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School of Doctoral Studies in Biological Sciences University of South Bohemia in České Budějovice Faculty of Science Dung beetles of Central Europe: Diversity and conservation. Ph.D. Thesis Mgr. Lucie Ambrožová Supervisor: Mgr. Lukáš Čížek, Ph.D. Institute of Entomology, Biology Centre, Czech Academy of Sciences Department of Zoology, Faculty of Science, University of South Bohemia Consultant: RNDr. František X. J. Sládeček, Ph.D. Institute of Entomology, Biology Centre, Czech Academy of Sciences Department of Zoology, Faculty of Science, University of South Bohemia České Budějovice 2023

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iii This thesis should be cited as: Ambrožová, L., 2023: Dung beetles of Central Europe: Diversity and conservation. Ph.D. Thesis Series, No. 1. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 209 pp. Annotation The thesis consists of three conservation-oriented studies, mainly focusing on the factors determining dung beetle diversity in Central Europe. We assessed the role of routine ivermectin treatment on diversity and functional performance of dung beetle community. Alternative forest managements of coppicing and additional topsoil removal were evaluated in terms of their suitability for increasing diversity of dung- inhabiting dung and rove beetles. Further, we examined environmental and management-related factors driving dung beetle β -diversity to facilitate conservation prioritization of Central European dung beetles. Declaration I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references. České Budějovice, ... 30. 11. 2022 Lucie Ambrožová

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vi List of papers and author's contribution The thesis is based on the following papers (listed chronologically): I. Ambrožová, L., Sládeček, F. X. J., Zitek, T., Perlík, M., Kozel, P., Jirků, M. & Čížek, L. (2021).

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Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities.

Agriculture, Ecosystems & Environment, 321, p. 107634. doi: 10.1016/j.agee.2021.107634. (IF = 6.576) LA led the field sampling, determined the sampled material, performed statistical analyses, and was responsible for the manuscript writing. Her contribution was 50 %. II. Ambrožová, L., Finnberg, S., Feldmann, B., Buse, J., Preuss, H., Ewald, J. & Thorn, S. (2022). Coppicing and topsoil removal promote diversity of dung- inhabiting beetles (Coleoptera: Scarabaeidae, Geotrupidae, Staphylinidae) in forests. Agricultural and Forest Entomology. doi: 10.1111/afe.12472. (IF = 2.126) LA participated in the field sampling, determined the sampled material, and was responsible for the manuscript writing. Her contribution was 40 %. III. Ambrožová, L., Čížek, L., Sládeček, F. X. J., Thorn, S. (2022).

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Understanding the drivers of β -diversity improves conservation prioritization for Central European dung beetles. Biological Conservation, 273,

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vii Co-author agreement Lukáš Čížek, the supervisor of this Ph.D. thesis and co-author of papers „

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viii Contents Introduction 1 1. Biology of dung beetles 4 2. Dung beetles and their ecosystem role 7 3. Diversity of Central European dung beetles 9 4. Major threats 11 4.1. Agriculture intensification and land-use changes 12 4.2. Antiparasitic treatment of livestock 14 4.3. Climate change 19 5. Conservation 20 6. Aims and scope of the thesis 24 7. References 25 Chapter I 49

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Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities.

Chapter II 93 Coppicing and topsoil removal promote diversity of dung-inhabiting beetles (Coleoptera: Scarabaeidae, Geotrupidae, Staphylinidae) in forests. Chapter III 153

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Understanding the drivers of β -diversity improves conservation prioritization for Central European dung beetles.

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1 Introduction

3 Introduction Numerous studies around the world have driven attention to the current decline of insect abundance and diversity (Carpaneto et al., 2007; Habel et al., 2016; Hallmann et al., 2017; Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019; van Klink et al., 2020). Insect decline is usually associated with anthropogenic influences, where habitat destruction, conversion (e.g., intensive agriculture), and climate change are usually listed among the main causes (Habel et al., 2019; Wagner, 2020). Insects provide various ecosystem services that bring direct benefits to humans (e.g., pollination, decomposition of organic matter, pest control, wildlife nutrition) (Losey & Vaughan 2006). Thus, insect decline may have a serious impact on ecosystem functioning and also on humans (Benton et al., 2002; Doube, 2018; Vanbergen and the Insect Pollinators Initiative, 2013). In this study, I focus on dung beetles (Coleoptera: Scarabaeidae, Geotrupidae), widely distributed coprophagous insects that use mammalian dung for feeding and breeding. By dung exploitation, they provide several keystone ecosystem services, such as dung decomposition, nutrient cycling, pest control (flies and livestock internal parasites), or secondary seed dispersal (Nichols et al., 2008). At the same time, they are one of the most affected insect groups by intensive agricultural practices and landscape changes (Sánchez-Bayo and Wyckhuys, 2019), with well-documented decline in diversity and biomass from many regions of the world (Bogoni et al., 2019; Carpaneto et al., 2007; Escobar et al., 2008; Horgan, 2007; Lobo, 2001). Therefore, dung beetles represent an ideal model group, frequently used also in studies of habitat change, agricultural management, and nature conservation (see, e.g., Roslin & Koivunen 2001; Buse et al. 2018). Here, I first introduce dung beetles with their biology and ecology to give a broader context to an otherwise more conservation-oriented study. Second, I review the patterns and drivers of the diversity of dung beetles in temperate, especially in

4 Central Europe, which is the focal region of my study. Later, I identify the main factors threatening dung beetle diversity, populations, and related ecosystem functions and services. This is followed by a discussion on the general conservation recommendations targeted on dung beetles, and case studies and examples of good practice from abroad are provided. At the end, I outline the aims and scope of the thesis, which are followed by three original papers coming out of my Ph.D. 1. Biology of dung beetles Mammalian dung is an ephemeral resource hosting numerous invertebrate taxa, including coprophages (i.e., Geotrupidae, Scarabaeidae, some Hydrophilidae and Staphylinidae, most of the flies and earthworms) as well as predators or parasites/parasitoids (i.e., mostly Staphylinidae, Histeridae and some flies species). In my thesis, I specifically focused on “dung beetles” (Scarabaeoidea: Scarabaeidae and Geotrupidae) (Hanski and Cambefort, 1991), as they are the most important agents in grazed ecosystems, providing several ecosystem services. The origin of coprophagy is usually associated with mammalian evolution (Ahrens et al., 2014; Arillo and Ortuño, 2008; Hanski and Cambefort, 1991). Coprophagy has probably evolved from saprophagy (Hanski and Cambefort, 1991). This shift is most notable in adult beetles who transited from chewing on hard organic particles (e.g., wood, fungi, litter) to consuming liquid organic matter (e.g., juice from decaying plant matter, bacterial albumens in decaying humus, liquid part of mammalian dung) for which they have specifically modified filtering mouthparts (Holter and Scholtz, 2007, 2005). Yet, some dung beetles species are not obligatory coprophages, as they can utilize or even prefer other organic material for successful larval development, such as rotting plants, roots, or very old dung (e.g., genus *Melinopterus*, *Nimbus*, *Chilothorax*, *Volinus*) (Landin 1961; Rössner 2012 and references herein; Buse et al. 2018; Floate 2021).

5 Mammalian, especially large herbivore dung, is the most common food source for dung beetles. This, seemingly a waste material, is in fact very rich in nutrients, such as proteins or carbohydrates. Essential nutrients come from the animal's digestive system. Excreted microbial symbionts together with intestinal epithelial cells, mucus, and water form the liquid part of the dung (Holter 2016). For feeding on dung juice, adult dung beetles have modified mandibles with a filtering apparatus to strain water and large particles out and with a grinding molar lobe to break down remaining smaller particles (Hata and Edmonds, 1983). Interestingly, this morphological adaptation for dung feeding has developed in several coprophagous taxa, including Scarabaeidae, Geotrupidae, and Hydrophilidae (Holter, 2004). Larvae have simple chewing mandibles and are likely to consume larger particles. According to Holter (2016), mobile larvae of Aphodiinae (Scarabaeidae) may feed on easily digestible dung components, probably dead and/or alive microbial biomass. Larvae of Scarabaeidae and Geotrupidae are restricted to the dung in their brood masses, where they are assumed to re-eat their own feces several times (Holter, 2016). However, the exact mechanism of reaching essential nutrients requires more detailed research; it is still not clear whether larvae use some mutualistic cellulose-degrading microorganisms (Schwab et al., 2016) or whether selective collection of dung for brood masses (avoidance of coarse fibres) or dung pre-digestion by mother ensures successful larval development (Byrne et al., 2013). In the way of resource utilization, dung beetles display several feeding and nesting strategies that have further implications for their role in the ecosystem and for the ecosystem services they provide (Nichols et al., 2008). First, adult beetles require maturation feeding, a short period (several days to weeks) when they gather energy and their reproductive organs develop to the mature stage (Doube, 1990; Hirschberger, 1998). Regarding the nesting strategies, we recognize three basic

6 functional groups, tunnelers (paracoprids), rollers (telecoprids), and dwellers (endocoprids) (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). This classification is, however, a simplified view of a more complex set of behaviors, where many exceptions and aberrations exist; for more details see Tonelli (2021). In general, tunnelers drag pieces of dung into vertical underground chambers close to the original dung deposition site, where females form dung into brood balls and lay one egg in each (Hanski and Cambefort, 1991). In the Central Europe, tunnelers are represented by coprophagous Geotrupidae, nearly all Scarabaeinae, and one Aphodiinae genus Colobopterus (Buse et al., 2018; Vitner, 1998). Rollers first form dung balls from freshly deposited dung and roll them some distance from the original site. Then, they usually bury them in the soil to establish a new nest and provide the offspring with food source (Nichols et al., 2008). In Central Europe, there are only a few roller species, i.e., *Sisyphus schaefferi*, *Gymnopleurus geoffroyi*, *G. mopsus*, *Scarabaeus typhon*. Dwellers lay eggs directly in the dung pat or at the dung/soil interface or slightly below the surface; larvae develop inside the dung mass (Hanski and Cambefort, 1991; Vitner, 1998). They are represented by nearly all Central European Aphodiinae coprophagous species (Buse et al., 2018), with an exception of aforementioned saprophagous genera.

7.2. Dung beetles and their ecosystem role Dung beetles are important agents in grassland and forest ecosystems, as they provide several ecosystem function by their feeding and breeding activities. Some of the functions are directly relevant to humans and can be perceived as ecosystem services with economic value. For example, Beynon et al. (2015) estimated the yearly price of four ecosystem services (reduced pest flies, reduced gastrointestinal parasites, reduced pasture fouling, and increased soil nutrients) provided by current UK dung beetle communities to ca. £367 million. Adult beetles coming to the fresh dung disintegrate it by creating galleries within the dung pat, which helps with faster weathering (Holter, 1979; Sands and Wall, 2017). As they utilize dung for their own consumption and to feed their larvae, dung beetles contribute to the initial stages of dung removal and provide some other ecosystem functions. The extent of the functions provided is largely dependent on dung beetle life strategy. From a functional perspective, tunnellers and rollers are disproportionally more important for dung removal (and related ecosystem services) than dwellers (Beynon et al., 2012; Milić et al., 2017; Rosenlew and Roslin, 2008; Tonelli et al., 2020). For other ecosystem functions, dung beetles accelerate nutrient cycling, contribute to bioturbation, soil fertilization and aeration, enhance plant growth, participate in secondary seed dispersal, suppress enteric parasites of grazing animals, or suppress fly development (Nichols et al., 2008). Physical removal of dung from the surface clears space for plant growth, as well as it reduces space for fly development. This became especially obvious in Australia, where native dung beetles were not able to remove all the dung produced in the growing cattle industry (Bornemissza, 1976). The pasture fouling led to extensive pasture loss as livestock avoided grazing in the area surrounding the dung deposits (Bornemissza, 1976; Doube, 2018). The accumulated dung provided space for the development of several species of pest dung-dwelling flies (e.g., *Haematobia*

irritans, *H. thirouxii*, *Musca vetustissima*, *M. autumnalis*), that seriously reduced livestock productivity and negatively affected human well-being (Doube, 2018). This was partially solved by introducing exotic dung beetle species that coped sufficiently with dung production (Pokhrel et al., 2021). Dung beetles suppress livestock parasites available on site by their mechanic damage and dung burial, which physically removes them from pastures (Coldham, 2011; Nichols and Gómez, 2014; Pokhrel et al., 2021). Species rich community of dung beetles can reduce the number of parasite larvae by up to 31% (Beynon et al., 2015; Sands and Wall, 2017). In New Zealand, the activity of introduced non-native dung beetle species reduced nematode numbers on grass around the dung pats by even 71% (Forgie et al., 2018). Eggs of gastrointestinal nematodes require oxygen for successful hatching but do not survive desiccation (Durie, 1975). The activity of dung beetles that aerate dung supports the development of parasite larvae under moist conditions, while they cause faster desiccation and suppress nematode larvae under dry conditions (Chirico et al., 2003). Beynon et al. (2015) estimated the economic benefit of dung beetles in suppressing livestock parasites to be about £197 million for the UK only. Dung beetles have also positive effect on soil and plants (Nichols et al., 2008), as decomposed dung improves soil with organic material and nutrients (Badenhorst et al., 2018; Bertone et al., 2006; Yamada et al., 2007). For example, bioturbation (mixing dung and soil) by dung beetles results in a significant increase in above and below-ground plant biomass (Bornemissza and Williams, 1970), plant height and grain production (Kabir et al., 1985) or digestibility and nutritional value of herbage (Bang et al., 2005). By tunneling and rolling behavior, dung beetles contribute to secondary seed dispersal (Milić et al., 2019), which is especially important for tropical forest regeneration (Andresen, 2002). By burying activities, dung beetles also reduce soil compaction and aerate soil (Badenhorst et al., 2018;

