermectin (a group of macrocyclic lactones that include abamectin, ivermectin, eprinomectin, and doramectin) (Ridsdill-Smith, 1988). This theme started to attract attention, especially of scientists who were concerned that this new livestock management practice could jeopardise the survival of the introduced dung beetles (Ridsdill-Smith, 1988; Wardhaugh *et al.*, 1998).

In the first steps of this research, the methodology aimed at observation of the effects of the antiparasitic products on the survival, reproduction activity, or removal rate of the coprophagous insects. Under field conditions, dung from treated and untreated cattle were monitored through time to evaluate the number of adult emergencies, colonisation of the dung patch, or removal rate by several studies (Sommer *et al.*, 1992) (Annex Section 6.A.I). In the laboratory, different concentrations of the veterinary products were evaluated to find the lethal concentration 50 (LC50) (Ridsdill-Smith, 1988; Floate, 2007) (Annex Section 6.A.II). Over time, the questions and the methodology have become more detailed: (i) evaluation of effects on the reproductive physiology and more specifications in the vital cycles of the different species (González-Tokman *et al.*, 2017); (ii) transgenerational effects in the progeny causing long term fitness consequence (Manning *et al.*, 2018); (iii) chemistry evaluation on the different veterinary products to identify the toxic compounds and their residual fate (Römbke *et al.*, 2010); and (iv) the toxic concentration of these products in faecal residues over time (Annex Section 6.A.III–V). In most recent articles there were introduction of other variables to explain the effects under different contexts. Some studies included agronomic variables such as livestock species and management (Tonelli *et al.*, 2017), or data about environmental conditions in different study sites (Webb *et al.*, 2010), or even the effects on the ecosystem (Hammer *et al.*, 2016) (Annex Section 6.A.VI–XI).

The effects of antiparasitic products on coprophagous insects were studied on a broader number of taxon than the other categories. The research articles on this subcategory included 16 studies where the effects where measured on dung beetles and flies (Iwasa *et al.*, 2008), seven articles about the impacts of the antiparasitic products on coprophagous fauna in general (insects and invertebrates) (Schoof and Luick, 2019), three where predatory beetles that fed on the coprophagous insects was also evaluated (Floate, 1998), only two studied the effects on flies (Sommera *et al.*, 2001) and one on earthworms (Svendsen *et al.*, 2003).

Changes in diversity by human land use: In diversity studies there were many research articles that compare study sites communities. In this subcategory we distinguish the articles where the objective of this comparison was to highlight the effects of human activities on the coprophagous insects.

In the research articles where taxonomic diversity is used, the most frequent studies were to compare the coprophagous communities in different types of productions: (i) agricultural and livestock production (Rodrigues *et al.*, 2013), (ii) traditional livestock and silvopastoral production (Mendivil Nieto *et al.*, 2020), (iii) differences between livestock and forest productions (Rangel-Acosta *et al.*, 2020), or (iv) between natural grassland and pastures (Treitler *et al.*, 2017) (Annex Section 6.B.I). In the research articles where assemblage diversity is used, we found comparison between livestock production in a gradient of human interventions, from open pastures, different grazing intensities, to silvopastoral production (Lobo *et al.*, 2006; Bouragba *et al.*, 2018). There were also assemblage comparisons between livestock and monocultures (Gómez-Cifuentes *et al.*, 2017), and livestock production and protected areas (Nependa *et al.*, 2021) (Annex Section 6.B.II). Most of the research articles studied the diversity of dung beetles, but there were five articles on coprophagous fauna in general, and one that studied flies diversity (Martínez-Sánchez *et al.*, 2000).

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In this subcategory we included research articles that used the advantage of all the knowledge about dung beetles such as habitat and food preferences, distribution, diversity in different types of land modification, and use these variables to identify land use indicators groups (Halffter and Arellano, 2002) (Annex Section 6.B.III).