9 Manning et al., 2016; Mittal, 1993). Tunneling behavior positively influences hydrological properties of the soil by increasing water infiltration and reducing surface water runoff (Brown et al., 2010). Aeration of dung and soil increases aerobic decomposition, decreases anaerobic decomposition and reduces methanogenesis (Penttilä et al., 2013). Dung beetles facilitate activity of other beneficial organisms. Activity of adult beetles and their larvae possibly attracts more earthworms to the dung, which speeds up dung decomposition in the later stage of dung succession (Doube, 2008; Holter, 1979). On the other hand, earthworm tunneling may disturb the feeding of dung beetle larvae and even completely override the effect of larval consumption on dung removal (Hirschberger and Bauer, 1994; N. M. O’Hea et al., 2010). Dung beetles often carry phoretic mites, that are mainly predators or parasitoids of flies (Krantz, 1998). Those mites then serve as vectors for several coprophilous fungi (Blackwell and Malloch, 1991). 3. Diversity of Central European dung beetles Dung beetle diversity is determined by several environmental factors, such as biogeography (Barragán et al., 2014; Davis et al., 2002), climate (Gebert et al., 2020), biotope (Frank et al., 2017; Stanbrook et al., 2021), soil (Davis, 2002; Salomão et al., 2022), herbivore species (Bogoni et al., 2016), season (Agoglitta et al., 2012), or elevation (Mantoni et al., 2021). These are further modulated by anthropogenic influences, such as grazing continuity (Buse et al., 2015), herd management (Jay-Robert et al., 2008; Perrin et al., 2021), environmental pollution (Verdú et al., 2018b), or land-use changes (Errouissi and Jay-Robert, 2019). In Europe, the diversity patterns of Scarabaeidae, Geotrupidae, and Aphodiinae do not fully overlap, as each of the groups has their distinct evolutionary history (Errouissi et al., 2004; Hortal et al., 2011). Scarabaeinae dung beetles, a

10 warm-adapted group (Davis and Scholtz, 2001), are more abundant and diverse in Southern Europe and in lowland localities (Lobo et al., 2002; Lumaret and Kirk, 1991). Hortal et al. (2011) suggest that Scarabaeinae assemblages in the central and northern parts Europe consist of large-range generalist with better tolerance to lower temperatures, who are a subset of the southern ones, which are more diverse and variable in composition. Aphodiinae dung beetles, better adapted to temperate or cold-temperate conditions, prevail in Central and Northern Europe and in mountains (Cabrero-Sanudo and Lobo, 2006; Hanski, 1991; Lumaret et al., 2022). Geotrupidae are only represented by 8 coprophagous species in Central Europe, while the center of their European diversity lies on the Iberian, Italian, and Balkan Peninsulas and on the islands in the Mediterranean Sea (Löbl and Löbl, 2016). Another aspect of dung beetle diversity is their functional diversity (i.e., “the kind, range and relative abundance of functional traits present in a given community”, Díaz et al. 2007), which largely determines the range of provided ecosystem functions (Manning et al., 2016; Milotić et al., 2017). It is clear that guilds are not equally efficient in dung removal (and related ecosystem functions), as rollers and large-bodied tunnelers are disproportionally more efficient than dwellers (Milotić et al., 2017; Tonelli et al., 2020). The Northern and Central European communities are dominated by dwellers, while large-bodied tunnelers are mainly represented by only several species of Geotrupidae and rollers are very scarce (Hortal et al., 2011). Therefore, the dung decomposition is slower than in southern regions, and it is often ensured by other soil macro-invertebrates, such as earthworms (Gittings et al., 1994; Milotić et al., 2019). Conserving functionally complete local assemblages should be, however, the main goal in grazed ecosystems in order to preserve all ecosystem functions (Milotić et al., 2019).

11 4. Major threats Apart from the worldwide insect decline (Habel et al., 2019; Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019; van Klink et al., 2020), there are specific concerns regarding dung beetle conservation. Seibold et al. (2019) associated the decline of terrestrial insects with land-use changes in forest and agricultural land at the landscape level. Habel et al. (2019) identified four main drivers of insect decline – habitat loss, increasing habitat isolation, decreasing habitat quality, and climate change. All of these also apply for dung beetles (Lumaret et al., 2022). Since they are diverse and ecologically important group, understanding what threatens them becomes a necessity for their effective protection. In the Central Europe, dung beetles are an insect group with one of the greatest share of threatened species, with 25-61 % species being included in national red lists (Schmidl & Büche in press; Holecová & Franc 2001; Głowaciński 2002; Paill & Mairhuber 2006; Juřena & Týr 2008; Rössner 2012; Král & Bezděk 2017). This situation is usually attributed to the habitat changes due to the abandonment of traditional grazing, agriculture intensification, and the decline of pasture area (Buse et al., 2015; Carpaneto et al., 2007; Tonelli et al., 2018). At the same time, changing climate and widespread use of antiparasitics pose an additional risk for dung beetle communities (Dortel et al., 2013; Lumaret et al., 2012; Lumaret and Errouissi, 2002). The key environmental and management factors determining dung beetle diversity have never been evaluated together to assess their relative strength, although this knowledge would allow for better targeted conservation actions.

12 4.1. Agriculture intensification and land-use changes As large wild herbivores are mostly extinct in Europe for centuries, European dung beetles are closely connected to the grazing of large domestic herbivores. Dung beetle populations thus react to the changes in agricultural practices. Until the 19th century, a substantial share of fallow land used for grazing, as well as animal draft power were part of the traditional farming (Kuskova et al., 2008). Therefore, dung of large herbivores was nearly omnipresent source. At the beginning of the 20th century, the stock of cattle substantially declined and horses nearly disappeared after WWII. Between the 1950s and 1960s (1970s in mountain areas), collectivization and intensification of agriculture took place all around the Central and Eastern European countries under communist rule (Bezák and Mitchley, 2014; Blacksell, 2010; Lipsky, 1995). Livestock were mostly kept and fed indoors rather than allowed to graze on pastures (Lerman et al., 2004), and if, then it was restricted to steep slopes or other localities of lower value (Bezák and Mitchley, 2014). In Czechia, large intensive grazing farms were established between the 1960s and 1980s, and around 1960s, grazing in newly established national parks and protected landscape areas was banned by law (Mládek et al., 2006). Thus, sources of livestock dung first almost disappeared from the landscape, or were later concentrated in more or less isolated patches around intensive farms. In the 1990s, political regime changed in Central and Eastern European countries. The proportion of abandoned agricultural land again increased due to the problems with restitutions and rural depopulation (Bezák and Mitchley, 2014; Skokanová et al., 2016). On the other hand, grazing returned to mountain, submountain and partly to protected areas in Czechia (Mládek et al., 2006). Since the beginning of the 21st century, Central European countries became part of the EU, and got access to substantial financial support derived from Common Agricultural Policy (CAP) (Bezák and Mitchley, 2014). Grazing again increased especially in mountain areas (Bezák and Mitchley, 2014), and it slowly returns also to lowlands. Overall, the Czech Republic lost nearly 60 % of pasture area between 1845- 1999 (Bičík et al., 2001), especially in lowlands (Bičík and Jančák, 2005). However, the decline of pasture area does not fully illustrate the magnitude of the decline of dung sources in the landscape, because it does not consider grazing abandonment on other land grazed only a part of the season, such as fields after the crop harvesting, meadows after hay cutting, wastelands, roadside ditches, or forests. Such changes in pasture extent and dung availability are likely the main reason why 61 % of Czech dung beetle species are currently red-listed (Král and Bezděk, 2017). Regarding the pasture management, low grazing intensity or abandonment decrease the alpha diversity and biomass of dung beetles, making especially dwellers and large-bodied species more prone to local extinctions (Tonelli et al., 2019, 2018, 2017). Since large-bodied dung beetles are the most efficient in dung removal (Nervo et al., 2014; Ortega-Martínez et al., 2016), their loss can be detrimental to the pasture functioning. In abandoned sites, the dung beetle assemblages tend to shift towards more opportunistic species, which depend on dung only in adult stage, while the larvae can be saprophagous – e.g., genus *Melinopterus* or *Chilothonax* (Tonelli et al., 2017). The following encroachment of shrubs and wood leads to additional loss of species richness (Errouissi and Jay-Robert, 2019). Species with lower dispersal abilities or higher habitat specialization are more prone to local extinctions due to stochastic events or habitat destruction (Roslin, 2000). This shortage of lowland pastures could have caused so many thermophilous species to become endangered (Král and Bezděk, 2017). One may argue that these dung beetle species could have survived in the landscape on the dung of abundant wild ungulates. However, Jay-Robert et al. (2008) reported a low efficiency of game dung in maintaining the original species pool, probably because it dries fast in open habitats and is not as suitable for larval development. Intensive farming with herbivore overabundance increases trampling, often leads to overgrazing and exposes bare soil. Although such pressure is often detrimental to many plant species (Fedrigo et al., 2018; Liu et al., 2022), it delivers large amounts of dung that could serve as an abundant food source for dung beetles. Negro et al. (2011b) reported that overgrazed sites had lower abundances and species richness of dung beetles than ungrazed sites, while my observations from overgrazed game reserves in Czechia suggest that they can be sometimes one of very few suitable sites for endangered species in given region (e.g., *Sisyphus schaefferi*, *Copris lunaris*). So far, only a few studies tested the role of vegetation cover with a special focus on bare soil on dung beetle diversity (e.g., Tocco et al. 2013; Tribble 2021).

4.2. Antiparasitic treatment of livestock One of the challenges of intensive agriculture is to deal with various ectoparasites and endoparasites that influence the health of livestock and the economy of meat and dairy industry (Corwin, 1997). Livestock parasites include internal (e.g., gastro- intestinal nematodes, lungworms) and external parasites (e.g., mites, lice, warbles). Some of the parasites are relatively harmless when in low concentrations, while higher parasitic load is usually a big problem for animal's health, and it can even lead to the animal's death. Thus, antiparasitics are often used as a cure and sometimes as a prophylaxis. Antiparasitic treatment not only improves animals' health and decreases their mortality, but also reduces the transmission of parasitic diseases among farm animals, to wildlife or even to humans (Liu and Weller, 1996). However, there are serious concerns about their undesired effect on non-target

15 organisms, such as dung-inhabiting insects or soil invertebrates (e.g., Goodenough et al., 2019; Lumaret et al., 2012; Römbke et al., 2010). The most common antiparasitics against gastrointestinal (GI) and external parasites are usually members of the following drug families – benzimidazoles, macrocyclic lactones, imidothiazoles, tetrahydropyrimidines, salicylanilids, and isoquinolines. Benzimidazoles (e.g., albendazole, fenbendazole, mebendazole, flubendazole) are used against wide range of GI nematodes, tapeworms and flukeworms (Floate et al., 2005). Benzimidazoles are excreted in dung and some in urine (Floate et al., 2005; Wardhaugh, 2000). They are assumed harmless to dung beetles (McKellar, 1997), while they might increase mortality of earthworms (Goodenough et al., 2019). Macrocyclic lactones (e.g., abamectin, ivermectin, doramectin, eprinomectin, moxidectin) are efficient against various GI nematodes and external arthropod parasites (Floate et al., 2005). Macrocyclic lactones are excreted in dung (Floate et al., 2005). They have negative impact on dung beetles and flies, decrease motility of earthworms, and impair reproduction of soil collembolans (Goodenough et al., 2019; Lumaret and Errouissi, 2002; Zortéa et al., 2017). Imidothiazoles represented by levamisole are efficient against GI nematodes, excreted mostly in urine, and have either low or no negative effect on dung fauna (Lumaret and Errouissi, 2002; McKellar, 1997). Tetrahydropyrimidines represented by pyrantel and morantel are efficient against roundworms, lungworms and bot flies (Floate et al., 2005). They are excreted in dung and urine and they likely have no insecticidal effects (Lumaret and Errouissi, 2002). Salicylanilids, represented by closantel, are efficient against nematodes, flukes and tapeworms, and they are excreted in dung (Floate et al., 2005). Its effect on non-target organisms requires more investigation, but Lumaret et al. (2013) do not assume closantel has a serious negative impact on dung fauna.

16 Macrocyclic lactones, and ivermectin in particular, are currently the most often used broad-specter antiparasitics in veterinary medicine (Laing et al., 2017; McArthur and Reinemeyer, 2014; Ōmura, 2008). They act through blocking neurotransmission on glutamate-gated chloride channels, which, for example, causes paralysis of pharyngeal and somatic muscles of GI parasites (Laing et al., 2017; Ōmura, 2008). However, these channels are present in all Ecdysozoa (Puniamoorthy et al., 2014), so the macrocyclic lactones are effective against all ecdysozoan parasites, including nematodes, and arthropods, while ineffective against tapeworms and flukes (Lophotrochozoa: Platyhelminthes). Macrocyclic lactones are poorly metabolized in animal organism, and their residues are mostly excreted with dung in active form (Norma M. O’Hea et al., 2010; Ōmura, 2008; Wratten and Forbes, 1996), where they can still affect dung-dwelling arthropods. Exposure to the residues of macrocyclic lactones has lethal and sublethal effects on dung beetles up to several weeks post-treatment, depending on the active compound and the way of application (Martínez et al., 2017; Norma M.

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O’Hea et al., 2010; Rodríguez-Vivas et al., 2020; Verdú et al., 2018a; Weaving et al., 2020). Floate et al. (Floate et al., 2005, 2002)

tested the effect of pour-on formulation of four macrocyclic lactones (abamectin, doramectin, eprinomectin, ivermectin, moxidectin) on dung-dwelling insect suppression. They found the longest and most adverse effect on dung-dwelling insects (in decreasing order) for abamectin, then doramectin, followed by

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eprinomectin and ivermectin, but no effect was observed for moxidectin.

The low toxicity of moxidectin was supported by numerous other studies (Doherty et al., 1994; Hempel et al., 2006; Jacobs and Scholtz, 2015; Junco et al., 2021; Strong and Wall, 1994; Suárez et al., 2009; Verdú et al., 2018a). Regarding the method of administration, macrocyclic lactones can be administered subcutaneously by injection, topically in the form of pour-on, or orally in form of a gel, paste, oral drench or sustained release bolus (a pill continuously releasing therapeutic doses of given medication for up to several months). Again, most of the studies were conducted on ivermectin, as it is available in all forms. Sustained release bolus has the most adverse effect on dung fauna, due to the very long period of excretion of high levels of residues (Herd et al., 1996). Although this method is already abandoned in most European countries, the rest of the world still uses it which makes this practice a serious threat to dung beetle communities (Errouissi and Lumaret, 2010). For the injectable and topical formulations of ivermectin, the highest concentration of eliminated drug usually occurs within 2-7 days post-treatment, but the long tail of low-concentration residues can last up to 6 weeks (Floate et al., 2005). On the individual level, ivermectin negatively affects foraging and reproduction (Norma M.