There is also a research article which studied the lead contamination produced by emissions from internal combustion engines that affect vegetation, cattle, cattle dung, and in consequence dung beetles (Robel *et al.*, 1981) (Annex Section 6.B.IV).

Geographic interest

The relationship between coprophagous insects and livestock production has a long research history. When organising the articles by a political geographic criterion Mexico, Australia, Brazil, and the United States were the countries with the highest number of publications (fig. 3). Nevertheless, the interest in this subject was well documented all around the globe. In this bibliographic search, 53 countries from the five continents have published articles. Analysing the research articles with an ecological geographic criterion, the most represented biome was the Temperate broadleaf forest (16%). The Mediterranean vegetation, the Temperate steppe, and the different types of forests (Tropical and Subtropical rainforest, Dry and Montane forests) were also biomes selected to perform these researches. In the driest biomes, there are fewer studies of the interaction between coprophagous insects and livestock production (fig. 4).

Mexico has a long history in the study of coprophagous insects and livestock production (50 research articles). Its first article in our literature search was published in 2002, and until 2010 all of them were related to the coprophagous insects Diversity (in the category of diversity), or in the Production practices impacts under the subcategory *Assemblage diversity* (fig. 5a). Once endemic diversity had been well studied, researchers started to evaluate and to publish numerous articles on the ecological function *dung removal*, and how this is affected by the antiparasitic products. But they also moved beyond, incorporating very often in their diversity studies complementary variables such as food selection, biological control, dung removal, and relating the results to the biological information of each group. Their research is mostly in forest type biomes, but they also had some studies on the xeric shrubland.

Australian (45 articles) research groups focused from the beginning on issues related with dung removal rate as a special function of coprophagous insects, and also the ecosystem service of pest flies biological control derived from it. In 1982, the research articles on biological issues start to appear, studying