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O’Hea et al., 2010; Rodríguez-Vivas et al., 2020), olfactory and locomotor abilities (Verdú et al., 2015) and mobility of adult beetles (Martínez et al., 2017; Pérez-Cogollo et al., 2017; Weaving et al., 2020), while it usually does not kill them. Ivermectin residues, however, substantially reduce larval survival (Martínez et al., 2017; Norma M. O’Hea et al., 2010; Pérez-Cogollo et al., 2017), decrease number and body size of newly emerged beetles (S. A. Beynon et al., 2012; González-Tokman et al., 2017), and change offspring sex-ratio in favor of males (González-Tokman et al., 2017).

Moreover, dung containing residues of ivermectin are more attractive to insects, that potentially puts survival of their offspring in the risk (Errouissi and Lumaret, 2010). Depending on the residue concentration, ivermectin can have lethal or sublethal effect on insect larvae up to 8 weeks post-treatment (Sommer et al., 1992; Suarez et al., 2003), or, if administered as intra-ruminal long-acting bolus, up to several months (Errouissi et al., 2001). Since it has a negative impact on beetle survival and reproduction, use of ivermectin raises concerns about its effect on community structure and ecosystem functioning.

18 On a community level, sites with macrocyclic lactone treatment (especially ivermectin) have substantially lower dung beetle abundance (Finch et al., 2020; Römbke et al., 2010; Verdú et al., 2018), biomass (Hutton & Giller, 2003; Tonelli et al., 2017; Verdú et al., 2018) and species richness (Hutton & Giller, 2003; Pecenka & Lundgren, 2019; Tonelli et al., 2017; Verdú et al., 2018) than control sites. Altered community structure and overall beetle abundance in turn affects community's functional performance in perturbed ecosystems (Beynon et al., 2012). For example, species-poor areas under warm climate emit 1.6- and 2.8-fold higher total CO₂ and CH₄, respectively, than sites without treatment (Verdú et al., 2020). Dung degradation is significantly prolonged when ivermectin residues are present in dung (Floate, 1998; Manning et al., 2017b, 2017a; Römbke et al., 2010). Up to 70 % lower dung removal capacity on routinely treated sites stems from reduced functional richness, particularly from the loss of large tunneling and rolling dung beetles (Tonelli et al., 2020). Treatment with macrocyclic lactones certainly threatens dung beetle diversity as well as the ecosystem services they provide. Most of the studies evaluated effects of macrocyclic lactones from various perspectives mostly following their administration in respective season. On the other hand, very few studies evaluated the real-life effects of routine, year-by-year treatment on dung beetle communities (e.g., Sherratt et al. 1998; Tonelli et al. 2020). Nevertheless, this knowledge is essential to determine the potential of antiparasitic treatments to seriously harm dung beetle communities and the ecosystem services they provide and to decide whether some regulations should be considered.

4.3. Climate change Although changes in land-use and agriculture are primary causes of the detected decline of dung beetles, climate warming can even accelerate the changes (Dortel et al., 2013). Increasing temperatures (and less predictable precipitation) may result in 19 northward, uphill, seasonal, or habitat shift of dung beetle assemblages in Europe. For example, a northward shift was estimated for many Scarabaeinae species of the Iberian Peninsula, where the shift of current species might be compensated by the arrival of more thermophilous ones (Dortel et al., 2013). Birkett et al. (2018) recorded an uphill shift of the low elevation limit of *A. lapponum* by 177 m over 57 years in northern England. The mean elevation shifted upward for the majority of species in the south-west Alps (19 of 30 species) and the Sierra Nevada (17 of 19 species) (Menéndez et al., 2014). Especially cold-adapted species occurring in mountains may be limited by shrinking or inaccessibility of suitable habitats (Dirnböck et al., 2011). Menéndez & Gutiérrez (2004) observed that some dung beetles can even change habitat associations or modify seasonal occurrence in response to changing climatic conditions so that their microclimatic requirements are met. They also pointed out that climate warming has the potential to alter or even generate new species interactions, such as competition for resources (Menéndez and Gutiérrez, 2004). On the other hand, the effect of climate change on dung beetles might not be only negative. Northward shifting ranges of many species may increase dung beetle diversity in certain regions (Dortel et al., 2013). We may even expect that ranges of some species may expand and they might be able to recolonize their former localities. As an example, several species formerly restricted to the warmest regions of the Czech Republic (e.g., *Coprimorphus scrutator*, *Rhodaphodius foetens*, *Geotrupes spinniger*) expanded their range to many highlands and even submountain regions within the last circa 20 years (Mertlik, 2019; Týr, 1999). This northward shift will favor Scarabaeinae over Aphodiinae (Dortel et al., 2013), which can in turn affect functional composition and performance of the community. In Central and Northern Europe, the higher representation of Scarabaeinae may increase dung removal and related ecosystem services (Milotić et

20 al., 2019). The question remains whether these potentially expanding species will be able to colonize new favorable areas, as their successful dispersal requires a good connectivity among pastured habitats (Dortel et al., 2013). Unfortunately, scenarios of land-use development predict more increased division of cattle breeding industry to intensive farming in favorable areas versus grazing abandonment (Schröter et al., 2005). 5. Conservation Dung beetle conservation is crucial for two main reasons – sustaining biodiversity, as they are one of the most threatened insect groups in Central Europe, and sustaining ecosystem services their communities provide. To allow natural restoration of dung beetle communities, it is necessary to eliminate or compensate for the main causes of their decline. In Central Europe, it is mainly habitat loss due to grazing abandonment and following habitat isolation (Buse et al., 2018, 2015). The goal is to create a fine network of suitable habitats, so that the grazed sites serve as stepping stones for natural re-colonization and long-term survival of dung beetle species in a landscape (Buse et al., 2015). This is especially important for red-listed species, as they require either

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large pastures (< 130 ha) or a coherent network of small pastures to ensure

their long-term survival (Buse et al., 2015). Since decades or even centuries are needed for the full community development, Buse et al. (2015) suggest to support establishment of new pastures preferably in the vicinity of existing pastures with longer grazing history. This could be achieved with only a low grazing intensity (Tonelli et al., 2019, 2018). Moreover, some habitat specialists may require more time and effort beyond the overall increase of pasture extend, with a special focus on their preferred habitats (Buse et al., 2015). For instance, for forest specialists, wild ungulate populations

21 accompanied with some type of disturbance (e.g., clearings used for pastoralism) worked better than wild ungulates only (Barbero et al., 1999). While increased number and extent of grazed sites is the main starting point for efficient dung beetle conservation, the quality of habitats determines its success. In general, grazing in heterogeneous habitats sustains more species than in homogeneous ones, as it provides living space for more species with different needs (Jay-Robert et al., 2008; Negro et al., 2011a). Low-quality biotopes, such as intensive farms or sites regularly treated with antiparasitics, have lesser abundance, species richness and host functionally less capable communities of dung beetles than organic farms with medium intensity grazing (Hutton and Giller, 2003; Tonelli et al., 2017; Verdú et al., 2018b). Abundant habitats of lower quality (e.g., intensive farms with excessive use of antiparasitics, timber production forests) may host common species with lesser specialization or even act as stepping stones for dispersing individuals, while they probably cannot ensure long-term survival of species with more specialized habitat requirements (Buse et al., 2015; Hodgson et al., 2011). Therefore, habitats of higher quality, such as rewilded areas, grazed reserves, or farms with more environmentally friendly grazing schemes, are needed. Another point of view can be a conservation of the most agriculture-relevant ecosystem services (dung removal, fly and parasite control, improved soil productivity). It is mainly dependent on the total abundance of dung beetles (Manning and Cutler, 2018) and presence of functionally most efficient large relocating beetles (tunnelers and rollers; Piccini et al. 2018; Tonelli et al. 2020). At the same time, body size (Larsen et al., 2008; Tonelli et al., 2018) and relocating behavior (Carpaneto et al., 2007; Lobo, 2001; Piccini et al., 2018) are related to the higher risk of extinction. As large relocating beetles in Central Europe are usually concentrated in warm lowlands (Lobo et al., 2002; Lumaret and Kirk, 1991), our conservation effort (i.e., support of grazing) should be first targeted in these regions.

22 To conserve ecosystem services provided by dung beetles, we should aim to reach high abundances and representation of large and relocating beetles, either by excluding their threats or by direct support of beetle populations. Dung beetles can be supported not only by extended conventional or organic grazing, but also by rewilding (Andriuzzi and Wall, 2018; Brompton, 2018). Rewilding is a modern approach of preserving larger reserves, allowing the environment to restore its natural state and processes, usually with help of introduced or repatriated predators and large herbivores that act as ecosystem engineers (e.g., wolves in Yellowstone, or cattle and horses in Oostvaardersplassen). Brompton (2018) showed on an example from the UK, that rewilded sites had significantly higher dung beetle diversity than organic farms, which she explains by higher ungulate diversity as well as more complex vegetation structure in rewilded sites. Similar observation comes from my own study, where rewilded site in Milovice (Central Bohemia, Czech Republic) hosted highest numbers of species and individuals from all sampled sites within the region of Elbe lowland (Ambrožová, unpublished). Such observations are relatively scarce and more research is still needed to properly evaluate the role of rewilding for dung beetle conservation. However, restored grazing of large herbivores in rewilded areas may bring an opportunity for conservation of threatened or even regionally extinct species by translocation, if the habitats required for the concerned species are preserved or renewed (and the basic translocation principles followed) (Andriuzzi and Wall, 2018; Bellis et al., 2019). Translocation of dung beetles has a long history – exotic species were introduced in Australia, New Zealand, Canada and USA, mostly as a biological control of flies and to help with dung degradation. In Australia, undegraded dung of introduced livestock became a massive resource of livestock GIT parasites (Doubé, 2018) and dung-breeding flies (*Musca vetustissima*, *Haematobia irritans irritans*), a

23 serious nuisance and a vector of parasites of cattle and humans (Da Cruz et al., 2002; Kunz, 1978; Shaw and Sutherland, 2006; Waterhouse, 1974). The situation significantly improved after the introduction of 43 exotic dung beetle species, mainly recruited from the large tunneling and rolling beetles of Southern Europe and South Africa (Bornemissza, 1976; Doubé, 2018; Edwards, 2007). In New Zealand, the introduction of 15 non-native species improved ecosystem functioning by reduced surface soil runoff by 49-97 % and reduced nematode numbers on grass by 71% (Forgie et al., 2018). Canada and USA introduced 10 and 29 dung beetle species, respectively, as a biological control of invasive horn flies (*Haematobia irritans irritans*) and to improve dung degradation (Pokhrel et al., 2021). In the United Kingdom, there are attempts to supply native dung beetles to farmers and horse owners to replenish their native populations, once the research is completed (Anonymous, 2018). This support of native species, in my opinion, can be an effective way of sustaining ecosystem services, especially suitable for highly fragmented landscape with isolated pastures.

24 6. Aims and scope of the thesis In this thesis, I focused on understanding the environmental drivers, the effect of site management and veterinary treatment on dung beetle communities in Central Europe. Dung beetles are one of the most affected taxa by modern agricultural practices, facing the severe decline and isolation of suitable habitats and their quality across the whole Europe. Thus, understanding the drivers of their diversity enables us to prioritize and better target future conservation efforts. Furthermore, I studied the effect of site management on dung beetle communities (use of veterinary medical products in pastures and opening a forest by coppicing and topsoil removal), both with an important overlap to practical conservation. Chapter I focuses on the routine treatment of grazing animals with ivermectin and its effect on dung beetle communities and their dung-removal potential, the key ecosystem service they provide. Twenty-six sites across the Czech Republic were sampled to test whether routine ivermectin treatment changes dung beetle community structure (α -diversity, abundance, biomass of guilds) and their potential to provide ecosystem services compared to the sites without any antiparasitic treatment. In the Chapter II, I studied the effect of special forest management on forest dung and rove beetles. The question was whether small scale measures, such as coppicing and topsoil removal, can increase dung beetle taxonomic and functional diversity. In the Chapter III, dung beetle communities across the Czech Republic were sampled to test the relative importance of environmental variables for dung beetle β -diversity. The aim was to reveal which environmental variables should be given the conservation priority to yield the highest γ -diversity of dung beetles on a country-wide scale. Furthermore, the optimal grazing regime to yield highest γ -diversity of dung beetles on a country-wide scale was simulated.

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Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities

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Agriculture, Ecosystems & Environment (2021) 321, 107634 DOI: 10.1016/j.agee.2021.107634 50 51 Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities

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Abstract Use of ivermectin in agro-ecosystems negatively affects non-target dung beetles, which provide keystone ecosystem services for pasture functioning. While the direct effects of ivermectin on dung beetles are at the center of scientific attention, its long- lasting effects on routinely treated pastures have not yet been studied on real communities and under field conditions. We focused on basic characteristics (species richness, abundance, biomass) and functionality (dung removal ability represented by guild composition) of dung beetle communities in response to ivermectin treatment. We selected 15 sites with routine ivermectin treatment and 11 without any treatment, both for at least five consecutive years prior to our sampling. We covered wide range of climatic conditions in the Czech Republic, seasonal variability, and sampled the dung of four main herbivore dung types. Additionally, we separated the samples from ivermectin treated sites into two categories, i) recently treated representing immediate effects (treated <8 weeks prior to sampling, expected lethal or sublethal levels of residues), and ii) long-ago treated representing lasting effects (treated >8 weeks, expected sublethal or inconsequential levels of residues). Ivermectin treated sites had ca. 35% lower species richness and 44% lower abundance per pat. Per pat biomass did not change. However, from a functional perspective, ivermectin use significantly decreased the biomass of beetles with high contribution to dung removal (relocating and dwelling beetles), while the biomass of beetles with low contribution (dung visiting adults with saprophagous larvae) was not affected. This was accomplished with decrease in per pat functionality at treated sites, i.e., the dung removal ability of the community. Our results highlight that the effects of ivermectin use can last far beyond its physical presence in the grazing system. Via its effects on dung beetles, routine antiparasitic treatment by ivermectin has negative consequences for both pasture biodiversity and ecosystem functioning. Therefore, all alternatives should be carefully considered to ensure that the positives of any antiparasitic treatment outweigh the damages. In areas where biodiversity is of concern, as well as in organic farming systems, all precautions should be taken to avoid excretion of toxic residues on-site.

Keywords: anthelmintics, decomposition, grazing, Geotrupidae, livestock management, Scarabaeidae 1.

Introduction Changes in agricultural practices are among the primary causes of the recent loss of biodiversity and ecosystem services (Foley et al., 2005, Tscharrntke et al., 2005, Newbold et al., 2015). Animal grazing, especially in biomes where large herbivores have always been prominent, could represent a profitable agricultural activity that also sustains biologically diverse, natural, or semi-natural ecosystems (Metera et al., 2010). Intensification of livestock production, however, has resulted in widespread use of antiparasitics, mostly macrocyclic lactones, that harm non-target organisms involved in pasture functioning (Hutton and Giller, 2003, Tonelli et al., 2017, Verdú et al., 2018). Use of antiparasitics could thus lead to loss of biodiversity as well as ecosystem services (Emmerson et al., 2016). Residues in dung of animals treated with antiparasitics have the potential to adversely affect dung-breeding insects, including dung beetles that accelerate dung removal, an ecosystem service crucial to pasture functioning (Sommer et al., 1992, Lumaret and Errouissi, 2002, Nichols et al., 2008). Dung removal involves rich communities of bacteria, fungi, annelids, and arthropods (Holter, 1977, Holter, 1979). Among them, dung beetles contribute most to the initial phases of dung removal (Lumaret and Kadiri, 1995, Tixier et al., 2015). They remove dung directly and/or their activity in dung pats enables the activity of other dung decomposing organisms such as earthworms, soil bacteria, and coprophilous fungi (Holter, 1979, 54 Blackwell and Malloch, 1991). Via dung removal, dung beetles decrease the survival of dung-inhabiting larvae of various pests, blood-sucking flies, and endoparasites (Edwards and Aschenborn, 1987, Sands and Wall, 2017), aerate the soil, thus allowing aerobic bacteria to reduce emission of methane from decomposing dung (Penttilä et al., 2013), affect plant fitness by dispersing seeds from dung (Milotić et al., 2019, DeCastro-Arrazola et al., 2020), and enhance soil fertility (Bang et al., 2005). Dung beetles thus promote resource cycling between plants and animals (Maldonado et al., 2019), and prevent dung accumulation on pastures (Beynon et al., 2015). Dung beetles are, however, among the terrestrial insects most affected by habitat loss, including agriculture intensification, accompanied by high usage of inadvertently harmful antiparasitics, such as ivermectin (Sánchez-Bayo and Wyckhuys, 2019). Due to its low cost and high efficiency against a broad spectrum of parasites, ivermectin is one of the most widely used antiparasitics (Guichon et al., 2000). It causes neural paralysis to Ecdysozoa (Puniamoorthy et al., 2014), making it effective against gastro-intestinal nematodes as well as both internal and external arthropod parasites (Campbell et al., 1983, Sutherland, 1990). Ivermectin is not fully metabolized by animals and is therefore excreted in its active form in dung (Campbell et al., 1983). This is a problem, since ivermectin residues are harmful to dung-feeding arthropods, including dung beetles (Floate, 2007, Lumaret et al., 2012). Depending on the treated herbivore species and the way of administration, the residues can affect dung beetles up to several weeks post-treatment (Sommer et al., 1992, Errouissi et al., 2001, Suarez et al., 2003). Ivermectin can be administered by several routes with different excretion times (in increasing order: oral, intramuscular, subcutaneous, topical, sustained release bolus) (Floate et al., 2005, Canga et al., 2009). 55 In adult beetles, ivermectin affects their reproduction (O'Hea et al., 2010, Martínez et al., 2017, Rodríguez-Vivas et al., 2020), foraging, olfactory and locomotor abilities (Verdú et al., 2015), and mobility (Martínez et al., 2017, Pérez-Cogollo et al., 2017, Weaving et al., 2020). Larvae are even more affected, as ivermectin residues substantially reduce their survival (O'Hea et al., 2010, Martínez et al., 2017, Pérez-Cogollo et al., 2017, Finch et al., 2020), decrease the number and body size of newly emerged beetles (González-Tokman et al., 2017), and change the offspring sex-ratio in favor of males (González-Tokman et al., 2017). Such adverse effects should lead to serious large-scale alteration of dung beetle communities and hamper the ecosystem service they provide in the form of dung removal. At the community level, use of ivermectin on livestock has been associated with reduced abundance and diversity of dung beetles (Hutton and Giller, 2003, Verdú et al., 2018), and the dung removal rate (Tonelli et al., 2020). Most studies compared dung beetle communities in dung of untreated and recently treated animals (e.g. Sutton et al., 2014). They thus focused on the immediate, direct effects, while long term effects of ivermectin use were rarely investigated (but see Verdú et al., 2018). Yet, these are potentially more important to pasture health. If dung beetle communities recover rapidly, then non-target effects regarding the use of ivermectin are not a serious issue. If, however, it has a lasting effect on dung beetle communities, then ivermectin usage does have a serious, persistent negative influence on dung beetles and the ecosystem services they provide. Information on this important issue is, nevertheless, insufficient, as most relevant studies (e.g. Verdú et al., 2018, Pecenka and Lundgren, 2019) were limited by the number of sites or spatial scale. Although dung removal is the main ecosystem service provided by dung beetles, not all species contribute equally. Their contribution depends on their size, 56 abundance and feeding/nesting strategy. Dung relocating species (i.e., tunnellers and rollers) contribute more than species who do not relocate (Beynon et al., 2012a, Nervo et al., 2014). Among non-relocating dung beetles, species with adults and larvae feeding in the dung (i.e., dwellers) contribute more to dung removal than species with mostly saprophagous larvae feeding on dung mainly as adults (i.e., visitors; genus *Melinopterus*, *Chilothonax*, *Oxyomus*) (Landin, 1961, Christensen and Dobson, 1976, Gittings and Giller, 1997, Finn and Gittings, 2003, Rössner, 2012 and references therein; Buse and Entling, 2020). Ivermectin may thus affect ecosystem services provided by dung beetles not only by decreasing overall abundance and biomass, but also by altering the functional composition of their communities. Indeed, several studies pointed to the reduced numbers of relocating beetles on ivermectin treated sites than the other guilds (Sands and Wall, 2018, Tonelli et al., 2020). However, we are not aware of any study, which would account for the difference between dwellers and visitors. Such an indiscriminate approach might systematically underestimate the effect of ivermectin on the ecosystem services provided by dung beetles. The aim of this study was to investigate how routine use of ivermectin affects dung beetle communities on a landscape scale and to assess its potential effect on ecosystem services the communities provide. Thus, we carried out an extensive, large-scale survey of dung beetles at 26 grazed sites across the Czech Republic. To quantify the effect of ivermectin and to distinguish the lasting from immediate effect, the samples were categorized as originating from recently treated (> 8 weeks post application), long ago treated (< 8 weeks post application) or never treated pastures. To account for the effects of herbivore species, seasonal and

geographic variability, our sampling included four main herbivore dung types (horse, cattle, sheep, and fallow deer), covered elevations from 180 to 800 m a.s.l., and nearly full seasonal variability. We then compared abundance, species richness, biomass, 57 functionality, and guild composition (i.e., relocators, dwellers, visitors) of dung beetle communities among the treatments. Finally, we discuss the importance of our findings for conservation of biodiversity and ecosystem services and pasture health. 2. Materials and methods 2.1. Study sites We sampled dung beetles at 26 livestock pastures and game reserves, 25 across the Czech Republic and one in Austria. The sampling covered four regions and an elevation range of 180–800 m a.s.l. The regions include the Bohemian Forest (average annual temperature 6 °C, average annual precipitation 1028 ± 7 mm, average altitude 801 ± 12 m), South Bohemia (8 °C, 732 ± 1 mm, 393 ± 3 m), Central Bohemia (9 °C, 523 ± 16 mm, 227 ± 19 m), and South Moravia (9 °C, 606 ± 24 mm, 268 ± 88 m). Sites were

grazed by different herbivores, including horse, large bovids (domestic cattle, wisent – generally referred to as cattle herein after), sheep, and fallow deer (Fig. 1, Appendix: Table A1). Livestock sites ranged from open pastures without trees to shrubby sites with a few solitary trees; game enclosures were mostly forested but with large open meadows. All study sites were in relative proximity to the forested areas (usually between 500 and 1000 m). The animals in our study sites were either treated with ivermectin (all animals on site at the same time) or not treated with any antiparasitic, both at least for five consecutive years, though usually much longer. The actual dates of ivermectin administration are given in the Appendix, Table A1. Ivermectin treatments were classified as (i) never treated (no ivermectin or other antiparasitic treatment), (ii) recently treated (animals treated less than eight weeks before

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sampling, expected lethal or sublethal levels of residues), and (iii) long ago treated (

antiparasitics administered more than eight weeks before the sampling; expected 58 sublethal or inconsequential levels of residue). The eight-week threshold between the recently and long-ago treatments represents up to six weeks when ivermectin residues can negatively affect development and survival of dung beetle larvae (Strong and Wall, 1994, Floate, 1998, O’Hea et al., 2010), plus a two-week buffer period. 2.2. Sampling Dung beetles (Coleoptera: Geotrupidae, Scarabaeidae) were collected in three sampling campaigns (May, July/August, October) in 2018 to cover three seasonally different dung beetle communities (Sladecek et al., 2013). We sampled beetles from all sites within one region in three days; all four regions were sampled within 20 days in each campaign. At each site, we sampled beetles from 10 (horse, cattle) or 20 (sheep, fallow deer) random dung pats and underlying soil from the most open parts of the pastures and game reserves. We sampled beetles from approximately 1 to 5 days old dung pats, which host the highest number of dung beetle species (Sladecek et al., 2013). Beetles were floated from dung (horse, cattle) in a bucket of water or directly collected from dung (sheep, fallow deer). All specimens were identified to species level. Species protected by law (Act No. 114/1992 Sb., Czech Law Collection) were counted in situ and released.

59 Fig. 1. Study sites. Distribution of study sites in four climatically and biogeographically distinct regions of the Czech Republic where dung beetle surveys were conducted in 2018 (Bohemian Forest: 1–6, South Bohemia: 7–9, Central Bohemia: 10–16, South Moravia: 17–26; site 23 is 0.5 km from the Czech border in Austria). For detailed characteristics of the study sites, see Appendix, Table A1. 2.3. Data For each sample (dung pat), we computed abundance, species richness, total biomass, the biomass of each ecological guild (see below), and functionality of the dung beetle community. We computed guilds’ biomasses as follows: guilds’ biomass [mg] = $(0.010864 \times \text{body length}^3 \times 3.16) \times \text{abundance}$ (Lobo, 1993), pooling the biomasses of all species for each guild (e.g., biomass of all dweller species for dwellers). Body sizes were obtained from Buse et al. (2018).

60 Dung beetles were classified into three guilds according to their feeding and nesting ecology: (i) relocators – all stages coprophagous, larvae develop in underground chambers in dung mass provided by their parents (Geotrupidae, Scarabaeidae: Scarabaeinae, Aphodiinae: genus *Colobopter*), (ii) dwellers – all stages coprophagous, larvae develop in dung pat (majority of Scarabaeidae: Aphodiinae), and (iii) visitors – adults coprophagous, saprophagous larvae do not primarily develop within dung pats (some Scarabaeidae: Aphodiinae genera, i.e.,

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Melinopterus, *Chilothorax*) (Landin, 1961, Christensen and Dobson, 1976, Halffter and Edmonds, 1982, Gittings and Giller, 1997, Rössner, 2012 and references therein; Buse

et al., 2018). By the nature of their life strategies, the guilds differ in their dung removing potential (Nervo et al., 2014). The potential is highest for relocators; coprophagous adults provision underground nests with dung for their coprophagous larvae before laying their eggs. Relocators thus physically remove dung from the surface, and the amount removed relates to the number of eggs laid. The potential of dwellers is lower since their larvae develop directly in the dung pat and contribute to removal through consumption, which depends on larval survival. Lastly, the potential of visitors is lowest; they contribute only via adult feeding because larvae develop usually independently on dung. To assess the dung removal ability of the studied communities, we computed the hypothetical functionality for each dung beetle community in each dung pat. Dung removal ability is determined by beetles' guild, size, and their abundance in a dung pat (Maldonado et al., 2019, DeCastro-Arrazola et al., 2020). The functionality was thus based on the biomass of each ecological guild adjusted by the guild's approximate dung removing potential. The arbitrary values for penalties were chosen to represent the natural disparity in dung degradation ability of dung beetle guilds, in the following order: relocators < dwellers < visitors. The biomass of 61 relocators therefore did not receive any penalty, dwellers were assigned a 50% penalty for their biomass, and visitors were assigned a 90% penalty for their biomass. The final formula for functionality was the following: functionality in each dung pat = (relocators' biomass in given dung pat*1) + (dwellers' biomass*0.5) + (visitors' biomass*0.1). For simplicity (as well as for lack of such information for the recorded species), we assumed that all adult beetles behave constantly and remove constant amount of dung mass over their occurrence.

2.4. Statistical analyses First, to confirm the homogeneity of sample distribution, we applied Patefield algorithm on the distribution matrix of treatments across herbivores ($T = 35.5$, $p = 0.9335$; (Blüthgen et al., 2006). In all analyses, one dung pat constitutes one sample. The effect of ivermectin treatment (never, long ago, recently) was the focal explanatory variable in all analyses. In addition, we fitted all models with the sampling campaign (date of sample collection as Julian date) as a fixed factor, and herbivore dung type (cattle, horse, sheep, fallow deer) and site as random factors. The significance of fixed factors was retrieved using the Anova function in the "car" package (Fox and Weisberg, 2019) in R 4.0.3 (R Core Team, 2020). We further tested differences among the ivermectin treatment levels (never, long ago, recently) in the "multcomp" package (Hothorn et al., 2008). All analyses were performed using generalized linear mixed effect models (GLMM) using the package "lme4" (Bates et al., 2015). For abundance and species richness, we fitted GLMMs with Poisson distribution of errors and diagnosed resulting models using the package "DHARMA" (Hartig, 2019). Since overdispersion was detected for abundance data, we added sample ID as an observation-level random effect (Harrison, 2014), which resolved the 62 problems with overdispersion. For overall community biomass, we analyzed the effect of ivermectin treatment using GLMM with Gamma distribution of errors. For biomasses of individual guilds, we first analyzed whether ivermectin treatment affects the probability of guild presence in dung pats. For this, we fitted three GLMMs with binomial distribution of errors using data on presence/absence of each guild in individual samples as response variables. Then we analyzed whether there is a difference in biomasses of guilds among ivermectin treatments. For the biomass of each guild, we used only samples where the particular guild was present. We then fitted a GLMM for the biomass of each guild with default model structure and Gamma distribution of errors with logarithmic link function. We analyzed the effects of ivermectin treatment on community functionality using default model structure and Gamma distribution of errors with logarithmic link function. We computed functionality for each sample in the whole data set. 3.