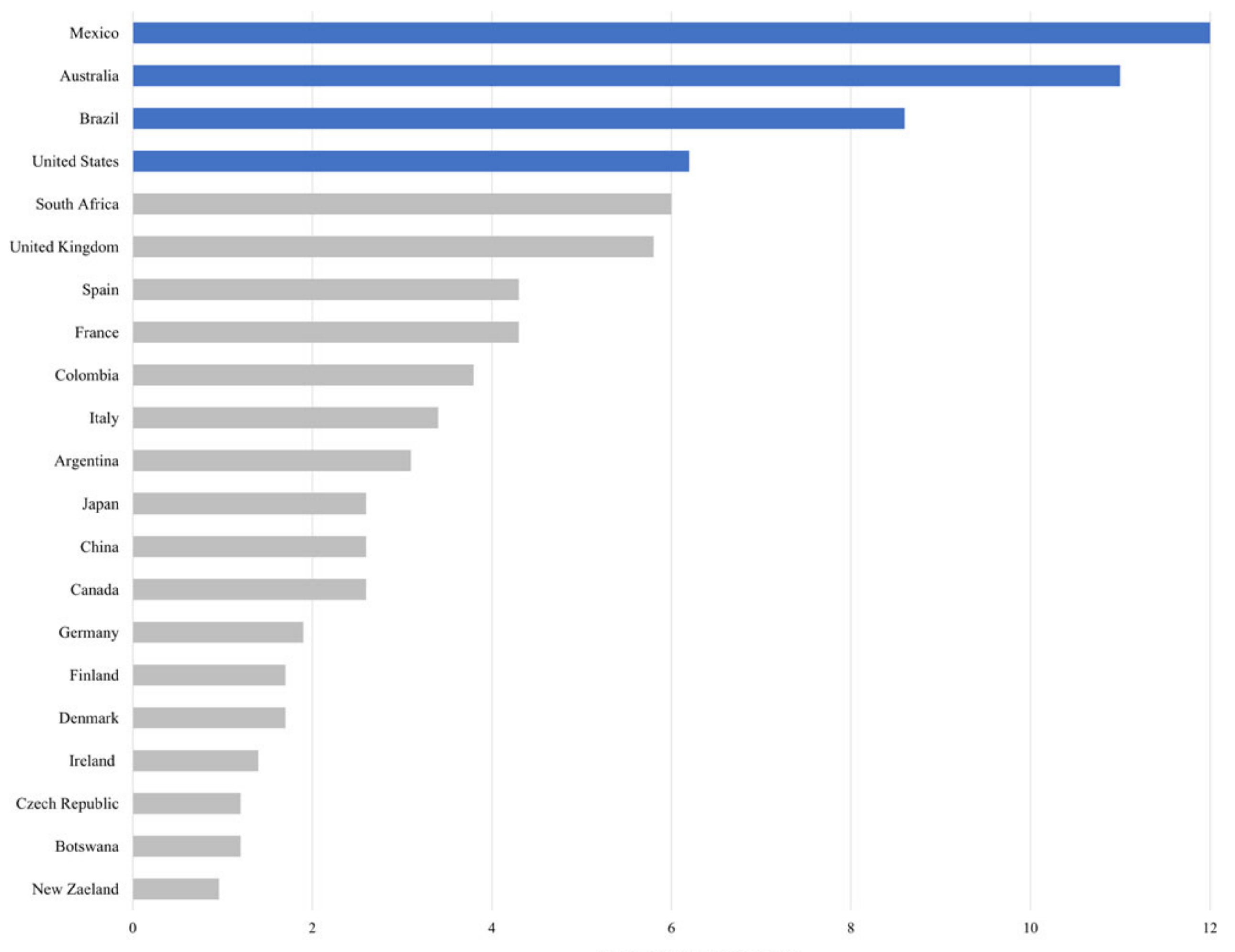

Figure 3. Percentage of research articles published on the first twenty one countries with the highest number of studies.

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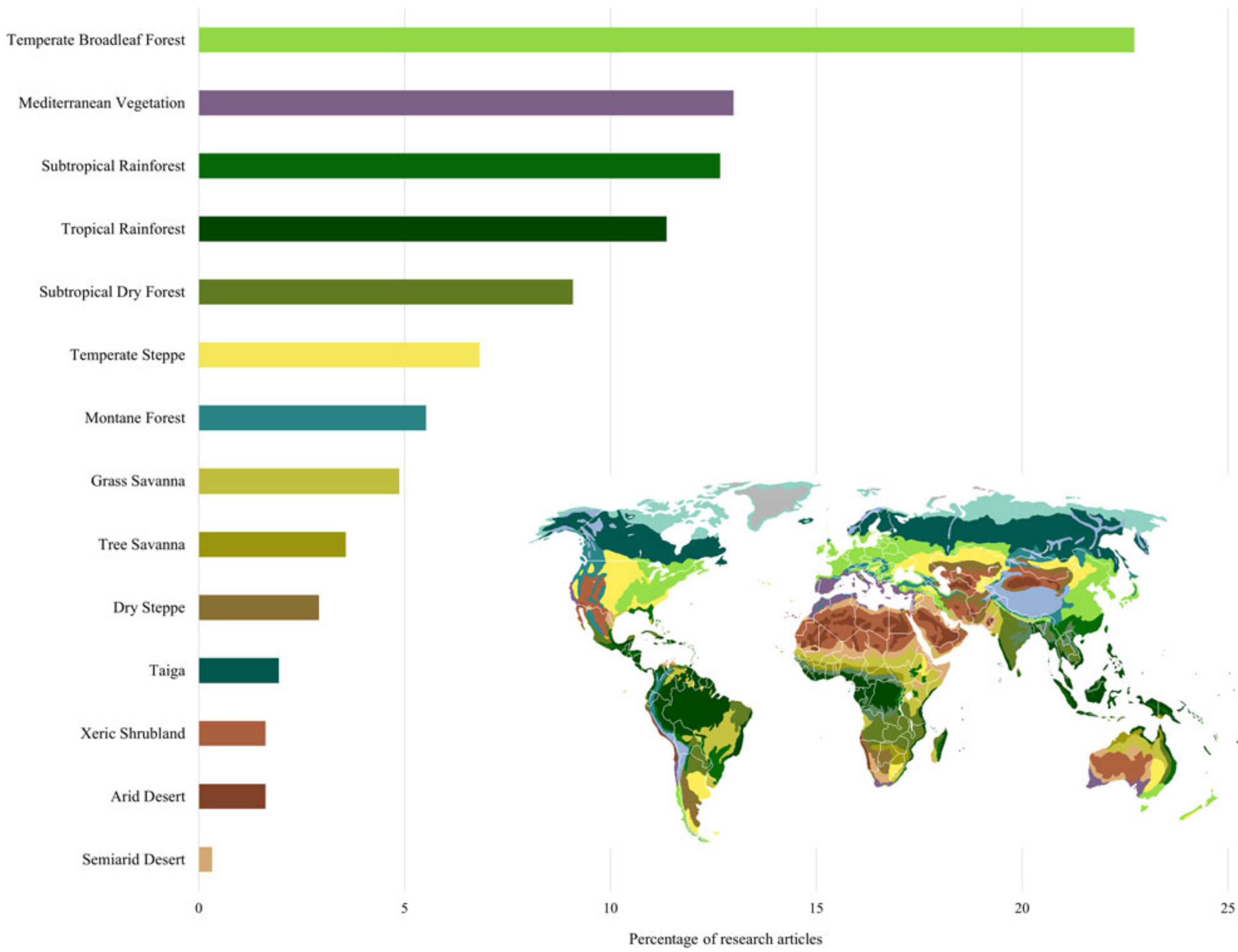

Figure 4. Percentage of biomes represented in the research articles.

specific attributes and food preferences (fig. 5b). In 1988, the first article appeared about the danger to coprophagous insects posed by the use of antiparasitic products in Australian livestock. During the next decade, this topic gained increased attention. Then they moved forward in evaluating the effect of different cattle diets in dung beetles (House and Simmons, 2007), and later in 2015 they resumed this research line adding the role of nutrient cycling (Joseph *et al*., 2015). They also published five reviews on different subjects of the relationship between coprophagous insects and livestock production. There are several types of biomes in Australia, most of the research sites were in forest type biomes, but they have two research articles in arid desert.

The articles from *Brazil* (36 research articles) were mostly related to diversity of the coprophagous insects (Fig. 5c). Most of them (14 articles) are from the subcategory *Taxonomic diversity* in Production practices impact, where diversity on different sites with distinct stages of human intervention is compared. In these different areas, some studies focused on the use of dung beetles as land use indicators. Also, the articles on the Diversity category from Brazil had the inclusion of ecological traits to complement the fauna description, such as biomass or body size measures, and seasonal variances. In the Biology category, food selection was well documented in their research articles. Half of the articles were performed in Mato Grosso do Sul state, and most of them in grass savanna biome (13 of the total 15 research articles in this biome are from Brazil, the others are from Uruguay and Tanzania).

The *United States* had the broadest variety of research topics (26 research articles). They started with biological control Ecosystem Service, centred on endoparasite control by dung beetles (fig. 5d). In the Ecological function category, they studied *dung removal*, and in the Production practices impacts, the effects caused by the antiparasitic products in the coprophagous insects. They have also published articles on biological aspects of this fauna including heterotrophic succession, survival and performance on different cattle diets and trophic nets. The diversity, both taxonomic and assemblage, was also used to describe the coprophagous insects on local sites, or to compare different biomes. The research articles are from the following three main biomes: Temperate Broadleaf Forest, Temperate Steppe and Subtropical Rainforest, but there is also one article from Montane Forest biome.