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Results In total, we sampled 31,578 individuals of 58 species of dung beetles. For the complete list of species, their abundances in all treatments and guild assignment, see Appendix, Table A2, and Tab. A3 for the list of species records per localities. Use of ivermectin did affect abundance, species richness and functionality but not total biomass of dung beetles (Table 1). Compared to never treated pastures, per pat abundance was reduced by 44% on long ago treated pastures, although only marginally

significant. Interestingly, dung beetle abundance did not differ between recently and never treated sites. (Table 2, Fig. 2A). In comparison with never treated pastures, per pat species richness was reduced by 29% and 37% on long ago and recently treated pastures, respectively (Table 2, Fig. 2B). Functionality in recently treated pastures was reduced by 64% compared to never treated pastures, and by 36% compared to long-ago treated pastures (Table 2, Fig. 2D).

63 Relocators were more likely to be present ($\chi^2 = 35.212$, $df = 2$, $p < 0.001$) in dung on never treated pastures, than in long ago (estimate = -1.175 , $z = -2.285$, $p = 0.054$) and recently treated dung (estimate = -2.769 , $z = -4.909$, $p < 0.001$), and also more likely in long ago than in recently treated pastures (estimate = -1.594 , $z = -5.118$, $p < 0.001$). Visitors were more likely to be present ($\chi^2 = 18.146$, $df = 2$, $p < 0.001$) in dung on recently treated pastures, than in dung on long ago (estimate = 1.128 , $z = 3.994$, $p < 0.001$) and never treated pastures (estimate = 1.379 , $z = 3.381$, $p = 0.001$). The probability of the presence of dwellers was not influenced by ivermectin treatment ($\chi^2 = 0.834$, $df = 2$, $p = 0.659$). Biomass of relocators and dwellers, but not visitors, was lower on recently treated than untreated pastures (Table 1). Compared to never treated pastures, per pat biomass of relocators and dwellers on recently treated pastures was reduced by 70% and 54%, respectively (Table 2, Fig. 3).

64 Table 1. Effects of ivermectin (Treatment), season, and dung type (herbivore) on dung beetle communities in dung pats. Summary of GLMER given for the two explanatory variables acting as fixed factors on dung beetle abundance, species richness, functionality, and total and individual guilds' biomass. Values presented are given by the Anova function in the R package car. See Methods for details. Significant results are in bold. χ^2 df p χ^2 df p Abundance Dweller biomass Treatment 12.416 2 0.002 Treatment 13.662 2 0.001 log(Season) 30.492 1 >0.001 log(Season) 88.285 1 >0.001 Species richness Relocator biomass Treatment 15.401 2 >0.001 Treatment 8.555 2 0.014 log(Season) 74.418 1 >0.001 log(Season) 9.843 1 0.001 Total biomass Visitor biomass Treatment 4.269 2 0.118 Treatment 0.745 2 0.689 log(Season) 38.369 1 >0.001 log(Season) 5.027 1 0.025 Functionality Treatment 10.074 2 0.006 log(Season) 19.412 1 >0.001

Table 2. Differences in dung beetle community structure between treatment regimes. Presented values were retrieved using Tukey's contrast in the R package "multcomp". Differences are given only for variables significantly affected by ivermectin treatment as a factor in our generalized linear models with mixed effects. Never = sites never treated with ivermectin, Long ago = sites treated > 8 weeks ago, Recently = sites treated > 8 weeks ago. For a detailed description of guilds and functionality, see text. Significant results are in bold. Estimate Std. Err. Z p Estimate Std. Err. Z p Abundance Dweller biomass Long ago – Never -0.596 0.282 -2.114 0.081 Long ago – Never -0.234 0.201 -1.165 0.469 Recently – Never -0.137 0.299 -0.457 0.887 Recently – Never -0.780 0.233 -3.343 0.002 Recently – Long ago 0.459 0.149 3.091 0.005 Recently – Long ago -0.546 0.173 -3.149 0.005 Species richness Relocator biomass Long ago – Never -0.339 0.109 -3.111 0.005 Long ago – Never -0.547 0.443 -1.235 0.419 Recently – Never -0.468 0.119 -3.992 >0.001 Recently – Never -1.193 0.486 -2.456 0.035 Recently – Long ago -0.128 -0.071 -0.816 0.158 Recently – Long ago -0.646 0.260 -2.481 0.033 Functionality Long ago – Never -0.573 0.348 -1.646 0.214 Recently – Never -1.012 0.370 -2.737 0.015 Recently – Long ago -0.439 0.177 -2.480 0.032

66 Fig. 2. Effects of ivermectin on abundance (A), species richness (B), total biomass (C), and functionality (D) of dung beetles in dung pats at sites never treated with ivermectin (Never), sites treated < 8 weeks ago (Long ago) and treated > 8 weeks ago (Recently). Functionality reflects dung removal potential of dung beetles in a dung pat depending on their biomass and guild. Middle points represent the model defined estimate of value per dung pat, error bars represent the standard error of mean. Horizontal lines denote statistical significance; + = $p \sim 0.05$, * = $p < 0.05$, ** = $p < 0.001$, *** = $p < 0.001$.

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Discussion Our results clearly demonstrate that ivermectin use leads to serious changes in dung beetle communities. First, dung of treated animals hosted communities poorer in species than untreated ones. Second, ivermectin use decreased the dung removal potential (functionality) of affected communities. Third, there is both short- and long-term effect of ivermectin use on dung beetle communities. Our sampling included the four main herbivore dung types of the temperate Europe; it nearly fully accounted

for seasonal, and partly also for climatic, variability. Therefore, we were able to generalize the effects of ivermectin use, alleviating the problems connected with spatiotemporal variability and preferences for the dung of certain herbivores. Below, we discuss the importance of our results for biodiversity conservation and pasture management and suggest alternative measures. 4.1. Short term vs. long term effects Ivermectin usually does not kill adult beetles but rather acts via larval survival and development (O'Hea et al., 2010, Martínez et al., 2017). Therefore, the observed community is a result of the effect of management on previous generation (i.e., we only see individuals that survived), and possible altered attraction/repellency of ivermectin residues currently present in the dung (Floate, 2007, Rodríguez-Vivas et al., 2020). The reason for splitting treated samples into recently and long-ago treated was to separate the effect of repeated treatment (i.e., long-ago, without residues) from the effect of repeated treatment possibly confounded with altered attractivity due to presence of residues (i.e., recently). We found that the species richness and functionality of dung beetle communities in recently and long ago-treated dung were substantially closer to each other than to untreated dung. Ivermectin use thus similarly affected certain aspects of dung beetle communities regardless of whether 68 a dung pat likely contained its residues or not. This shows that the effect of its use on dung beetle communities lasts much longer than the ivermectin in the grazing system itself. On the other hand, no observed difference in abundance between never treated and recently treated sites suggest, that presence of ivermectin residues may act as an attractant for dung beetles (Floate, 2007, Errouissi and Lumaret, 2010). All our study sited with ivermectin were treated for at least five consecutive years, though possibly much longer. The herein described patterns are therefore most likely the result of repeated, long-term use. Effects of single or occasional use of ivermectin should be less severe (Krüger and Scholtz, 1998). On the other hand, the rather low difference between recently and long-ago treated pastures suggests that recolonization is a slow process. This question requires further investigation, as our data do not allow for such conclusions. Nevertheless, they clearly show that the effects of ivermectin use on dung beetle communities last longer than the physical presence of its residues in dung. 4.2. Biodiversity concerns Insect decline is among intensively discussed and closely observed global problems. In our study, routinely treated sites hosted communities with 44% lower abundance (although marginally significant) and ca. 35% lower species richness than untreated sites. This suggests that when widespread, the use of ivermectin could be among the most important factors contributing to the decline of dung beetles, as numerous other studies have already associated lower dung beetle abundances (Hutton and Giller, 2003, Beynon et al., 2012b, Verdú et al., 2018, Pecenka and Lundgren, 2019) and species richness (Krüger and Scholtz, 1998, Verdú et al., 2018, Pecenka and Lundgren, 2019) with ivermectin treatment. This is of serious concern, as species richness of sampled communities was already depleted during the past century, when intensification of agriculture altered

69 agricultural production, the landscape, and biodiversity in the Czech Republic. Dung beetles were affected by the decline of pasturing, followed by rapidly diminishing areas of pastures and grasslands (Skaloš, 2006, Woodcock et al., 2008). During the communist era (1948–1989), most cattle were kept indoors, and the number of horses crashed from ca 420 thousand to ca 25 thousand (Czech Statistical Office, www.czso.cz/csu/czso/zem_ts). Remaining pastures were mostly found at higher elevations, as the soil was deemed too productive in lowlands to be grazed. Unsurprisingly, dung beetles were heavily affected. Of the 100 dung beetle species known from the Czech Republic, 9 species are extinct in the whole Czech Republic, 24 species considered regionally extinct in Bohemia or Moravia (Juřena and Týr, 2008), and 61 are red-listed (Král and Bezděk, 2017). Ivermectin was discovered in the 1970s and introduced as a commercial product for animal health in 1981 (Crump and Omura, 2011). Its introduction to the Czech Republic in the 1980s coincided with the lowest numbers of grazing animals in recent history. Thus, it was probably the last factor contributing to the decline of dung beetles already hit by the intensification of agriculture. Any further decline might cause further extinction of already threatened species (Tonelli et al., 2020). Our results point out that the use of ivermectin does have lasting effects and eliminates approximately one third of species from the dung pat community. Potential recolonization could be seriously hampered by fragmented landscape, since species rich dung beetle communities require large pastures with continuous grazing (Collinge, 2000, Buse et al., 2015). In other words, once the species are lost, even habitat restoration cannot guarantee the recovery of the original community (Audino et al., 2014). This is a serious concern, considering that most of our study sites were located in protected areas, where conservation of biodiversity should be among the primary goals. Therefore, in protected areas, administration of antiparasitics should be of great concern to nature conservation managers.

70 4.3. Ecosystem services concerns Ecosystem services provided by dung beetles are mainly connected with dung removal, which is strongly determined by their abundance, biomass and life strategy (Manning and Cutler, 2018, Piccini et al., 2018, Maldonado et al., 2019). In our study, ivermectin use marginally decreased abundance and at the same time it had no effect on biomass. From this point of view, the dung removal capacity remained seemingly unaffected. However, we observed a shift in guild composition in treated dung. Guilds contributing the most to dung removal (i.e., relocators and dwellers) decreased significantly, while the biomass of beetles with low contribution (i.e., visitors) remained unchanged. Once guild contribution to dung removal has been accounted for, it became clear that the functionality (total biomass weighed by each guild's contribution to the dung removal) in ivermectin-treated dung is dramatically reduced. The functionality in ivermectin-treated dung was reduced substantially (64% in recently treated dung). This pattern mainly reflects the different response of relocators and visitors. Our results are in agreement with Tonelli et al., 2017, Tonelli et al., 2020, Sands and Wall (2018), who found reduced biomass of relocating beetles in treated pastures. Hence, we provide additional evidence that ivermectin suppresses relocating dung beetles. As relocators are the most efficient guild in dung removal (Tonelli et al., 2020), such reduction can lead to a substantial decrease in the accompanying ecosystems services. For example, Tonelli et al. (2020) reported that dung removal decreased by 70% in the areas with long-term use of antiparasitics. Also other ecosystem services, such as seed dispersal, parasite control or enhanced nutrient cycling might be reduced with the decline of relocating beetles (Milotić et al., 2017). Theoretically, decline of relocating beetles can lead to the stage when each round of antiparasitic treatment necessitates further intensification of

71 antiparasitics administration due to the dung accumulation on pastures and subsequent easier spread of parasites. Visitors, on the other hand, tend to have high biomasses in all treatments but their real contribution to dung removal and subsequent ecosystem services is probably very low. We assume that their larvae are less likely to be exposed to toxic levels of ivermectin residues, as they primarily feed on decomposing organic matter outside of dung (e.g. Landin, 1961; Gittings and Giller, 1997; Finn and Gittings, 2003; Rössner, 2012). The other reason for lesser effect of ivermectin on visitors' populations might be their polyvoltinism and higher fecundity, compared to the other dwellers (Stebnicka, 1973, Gittings and Giller, 1997). Therefore they may not lose significant biomass on treated sites and could even compensate for the biomass decline of other two guilds. It is important to note, however, that we did not find significant lasting effect of ivermectin use on functionality (although the mean functionality was lower in long ago treated dung than in never treated dung). Thus, we cannot dismiss the possibility of community recovery after ivermectin treatment. Nevertheless, this observation might stem from overall high variability of our data, therefore we encourage further studies dealing with the lasting effects of ivermectin use on the landscape scale.

4.4. Management recommendations Widespread use of ivermectin poses serious threats to dung beetle species richness and the ecosystem services provided by them (dung removal, parasite control) (Sands and Wall, 2017, Verdú et al., 2018). That in turn could have significant economic consequences (Beynon et al., 2015). Therefore, measures to reverse or minimize dung beetle loss should be applied. As ivermectin (over)use is a symptom of agricultural intensification, one possibility is to return to traditional practices such

72 as low intensity cross and rotational grazing, where possible (Pecenka and Lundgren, 2019), to aid the natural control of parasite infections. When antiparasitic use is inevitable, treating during periods of low dung beetle activity, treating only a fraction of animals in the herd at a time, or keeping animals in stables for at least the first two weeks after the treatment can lower the negative impact on dung beetles (Webb et al., 2010). Alternatively, use of other antiparasitics with lesser (or no) impact on dung beetles, which do not hamper dung removal by beetles, should be encouraged (Lumaret and Errouissi, 2002, Sutton et al., 2014). Such alternatives include certain benzimidazoles (Lumaret and Errouissi, 2002), praziquantel (Hempel et al., 2006), or moxidectin (Floate et al., 2005). However, it is important to note that repeated use of any antiparasitic leads to the development of parasite resistance against certain compounds and subsequent loss of efficacy (Kaplan, 2004, Geurden et al., 2015). Also, even dung beetle-friendly benzimidazoles may disrupt dung removal via their negative effect on earthworms (Goodenough et al., 2019), another important dung removal agent in temperate regions. Importantly, antiparasitic medications should be targeted and based on thorough parasitological screening of herds, a practice not common in many developed regions. Therefore, all alternatives should be carefully considered before each intended antiparasitic treatment in order to decide whether the positives of the treatment outweigh the damages to non-target organisms and ecosystem services. Great attention should be paid to the administration of antiparasitics especially in protected areas. 5.

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Conclusions We have found serious differences in diversity and guild composition of dung beetle communities between sites where animals are treated with ivermectin and sites without treatment. Use of ivermectin as a veterinary drug decreases species richness and seriously affects the functionality of non-target dung beetle communities via 73 changes in guild composition. If the current practice of treating grazing animals with ivermectin continues, in addition to the isolation of grazed sites, ecosystem

services provided by temperate dung beetles could be seriously hampered or even permanently lost, leading to insufficient dung removal, insufficient reduction of greenhouse gasses, weakened natural parasite control, and substantial economic losses.

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APPENDIX Table A1: List of study sites with their main characteristics. Numbers correspond with the site numbers on the map (Fig. 1). Treated = date of ivermectin administration, dash stands for no antiparasitic treatment, rec = recently treated (>8 weeks prior to sampling campaign), long = treated long ago (<8 weeks prior to sampling campaign), never = not treated. Protection = highest legal protection: NP = national park, PLA = protected landscape area, NR = nature reserve; * = missing autumn samples; AU = Austria. region site herbivore treated spring summer autumn protection species abundance GPS lat N long E 1C South Bohemia Haklovy Dvory cattle 1.4. rec long long 18 796 48.987 14.408 2H Haklovy Dvory horse 1.3. rec long long 13 1188 48.997 14.389 3F Haklovy Dvory fallow deer 1.3. rec long long 8 139 48.997 14.393 4C Bohemian Forest Nová Pec cattle 31.7. long long long NP 15 827 48.784 13.930 5H Nová Pec horse 30.4. rec long long NP 17 1552 48.780 13.931 6S Nové Údolí sheep 30.4. rec long long NP 12 187 48.829 13.797 7S Slunečná sheep 2.1. long long long NP 16 287 48.809 13.971 8C Stožec* cattle - never never never NP 15 496 48.856 13.822 9H Stožec horse 20.5. long long long NP 11 2494 48.853 13.827

region site herbivore treated spring summer autumn protection species abundance GPS lat N long E 10C Central Bohemia Benátky nad Jizerou – Traviny cattle (wisent) - never never never NR 19 2894 50.284 14.870 11H Benátky nad Jizerou – Traviny horse - never never never NR 24 981 50.284 14.870 12H Lipník horse 1.4. rec long long 18 132 50.270 14.920 13C Milovice cattle - never never never NR 20 1978 50.236 14.889 14H Milovice horse - never never never NR 26 1149 50.236 14.889 15C Milovice – Tankodro m cattle 1.4. rec long long 17 1323 50.248 14.847 16F Žehuňská obora fallow deer - never never never 20 488 50.152 15.336 17F South Moravia Bulhary fallow deer 1.3. long long long PLA 26 1164 48.811 16.720 18H Havraníky horse 1.1. long long long NP 18 610 48.811 15.999 19H Havraníky horse - never never never NP 21 775 48.806 15.990 20H Lednice* horse 1.4. rec long - PLA 22 299 48.809 16.802

region site herbivore treated spring summer autumn protection species abundance GPS lat N long E 21H Mašovice horse - never never never NP 22 776 48.845 15.967 22H Mašovice horse 1.9. long long rec NP 17 638 48.850 15.966 23C Mitterhof (AU) cattle 30.8. long long rec 26 1588 48.773 16.446 24H Hlohovec – Nesyt horse - never never never NR 24 2968 48.766 16.727 25C Skalky u Sedlece cattle - never never never NR 32 4777 48.774 16.672 26S Skalky u Sedlece sheep - never never never NR 27 1090 48.773 16.677

90 Table A2. List of recorded species, their guild assignment, and abundances in study treatments. D = dweller, R = relocater, V = visitor, never = never treated with ivermectin, long ago = treated with ivermectin < 8 weeks prior to sampling, recently = treated with ivermectin > 8 weeks prior to sampling. family treated species guild never long ago recently Geotrupidae Anoplotrupes stercorosus (Scriba, 1791) R 9 34 6 Geotrupes spiniger (Marsham, 1802) R 66 76 7 Geotrupes stercorarius (Linnaeus, 1758) R 14 9 0 Trypocopris vernalis (Linnaeus, 1758) R 66 21 0 Scarabaeidae Acanthobodilus immundus (Creutzer, 1799) D 0 0 3 Acrossus depressus (Kugelann, 1792) D 7 34 38 Acrossus luridus (Fabricius, 1775) D 1140 252 18 Acrossus rufipes (Linnaeus, 1758) D 7 32 0 Agrilinus ater (De Geer, 1774) D 43 14 1 Ammoecius brevis Erichson, 1848 D 0 1 0 Aphodius pedellus (Degeer, 1774) D 569 145 223 Bodilopsis rufa (Moll, 1782) D 115 145 84 Bodilus ictericus (Laicharting, 1781) D 0 0 47 Bodilus lugens (Creutzer, 1799) D 4 67 1 Calamosternus granarius (Linnaeus, 1767) D 44 118 239 Colobopterus erraticus (Linnaeus, 1758) R 708 442 48 Coprimorphus scrutator (Herbst, 1789) D 163 22 1 Copris lunaris (Linnaeus, 1758) R 1 2 0 Esymus pusillus (Herbst, 1789) D 379 28 87

91 family treated species guild never long ago recently Euheptaulacus porcellus (Frivaldszky, 1879) D 3 0 0 Euoniticellus fulvus (Goeze, 1777) R 152 586 0 Euorodalus coenosus (Panzer, 1798) D 20 8 1 Euorodalus paracoenosus (Balthasar & Hrubant, 1960) D 11 2 2 Eupleurus subterraneus (Linnaeus, 1758) D 18 1 37 Chilo thorax distinctus (Müller, 1776) V 2812 759 362 Labarrus lividus (Olivier, 1789) D 0 2 0 Limarus maculatus (Sturm, 1800) D 13 1 0 Melinopterus consputus (Creutzer, 1799) V 3 65 2 Melinopterus prodromus (Brahm, 1790) V 2091 648 911 Melinopterus sphacelatus (Panzer, 1798) V 320 3464 1387 Nimbus contaminatus (Herbst, 1783) V 42 157 0 Nimbus oblitteratus (Panzer, 1823) V 84 44 0 Onthophagus coenobita (Herbst, 1783) R 123 19 7 Onthophagus fracticornis (Preyssler, 1790) R 495 157 55 Onthophagus furcatus (Fabricius, 1781) R 55 0 0 Onthophagus illyricus (Scopoli, 1763) R 187 35 0 Onthophagus joannae Goljan, 1953 R 851 122 7 Onthophagus lemur (Fabricius, 1781) R 1 0 0 Onthophagus medius (Kugelann, 1792) R 2 0 0 Onthophagus nuchicornis (Linnaeus, 1758) R 193 25 1 Onthophagus ovatus (Linnaeus, 1767) R 2430 192 31 Onthophagus ruficapillus Brullé, 1832 R 212 269 0 Onthophagus semicornis (Panzer, 1798) R 5 0 0

92 family treated species guild never long ago recently *Onthophagus similis* (Scriba, 1790) R 13 3 0 *Onthophagus taurus* (Schreber, 1759) R 0 1 0 *Onthophagus vacca* (Linnaeus, 1767) R 56 52 0 *Onthophagus verticicornis* (Laicharting, 1781) R 451 31 0 *Otophorus haemorrhoidalis* (Linnaeus, 1758) D 3552 395 481 *Oxyomus sylvestris* (Scopoli, 1763) V 12 3 0 *Phalacrothothus biguttatus* (Germar, 1824) D 3 0 0 *Plagiogonus arenarius* (Olivier, 1789) D 21 0 0 *Planolinus fasciatus* (Olivier, 1789) D 1 67 0 *Rhodaphodius foetens* (Fabricius, 1787) D 237 114 1 *Sigorus porcus* (Fabricius, 1792) D 10 2 3 *Sisyphus schaefferi* (Linnaeus, 1758) R 239 129 0 *Subrinus sturmi* (Harold, 1870) D 53 1 1 *Teuchestes fossor* (Linnaeus, 1758) D 211 171 75 *Volinus sticticus* (Panzer, 1798) V 55 57 24

93 Chapter II Coppicing and topsoil removal promote diversity of dung-inhabiting beetles (Coleoptera: Scarabaeidae, Geotrupidae, Staphylinidae) in forests Agricultural and Forest Entomology (2022) 24 (1), 104-113 DOI: 10.1111/afe.12472
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95 Coppicing and topsoil removal promote diversity of dung-inhabiting beetles (Coleoptera: Scarabaeidae, Geotrupidae, Staphylinidae) in forests Lucie AMBROŽOVÁ 1,2,3,* , Sven FINNBERG 4 , Benedikt FELDMANN 5 , Jörn BUSE 6 , Henry PREUSS 7 , Jörg EWALD 7 , Simon THORN 3 Affiliations: 1 Faculty of Science, Department of Zoology, University of South Bohemia in České Budějovice, Branišovská 1760, 37005, České Budějovice, Czech Republic 2 Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 1160/31, 37005 České Budějovice, Czech Republic 3 Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology (Zoology III), Julius Maximilians University Würzburg, Glashüttenstraße 5, 96181, Rauhenbrach, Germany 4 Waldhaus 1, 91459, Markt Erlbach, Germany 5 Juistweg 1, 48159, Münster, Germany 6 Department for Ecological Monitoring, Research and Species Protection, Black Forest National Park, Kniebisstraße 67, 72250, Freudenstadt, Germany 7 Institute for Ecology and Landscape, Weihenstephan University of Applied Sciences, Hans-Carl-von-Carlowitz-Platz 3, 85354, Freising, Germany * Corresponding author: Lucie Ambrožová, Tel.: +420 385 310 350; Fax: +420 387 775 980; e-mail: l.ambrozova@seznam.cz

96 Abstract 1. Central European forests experience a substantial loss of open-forest organisms due to forest management and increasing nitrogen deposition. However, management strategies, removing different levels of nitrogen, have been rarely evaluated simultaneously. 2. We tested the additive effects of coppicing and topsoil removal on communities of dung-inhabiting beetles compared to closed forests. We sampled 57021 beetles, using baited pitfall traps exposed on 27 plots. 3. Experimental treatments resulted in significantly different communities by promoting open-habitat species. While alpha diversity did not differ among treatments, gamma diversity of Geotrupidae and Scarabaeidae and beta diversity of Staphylinidae were higher in coppice than in forest. Functional diversity of rove beetles was higher in both, coppice and topsoil-removed plots, compared to control plots. This was likely driven by higher habitat heterogeneity in established forest openings. Five dung beetle species and four rove beetle species benefitted from coppicing, one red-listed dung beetle and two rove beetle species benefitted from topsoil removal. 4. Our results demonstrate that dung-inhabiting beetles related to open forest patches can be promoted by both, coppicing and additional topsoil removal. A mosaic of coppice and bare-soil-rich patches can hence promote landscape-level gamma diversity of dung and rove beetles within forests. Keywords: Dung beetle, forest management, functional diversity, insect decline, nitrogen uptake, rove beetle.

97 Introduction The conversion and degradation of natural habitats is causing global biodiversity declines (Newbold et al., 2015). Terrestrial insect abundance has declined by ~9% in past decades (van Klink et al., 2020), with adverse effects on ecosystem functioning, including the provision of food sources for higher trophic levels (Bowler et al., 2019), and nutrient cycling (Yang & Gratton, 2014). While insect decline is particularly strong in landscapes dominated by agriculture, forests experienced a decline of e.g., 41% arthropod biomass in Germany between 2008 and 2017 (Seibold et al., 2019). This loss has been attributed to the combined effects of e.g., removal of large old trees (Lindenmayer et al., 2014), homogenization of forest structures and increasing canopy closure (Miklín et al., 2018; Thorn et al., 2020), cumulative uptake of nitrogen (Midolo et al., 2019) and the abandonment of traditional forest management (Benes et al., 2006; Weiss et al., 2021). Traditional forest management, such as pollarding, wood pastures and coppicing, has promoted forest heterogeneity and hence enabled the co-existence of species with various habitat requirements (Sebek et al., 2013; Helbing et al., 2014; Horak et al., 2014). The abandonment of coppicing has caused an unprecedented decline of light-demanding species across European landscapes (Benes et al., 2006; Streitberger et al., 2012; Müllerová et al., 2014). Hence, coppicing is currently used to support specialized plants (Vild et al., 2013; Douda et al., 2017; Lanta et al., 2020), saproxylic beetles (Vandekerckhove et al., 2016) or butterflies (Fartmann et al., 2013; Sebek et al., 2015; Dolek et al., 2018). Nitrogen deposition changes plant species composition towards communities composed of more nutrient-demanding species with greater biomass and lower diversity (Hautier et al., 2009). Therefore, a simplified plant community hosts simplified communities of insects with lower richness but higher abundances (Haddad et al., 2000). Hence, nitrogen removal has been suggested to restore