Discussion

The studies of the relationship between coprophagous insects and livestock production are abundant in the scientific bibliography. There are two main approaches to differentiate in the research articles analysed in this review: (i) ecological features and (ii) production impacts. On the one hand, half of the scientific literature

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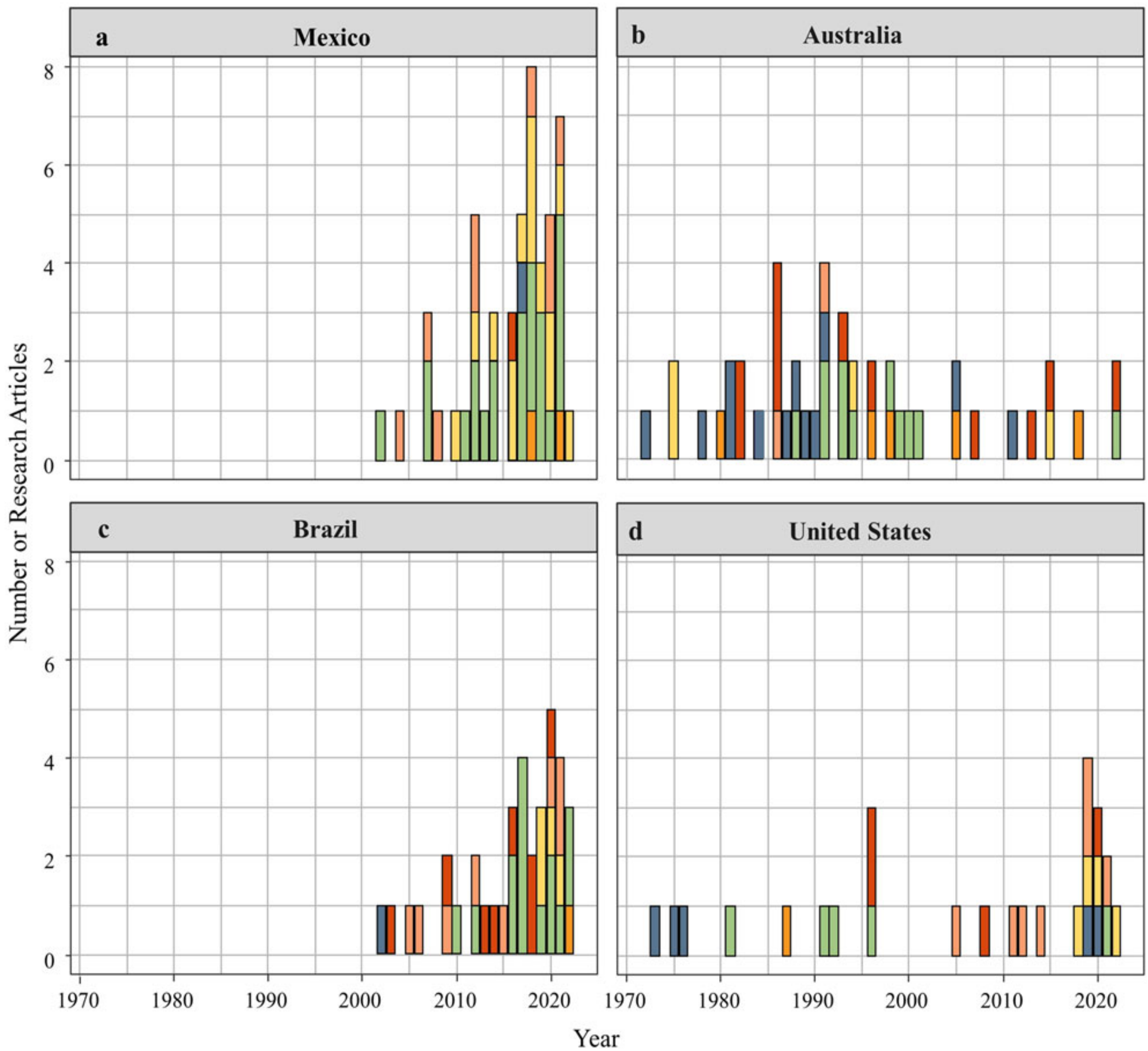

e Number of research articles in each category

	Biology	Diversity	E. Functions	E. Services	P. P.Impacts	Review	Total
Mexico	1	9	14	1	23	2	50
Australia	11	2	4	12	11	5	45
Brazil	8	8	4	1	14	1	36
United States	4	7	4	5	5	1	26