98 ecosystems and to manage nitrogen-limited habitats such as heathlands (Niemeyer et al., 2007). Nitrogen accumulation can be reduced by prescribed burning (Hubbard et al., 2004), grazing, mowing (Jones et al., 2017), litter harvesting (Sayer, 2006), removal of tree-biomass and logging residues (Lundborg, 1997) or humus and topsoil removal (Prietzl & Kaiser, 2005; Tarvainen et al., 2011). However, such measures might only have a short-term effect, given the continuous atmospheric nitrogen deposition, yet topsoil removal is one of the most efficient and long-lasting measures (Jones et al., 2017; Neff et al., 2020). Topsoil removal was implemented to restore plant communities (Hölzel & Otte, 2003; Kiehl et al., 2010), support the re-establishment of light-demanding herb species (Emsens et al., 2015), restore communities of herbivorous insects (Neff et al., 2020) and support thermophilic and epigeic arthropods, such as many carabids and spiders (Borchard et al., 2014). So far, topsoil removal has been barely applied in forest ecosystems (but see Ewald & Pyttel, 2016; Soto & Puettmann, 2018). While both, topsoil removal and coppicing, remove nitrogen to a certain degree, studies investigating the effects of topsoil removal and coppicing have mainly focused on either the one or the other (Šipoš et al., 2017; Neff et al., 2020). Yet, changes in forest management are accompanied by a continuous aerial nitrogen input (Bobbink et al., 2010). Hence, potential forest biodiversity conservation measures need to account for both, while it remains unclear whether nitrogen removal, e.g., topsoil removal, on top of tree-biomass removal by coppicing has additional benefits for biodiversity. Primeval European forests were likely more open than managed forests today, due to natural disturbances, e.g., windthrows, insect outbreaks, fires and grazing of large herbivores, creating temporal gaps and increasing forest heterogeneity (e.g. Bradshaw et al., 2003). The anthropogenic suppression of the effects of natural disturbances (Wohlgemuth et al., 2002; Thorn et al., 2017), the

99 lack of large herbivore grazing (Vera, 2000) and the transition from traditional forest management to modern forestry (Douda et al., 2017) additionally contributed to a decline of species associated with light forests. Dung beetles (Scarabaeidae, Geotrupidae) and rove beetles (Staphylinidae) provide important ecosystem functions in forests (Symondson et al., 2002; Nichols et al., 2008). The majority of dung beetle species is linked to open and semi-open habitats (Buse et al., 2018) and around half of Central European species are currently red-listed (Buse et al., 2015). Hence, dung-inhabiting beetles are commonly used bioindicators (Bohac, 1999; Spector, 2006). Most species of Aphodiinae (Scarabaeidae) feed and develop directly in the dung pile, while most of the Geotrupidae and Scarabeinae (Scarabaeidae) relocate dung into their underground nests to provision their offspring (Nichols et al., 2008; Noriega et al., 2021). Via these activities, they contribute to enhanced nutrient cycling, secondary seed dispersal or parasite and fly suppression (Nichols et al., 2008; Maldonado et al., 2019; Milotić et al., 2019). The species-specific contribution to dung removal, strongly depends on species ecological and morphological traits, such as nesting strategy, foraging behaviour and body size (Milotić et al., 2019; de Castro-Arrazola et al., 2020; Tonelli et al., 2020). Rove beetles are often the most numerous dung-inhabiting insects (Hanski & Hammond, 1986). Dung-associated rove beetles are mostly predators (and parasitoids) feeding on other dung-inhabiting insects, which makes them important biological control agents of e.g., larvae of dung breeding pest flies (Maus et al., 1998; Cabrera Walsh & Chani Posse, 2003). For instance, the large rove beetle species *Emus hirtus*, is a major predator in dung of various herbivores and preys on dung beetles in their galleries (Biel et al., 2014). A minority of rove beetle species are phytosaprophagous-coprotophagous (Freude, 2009). The maintenance of dung-inhabiting beetle functional diversity has hence recently

100 become a conservation goal beyond the protection of taxonomic diversity (Barragán et al., 2011; Milotić et al., 2019). We applied experimental coppicing and topsoil removal to test if taxonomic and functional diversity of dung-inhabiting beetle communities can be promoted by forest opening and topsoil removal. Furthermore, we discussed the effects of experimental treatment on red-listed species. Methods Study area and experimental design Our study was conducted near the city of Bad Windsheim in north-western Bavaria, Germany (49°32' N 10°23' E, around 350 m asl). In this area, the mean annual temperature was 9.2°C and the mean annual precipitation was 593 mm between 1991 and 2020 (station 'Kaubenheim', www.am.rlp.de). Forest stands in the study area are dominated by sessile and common oaks *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L., with lower percentages of beech *Fagus sylvatica* L., Scots pine *Pinus sylvestris* L. and spruce *Picea abies* (L.) H. Karst., as well as a high variety of around 60 other tree and shrub species. Beside high-stem forests, the study area is partly managed as coppice with standards, thus promoting sun-exposed forest structures and *Q. petraea*. Forests are inhabited by wild ungulates (roe deer, wild boar) while the sampling area is embedded in a landscape with long grazing tradition of moving herds of sheep. The earliest signs of grazing in the area date back to 1365 (Schultheiß, 1963). Coppicing in the above-described forests was applied in three randomized blocks of around 1.5 ha size each around Bad Windsheim in January 2019. Within each of the blocks, 10 cm of topsoil was removed on three patches of 20 × 20 m in size. Topsoil removal was performed by means of an excavator during daylight for several days in February 2019. The same plots were replicated in the coppiced area

101 nearby without topsoil removal and in adjacent forest (coppice with standards after 20 years without logging) serving as control, as it is the original forest, where coppicing and topsoil removal were applied. In total, we applied 27 plots (Fig. 1). The mean distance between plots was 640 m overall (60 m within blocks). On each plot, we exposed temperature loggers (model EL-USB-1, Easylog) from the beginning of April to the end of August 2020 and recorded the ground surface temperature every hour. We took one hemispherical photograph (Sigma EX DC 4.5 mm lens) in the middle of each plot and one in each corner in July 2020, resulting in five photographs per plot. These photographs were processed by means of the software HemiView (Version 2.1, Delta-T Devices) to yield the global site factor as a measure of solar radiation for each plot (Rich et al., 1993). Total vegetation cover was assessed based on the sum of cover in moss, herb and shrub layer, surveyed on a 100 m² on each plot.

102 Figure 1 Experimental design to investigate the effects of coppicing and topsoil removal on communities of forest-dwelling dung beetles. Three experimental blocks were distributed to the forestry district of Bad Windsheim, where each experimental block contains three untreated forest plots, three coppices and three coppices with additional topsoil removal. The inset shows the baited pitfall trap used in our study. Source of map: Bing maps via openmaps.

103 Beetle sampling and ecological traits In each of 27 plots, one dung-baited trap (Lobo et al., 1988) was exposed for 1 week in three sampling campaigns, i.e., May, July and October in 2020, to cost-effectively cover the seasonal variability in the beetle community (Sladeczek et al., 2013). A metal wire mesh (19 mm) carried the dung bait and was placed on the top of the 5 L bucket sunk in the soil with the upper edge levelled up to the soil surface. Traps were baited with homogenized fresh cattle *Bos primigenius* f. *taurus* (Linnaeus, 1758) dung collected from local cattle herds nearby, which were not treated with anthelmintics for at least 4 months. The size of the baits was standardized to 400 g. Baits were stored frozen prior to their exposition to avoid prior decomposition and thawed before use. All traps were filled with a saturated salt solution with detergent to preserve trapped specimens. In all sampling campaigns, traps were exposed for 1 week and collected from the field afterwards. All trapped beetles of the families Scarabaeidae, Geotrupidae and Staphylinidae were identified to the species level. Taxonomy follows Löbl and Löbl (2015, 2016). We extended published information on morphological and ecological traits of dung beetles and rove beetles, which represent the body size, general lifestyle and reproductive characteristics of each species, based on Buse et al. (2018), Freude (2009), Assing and Schülke (2012), Meineke et al. (2017) and Lipkow (2011). For complete list of traits, see Tables S1 and S2. Data analysis All statistical analyses were carried out in R version 4.0.2 (www.r-project.org). Prior to statistical analysis, all samples were accumulated to the plot level. First, we compared ground surface temperatures, global site factor, and vegetation coverage across treatments. Therefore, we modelled the mean hourly ground surface temperatures in all plots by generalized additive models with gaussian error

104 distribution. We included the daytime within the respective treatment as smooth term, the Julian date as linear predictor and block and plot identity as random effect to control for repeated measurements. Global site factor and total vegetation cover were compared between treatments using linear mixed models for gauss-distributed data provided by the 'lme4' r-package (Bates et al., 2015). The treatment (coppice/topsoil-removed/forest) was selected as response variable and the experimental block and plot was added as a random effect to account for the nested study design (Fig. 1). We analysed species alpha diversity by comparing the mean number of species collected in managed and unmanaged plots by using generalized linear mixed models for poisson-distributed data (Bolker et al., 2009). We selected the number of species as response variables and added the treatment as predictor. Additionally, we added the experimental block as a random effect. Pairwise comparisons between treatments in all models were conducted by means of multiple comparisons for parametric models with simultaneous adjustment of p-values based on the single-step method, provided by the function 'glht' from r-package 'multcomp' (Hothorn et al., 2008). This model was repeated for the number of species of relocating dung beetle species (all species of the genus *Onthophagus* Latreille, 1802, *Anoplotrupes stercorosus* (Scriba, 1791), *Colobopterus erraticus* (Linnaeus, 1758) and *Sisyphus schaefferi* (Linnaeus, 1758)) and dwellers (i.e., all others) (Buse et al., 2018). To reveal single species which respond by changes in their abundance to the respective treatments, we repeated the poisson-linear mixed model for the abundance of each species separately as response variable. We selected the treatment as predictor, the experimental block as random effect and added an observation-specific random effect to account for possible poisson- overdispersion (Elston et al., 2001). We estimated the degree of correlation of the model for alpha diversity residuals with geographic coordinates by means of spline

105 correlograms (Bjørnstad & Falck, 2001), provided by the r-package 'ncf' to detect possible spatial autocorrelations. Based on 1000 bootstrap iterations, we did not detect any spatial dependency in our model outputs (Fig. S1). We selected the distribution of functional traits in the functional space as a measure for functional diversity of dung beetle and rove beetle assemblages. Therefore, we used the abundance-weighted mean pairwise distances between co- occurring species in a functional space (Webb et al., 2008). Gower distances were computed using the function 'daisy' in the r-package 'cluster' (Gower, 1971). However, the observed functional diversity can be correlated to the number of species in a local community. Thus, we used null models that standardize the observed functional diversity across multiple sampling locations to the diversity expected when species are randomly selected from a regional species pool (Gotelli, 2000). The regional species pool of the present study was defined as all species recorded within our plots. Resulting standardized functional diversity values ≥ 0 indicate higher diversity per number of species than expected by chance and vice versa (Pausas & Verdú, 2010). Standardized functional diversity was modelled with the same model term as alpha diversity, but with a gaussian error-distribution. To analyse the effects of our experimental treatments on species communities, we used permutational multivariate analysis of variance (Legendre & Anderson, 1999), provided by the 'vegan' r-package (Oksanen et al., 2020). Here, Bray-Curtis distances were used to derive the associated resemblance matrices. Community composition was visualized using non-metric multidimensional scaling (square root transformation, Wisconsin double standardization; Minchin, 1987). P- values were adjusted using Bonferroni correction for multiple testing due to pairwise comparisons among treatments. In order to compare gamma-diversity among treatments, we used the analytical framework published by Chao et al. (2014), which is implemented in the

106 r-package 'iNEXT' (Hsieh et al., 2016). Here, species accumulation curves with confidence bands based on bootstrap replicates allow the comparisons of observed gamma diversity and sample coverage standardized by sampling effort. Pairwise dissimilarities within treatments were subjected to a multivariate homogeneity of group dispersions analysis (Anderson et al., 2006), which was calculated by means of the function 'betadisper' in the 'vegan' r-package (Oksanen et al., 2018). This analysis tests whether the average distance to the centroid of a given treatment (β -dispersion), differs between treatments. High β -dispersion indicates heterogeneous communities, while low β -dispersion indicates homogenous communities. Results In total, we recorded 49 448 specimens belonging to 28 species of dung beetles (19 species of Scarabaeidae: Aphodiinae, eight species of Scarabaeidae: Scarabaeinae, one species of Geotrupidae), and 7573 specimens belonging to 99 species of rove beetles (Staphylinidae). See Table S3 for the complete list of species. Sample coverage analysis revealed high sample completeness for both groups around 90% (Fig. S2). The number of species per plot (alpha-diversity) did not differ among treatments, as indicated by generalized linear mixed models (Fig. S3, Table S4) and rarefaction-extrapolation curves, respectively (Fig. 2). However, the total number of species (gamma-diversity) of dung beetles in coppice was higher than that in forest (Fig. 2). The mean number of relocating and dwelling dung beetles did not differ among treatments (Table S4). Additionally, the highest temperature fluctuations were measured in topsoil-removed plots (8–30 °C), lesser in coppice (9–28 °C) and the lowest in forest (12–24 °C; Fig. 3a). Topsoil-removed plots received the highest amount of solar radiation, followed by coppice and forest (Fig. 3b, Table S5). Vegetation cover was significantly higher in coppice than in topsoil-removed plots (Fig. 3c, Table S6).

107 Figure 2 Plot-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the sample size taken) of (a) dung beetles and (b) rove beetles sampled in baited pitfall traps on topsoil-removed plots, coppices and forest plots. Transparent shading indicates 95% confidence intervals based on 200 bootstrap replicates (see Fig. S2 for sample coverage).

108 Figure 3 (a) Mean hourly ground surface temperatures in study treatments. Temperature loggers (model EL-USB-1, Easylog) from the beginning of April to the end of August 2020 and recorded the ground surface temperature every hour, (b) global site factor, indicating the amount of solar radiation, (c) total vegetation cover based on the sum of cover in moss, herb and shrub layer on a 100 m² plot. Uppercase letters indicate statistically significant differences (see Tables S5 and S6 for statistical details).