Figure 5. Temporal interest evolution on each category in the four countries with more research articles: (a) Mexico, (b) Australia, (c) Brazil, (d) Unites States, (e) Number of research articles by category and total amount between 1970 and July 2022.

focuses on coprophagous ecological features that can benefit livestock production. On the other hand, the production impacts approach includes the research studies based on the manner in which the production and the management practices affects the coprophagous fauna.

Concerning the first approach, biological issues are necessary to understand the role of the coprophagous fauna in livestock production. The research articles that follow this approach generated diverse information with respect to some main themes: (i) vital cycles and distribution, providing knowledge regarding the location and moment of the year when the coprophagous can be found; (ii) food preference, informing the likelihood to find the community on domestic livestock dung. Under this approach all diversity studies helped to characterise the coprophagous fauna

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related to livestock production in a great amount of study sites worldwide. In the case of the specific ecosystem functions studied, all of them were related with the direct benefits of knowing and protecting this fauna. As mentioned in the results section, dung removal was one of the most studied topics, and this function was related to biological control of endo- and ecto-parasites, a very important ecosystem service of this fauna.

The effect on greenhouse gas emissions was another studied ecosystem service that results from the coprophagous' dung removal. However, there are other important topics in the Ecological Functions category which need to be more deeply studied. Soil modification, both chemical and physical, is a relevant theme in the interaction between coprophagous fauna and plant development. Nutrient cycling gives a promising scenario on the fate of dung buried by coprophagous insects. The few available studies helped in understanding how the coprophagous fauna was modifying the nitrogen volatilisation and increasing the amount of available nutrient compounds in soil. For example, some research articles explained how soil modification performed by dung beetles can change by the assemblage diversity, proportions of dweller and tunneller species (Cheng *et al.*, 2022), or by the temporal diversity (Guo *et al.*, 2021), how this activity is influenced by canopy cover (Gómez-Cifuentes *et al.*, 2020) or by contrasting livestock management (Barragán *et al.*, 2022). There was also evidence that dung beetles increased the porosity in at least the first 10 cm of soil, and the infiltration ratios and air permeability at this depth were also increased when dung beetles were present (Bang *et al.*, 2005). The information on physical modification in soil promoted by tunneller species needs future research.

Seed dispersal is another understudied ecological function reported to coprophagous insects in a livestock production context (Annex Section 4.C). In the few articles in this review, most of the experiments were performed in temperate grassland sites, with dung from different types of domestic animals (cattle, sheep, horses). In a silvopastoral context in Mediterranean vegetation, the role of dung beetles in oak seedling establishment through the passive burial by bioturbation was verified (Leiva and Sobrino-Mengual, 2022). However, there is more bibliography about this ecological factor in natural environments (mainly on dung beetles), suggesting that there is a need for more interdisciplinary research in this matter. For example, the seed survival and emergence with the help of dung beetles depends on the size of the seed, the size of the beetle and the beetles' dung processing method, and of course, the assemblage diversity (Andresen and Feer, 2005). Notwithstanding the natural or productive contexts, the conclusions were similar. Finding if the dispersal promoted by the dung beetles is positive for the seed and vegetation community needs future research. These variables are still lacking in the research on livestock production contexts.

The second approach, where the focus is the effects of the livestock production on the coprophagous fauna, have two main branches, both related with management practices: (a) the systematic use of veterinarian antiparasitic products on livestock, and (b) the change of habitat by land use. These themes were relevant since they tackled the relationship between coprophagous fauna and livestock because to accomplish the benefits to the production, which is necessary also to understand the possible consequences of the practices. In this regard, the antiparasitic effect on the coprophagous fauna, was the most studied topic, and many researches focused on very specific modifications in the coprophagous fauna biology (e.g. reproductive physiology, transgenerational effects), as well as on profound knowledge of the chemical compounds in the veterinary products and its consequences.

The research articles where the effects of changes in the land use on coprophagous fauna were revisted focused on the communities identity under different situations. These comparisons helped to understand the distribution, habitat preferences, and adaptive capacities of the studied fauna. Also, several articles make proposals of indicator species aimed at differentiating between good and bad production practices and land degradation processes.

When we looked at the ecological geographic criterion, it is not surprising that forests and temperate biomes were the most studied in this subject. In those biomes, livestock production, in particular cattle, is a relevant agricultural and economic activity. But there is much less knowledge in more arid biomes. There are other types of domestic livestock produced in those places such as sheep, goats, camels, and the role of the coprophagous insects is also very important but less documented.

In a livestock production context based on grasslands, the research on how the action of the coprophagous insects affects the vegetation community and primary production is lacking. There is information about this interaction where plant growth was higher with dung beetles activity, and also the nutrition value from those plants was increased in comparison with the control (Bang *et al.*, 2005). For example, the performance of a wheatgrass with the fertilising effects of dung beetles caused an increase in crude protein of the grass over the control (Macqueen and Beirne, 1975b). Further research is needed in the relationships between coprophagous insects and soil and vegetation dynamics under different livestock production systems and management to better orient decision making at a farm level.

In an agroecosystem, understanding the main ecological variables affecting performance at a system level is key to better orient management. Plants are used as food for livestock. Dung from these herbivores is the food and nesting resource for the coprophagous insects, and it provides more available nutrients for plants when it is buried in the soil. This benefic circle depends on many other features that affect this interaction and each component in different ways. For example, the type of soil, the climatic conditions, the assemblage of the coprophagous insects, the seed banks, and the pastoral management. Further research is needed to deeply understand these interactions, aimed at improving livestock management at a farm level.

Conclusions

This literature review focused on the relationship between coprophagous insects and livestock production, with focus on dung beetles, corroborating that it is an issue that has been studied for at least fifty years. The main interest was posed on dung removal ecology function performed by the coprophagous insects in livestock production contexts, and how this action support the ecosystem service of biological control of parasites. Related with the production practices impacts, the effects of veterinary products on the coprophagous insects was also a much studied theme. In some regions, there is a deeper knowledge about the distribution of species during the year and their biological requirements (e.g. Brazil, Mexico). However, there is still a lack of information about some specific ecosystem functions such as soil modification, which is relevant to better understanding the ecological processes influencing livestock production performance and sustainable environmental management. On this matter, *Nutrient cycling*, in particular studies on the chemical changes in soil and the availability of nutrients for plants mediated by coprophagous insects processes need further research. *Bioturbation* also needs deeper attention, since coprophagous fauna modifies the physical structure of soil, research studies might explore its implications in the context of anthropogenic disturbances such as soil compaction, and under scenarios of increasing climatic variability with extreme events (e.g. droughts, floods).

In addition to soil modification issues, we identified the following gaps of knowledge:

– *Effects on primary production and vegetation diversity*, forage is a key resource in pastoral systems, so these are critical research theme. The improvement in nutrient availability, the seed dispersal, germination and establishment of the adult plant are information gaps in this kind of agroecosystem.
– *Climate change mitigation*, including carbon sequestration, greenhouse gas emissions. This information may be included in studies of carbon net balance (footprint) of pastoral systems, which is currently neglected or not considered.
– *Arid biomes*, the information on the interaction between coprophagous insects and livestock production in these environments is poorly studied, future research should be addressed in these biomes.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485323000494

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