109 Five dung beetle species, namely, *Euorodalus paracoenosus* (Balthasar & Hrubant, 1960), *Melinopterus prodromus* (Brahm, 1790), *Onthophagus fracticornis* (Preysslser, 1790), *Onthophagus ovatus* (Linnaeus, 1767), *S. schaefferi* and four rove beetle species, *Anotylus tetracariniatus* (Block, 1799), *Eurodotina inquinula* (Gravenhorst, 1802), *Atheta longicornis* (Gravenhorst, 1802), *Tinotus morion* (Gravenhorst, 1802), were significantly more abundant in coppices. One dung beetle (*E. paracoenosus*) and two rove beetle species (*Anotylus inustus* (Gravenhorst, 1806), *Aleochara curtula* (Goeze, 1777)) were significantly more abundant in topsoil-removed plots (Figs S4 and S5, Table S7). Also, several species were significantly more abundant in forest, while rarely present in coppiced and topsoil- removed plots, including *Anoplotrupes stercorosus*, *Limarus maculatus* (Sturm, 1800), *Volinus sticticus* (Panzer, 1798), *Acrolocha amabilis* (Heer, 1841), *Omalium rivulare* (Paykull, 1789), *Bisnius fimetarius* (Gravenhorst, 1802), *Platydracus chalcocephalus* (Fabricius, 1801), *Tachinus humeralis* Gravenhorst, 1802 and *Oxypoda acuminata* (Stephens, 1832). Functional diversity of dung beetles was highest in forest, lower in topsoil- removed plots, and coppice hosted the functionally least diverse community (Fig. 4a). Functional diversity of rove beetles was increased by both, coppicing and topsoil removal, compared to forest control (Fig. 4b, Table S8).

110 Figure 4 Functional diversity, measured as standardized mean pairwise distances between co- occurring species in the functional space, of (a) dung beetles and (b) rove beetles sampled in baited pitfall traps on topsoil-removed plots, coppices and forest plots. Uppercase letters indicate statistically significant differences.

111 Communities of dung beetles found in coppice and topsoil-removed plots were similar but differed from communities found in forest (Fig. 5a, Table S9). Communities of rove beetles differed among all three experimental treatments (Fig. 5b, Table S9). Beta-diversity of dung beetles did not differ between any pair of treatments (Table S10). However, beta-diversity of rove beetles was lower in forest compared to coppice (Table S10).

112 Figure 5 Non-metric multidimensional scaling of species (black dots) of (a) dung beetles and (b) rove beetles from baited pitfall traps in topsoil-removed plots, coppice and forest plots (symbols). Polygons depict minimum convex hulls encompassing all plots of a respective treatment to indicate beta-dispersion.

113 Discussion The total number of dung beetle species was higher in coppice and topsoil-removed plots compared to forest control plots. However, the mean number of dung and rove beetle species per plot did not statistically differ among treatments. Functional diversity of rove beetles was increased by coppicing and topsoil removal, while dung beetles had highest functional diversity in forest, followed by topsoil-removed and coppice, respectively. Species communities of rove beetles differ in all pairwise comparisons and their beta-diversity were higher in coppices compared to untreated forest control plots. Topsoil removal can eliminate nitrogen and exposes large patches of bare soil (Jentsch et al., 2009). As the bare ground usually absorbs more heat, the surface gets warmer and drier than on sites with forest litter (Sayer, 2006). Warmer, drier and sun-exposed patches inside a forest matrix might enable the co-existence of open habitat and forest species on small spatial scales (Warren & Büttner, 2008). This is confirmed by our temperature data (Fig. 3a), revealing large differences in temperature amplitudes among our treatments, with the greatest differences in topsoil-removed plots and the lowest in forest. After topsoil removal, biological communities usually tend to shift towards less nutrient demanding, xero/thermo/heliophilic species or species of initial succession stages (Jentsch et al., 2009; Kiehl et al., 2010; Tropek et al., 2017; Volf et al., 2018). In our study, dung beetles of conservation concern, i.e., *E. paracoenosus* and *S. schaefferi* (Fig. S4) were predominantly caught in coppices and topsoil-removed plots (Table S3). *Onthophagus illyricus* (Scopoli, 1763) and *Onthophagus medius* (Kugelann, 1792), both are species of conservation concern, were exclusively found on managed plots. Also, we found significantly higher abundances of *E. paracoenosus* and *Anotylus inustus* on topsoil-removed plots than in coppiced and forest plots. Both species prefer warm habitats (Assing & Schülke, 2012; Buse et al., 2018) and likely

114 benefitted from warmer microclimate in topsoil-removed plots. Also, high, yet not significant, abundances of the ball-rolling dung beetle, *S. schaefferi*, were found in topsoil-removed plots. Patches of bare soil and low vegetation cover are critical for survival of many threatened organisms including plants (Česonienė et al., 2019), bees (Heneberg et al., 2016), and spiders (Krause et al., 2011), as well as ground beetles (Volf et al., 2018; Růžicková & Hykel, 2019). Our results indicated that bare soil, created by topsoil removal, is important also to some dung-inhabiting beetles. Hence, measures ensuring the presence of insolated patches of bare soil would benefit a wide array of specialized organisms and should be considered as a conservation measure for sustainable forest management (Borchard et al., 2014; Buckley, 2020). For practical applications further studies are needed to evaluate different patch sizes. Here, we show that already small patches of 400 m² are sufficient to support species of conservation concern. Beta dispersion analyses revealed larger turnover of rove beetle species within coppices (Table S10) compared to forest control plots, i.e., coppicing seems to create largely heterogeneous habitat conditions for rove beetles. The more heterogeneous habitat could be created by the simultaneous presence of legacies from the original forest, such as solitary standing trees, and the exposition of bare soil e.g., due to logging operations. This assumption is supported by higher beta-diversity in coppices, observed for plants (Kopecký et al., 2013; Bartha et al., 2020), birds (Battisti & Fanelli, 2011; Mentil et al., 2018), butterflies, amphibians, reptiles and small mammals (Buckley, 2020). More heterogeneous habitats, i.e., more niches, in coppice and topsoil-removed plots may also support a higher functional diversity of rove beetles (Fig. 4b). Untreated forest plots hosted dung beetle communities with typical forest species, such as the relocating species *Anoplotrupes stercorosus*, *Onthophagus verticicornis* (Laicharting, 1781), *O. coenobita* (Herbst, 1783) and the dung-

115 dwelling species *Acrossus depressus* (Kugelann, 1792), *Limarus maculatus* and *Volinus sticticus* (Buse et al., 2018). The dung-relocating (tunnelling) beetles are particularly important for dung removal in forests (Buse & Entling, 2020). This might also be reflected by higher functional diversity of dung beetles in forests, compared to coppice or topsoil-removed plots (Fig. 4a). Here, the lack of very large relocators in coppice and topsoil-removed plots could contribute to decreased functional diversity. However, an additional topsoil removal might promote higher abundances of other functionally distinct species, such as *S. schaefferi*, the only roller in our study. Recommendations for management Coppicing and topsoil removal had distinct effects on species communities of dung beetles and rove beetles. The effects of additional topsoil removal on the taxonomic diversity of dung and rove beetle communities were relatively small, compared to the effects of coppicing alone. However, additional topsoil removal buffered the slightly negative effects of coppicing on the functional diversity of dung beetles (Fig. 4a). Coppices showed significantly higher abundances of species of high conservation value, such as *E. paracoenosus* and marginally significant also *S. schaefferi*. Those species, together with other protected or rare invertebrates, birds and plants related to coppices (Benes et al., 2006; Spitzer et al., 2008; Buckley, 2020), justify continuous coppicing. By contrast, the abandonment of coppicing or coppice conversion to high forest might lead to local disappearance of light-demanding organisms (Kopecký et al., 2013; Buckley, 2020). Shade-tolerant species would remain largely unaffected since their required habitat remains available in currently most preferred closed-canopy high-stand forests (Buckley, 2020). However, the benefits of topsoil removal should be carefully weighed against its potentially high costs. Other measures creating bare soil patches, such as

116 prescribed burning, might be a suitable substitute for topsoil removal to create patches of bare soil. We presented the short-term biological response, while topsoil removal might result in a delayed succession of the respective plots, which may maintain open forest for a longer-time span. Conclusions Dung and rove beetles contribute to nutrient cycling and provide important ecosystem services in forests, such as dung removal and pest control. However, numerous species, including red-listed species, depend on open patches within a forest matrix. Our results demonstrate that taxonomic and functional diversity of those species can be promoted by coppicing, and additional topsoil removal. A mosaic of coppice and bare-soil-rich patches can hence promote landscape-level gamma diversity of dung and rove beetles within forests. Acknowledgements We thank Elisa Stengel, Lisa Rauscher and Heinz Bußler for their support during field work. Furthermore, we would like to thank the responsible local conservation authorities, namely, Angelika Bader, Claus Rammler and Michael Sauer, for supporting the establishment of the experimental treatments in this study. Finally, we would like to thank Lukáš Čížek for his insightful comments on an earlier version of the manuscript.

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Appendix S1. Supporting information Figure S1: Spline correlogram of the number of collected dung beetle species. The figure indicates the lack of spatial dependencies in the model residuals (black line in the centre of grey confidence shading). Table S1: Dung beetle species' traits. Size = mean body size [mm], repr = reproduction type, larva = larval feeding, imago = adult feeding, spec = dung specialization of adult (sum of dung types of used animals), activ = active months per year, RWL = relative wing length (wing to elytron length ratio), alt_m = altitude – montane, alt_a = altitude alpine, alt_l = altitude lowland, D = dweller, R = relocater, NA = not known, C = coprophagous, PS-C = phytosaprophagous- coprophagous, PS = phytosaprophagous, S = saprophagous. species size repr larva imago spec activ RWL alt_m alt_a alt_l *Acrossus depressus* 7.5 D C C 8 7 2 1 0 0 *Acrossus rufipes* 12 D C C 9 9 2.1 1 1 1 *Agrilus ater* 5.3 D C C 7 7 2.3 1 1 1 *Bodilopsis rufa* 6.3 D C C 8 7 2.2 1 1 1

130 species size repr larva imago spec activ RWL alt_m alt_a alt_l Anoplotrupes stercorosus 16 R C C 7 10 1.8 1 1 1 Aphodius pedellus 6.5 D PS-C C 8 10 2.2 1 1 1 Calamosternus granarius 5 D PS-C PS-C 9 11 1.9 1 0 1 Chilo thorax distinctus 5 NA PS C 8 12 2.1 1 0 1 Colobopterus erraticus 6 R C C 8 9 2.3 1 1 1 Esymus pusillus 4 D C C 7 7 2.2 1 1 1 Euorodalus paracoenosus 4.5 D NA C 5 6 1.8 1 0 1 Limarus maculatus 5 D C C 8 7 2 1 0 1 Melinopterus prodromus 6.3 NA S C 9 12 2.2 1 1 1 Melinopterus sphacelatus 5 NA S C 8 12 2.3 1 1 1 Nimbus contaminatus 6.3 D S C 9 9 2.1 1 0 1 Onthophagus coenobita 8 R C C 8 8 3.1 1 0 1 Onthophagus fracticornis 8.5 R C C 8 12 2.2 1 1 1 Onthophagus illyricus 8.5 R C C 5 6 2.1 1 0 1 Onthophagus medius 11 R C C 3 5 3 1 0 1 Onthophagus ovatus 5 R C C 8 12 2.6 1 1 1 Onthophagus similis 5.5 R C C 9 8 2.9 1 1 1 Onthophagus verticicornis 8 R C C 8 6 2.1 1 0 1

131 species size repr larva imago spec activ RWL alt_m alt_a alt_l Otophorus haemorrhoidalis 4.5 D C C 8 9 1.9 1 1 1 Parammoecius corvinus 3.8 D NA C 6 11 2.3 1 1 1 Planolinus fasciatus 4.3 D C C 7 12 2.5 1 0 1 Sisyphus schaefferi 10 R C C 7 7 2.5 1 0 1 Volinus sticticus 4.8 D NA C 7 10 2.1 1 1 1

132 Table S2: Rove beetle species' traits. Size = mean size [mm], feeding mode = feeding habitat, R = rotting material, G = ground, CR = carnivore, P = parasite, PS- C = phytosaprophagous-coprophagous. species size feeding mode feeding Acrolocha amabilis 2.25 R CR Acrolocha pliginskii 2.65 R CR Acrolocha sulcula 2.65 R CR Acrotona benicki 2 R CR Acrotona muscorum 2.05 R CR Acrotona parvula 2.15 R CR Aleochara bipustulata 4 R P Aleochara curtula 6 R P Aleochara intricata 4.25 R P Aleochara lanuginosa 4.25 R P Amischa nigrofusca 2.25 G CR Anotylus hamatus 2 R PS-C Anotylus inustus 3.7 R PS-C Anotylus mutator 3.9 R PS-C Anotylus sculpturatus 3.9 R PS-C Anotylus tetracarinaratus 1.95 R PS-C Anthobium unicolor 3.25 G CR Astenus gracilis 3.25 G CR Atheta cadaverina 2.9 R CR Atheta cauta 2.1 R CR Atheta cinnamoptera 2.65 R CR Atheta crassicornis 3.1 R CR Atheta episcopalis 3.25 R CR Atheta fimorum 2.3 R CR Atheta fungicola 3.1 R CR Atheta fungivora 2.85 R CR Atheta gagatina 2.4 R CR

133 species size feeding mode feeding Atheta indubia 2.1 R CR Atheta inquinula 1.15 R CR Atheta intermedia 3.15 R CR Atheta laevana 2.55 R CR Atheta laticollis 2.65 R CR Atheta liliputana 1.75 R CR Atheta longicornis 3.25 R CR Atheta marcida 3.25 R CR Atheta nigripes 2.7 R CR Atheta oblita 2.2 R CR Atheta puberula 2.3 R CR Atheta putrida 3.2 R CR Atheta ravilla 2.7 R CR Atheta sodalis 2.75 R CR Atheta sordidula 1.5 R CR Atheta triangulum 3.55 R CR Autalia longicornis 2.9 R CR Autalia rivularis 1.9 R CR Bisnius fimetarius 6.75 R CR Dinaraea angustula 3.35 G CR Drusilla canaliculata 4.9 G CR Gabrius piliger 4.5 R CR Gabrius splendidulus 5 G CR Gyrohypnus fracticornis 7.5 R CR Ilyobates nigricollis 5.75 G CR Ischnosoma longicorne 5 G CR Leptacinus sulcifrons 4.25 R CR Lesteva longoelytrata 4 G CR Liogluta alpestris 3.75 R CR Liogluta granigera 3.9 R CR Nehemitropia lividipennis 3.25 R CR

134 species size feeding mode feeding Ocalea badia 3.85 G CR Ocy pus nitens 16 R CR Olophrum assimile 4.25 G CR Omalium rivulare 3.75 R CR Ontholestes murinus 12.5 R CR Oxypoda acuminata 5 R CR Oxypoda brevicornis 2.85 G CR Oxypoda opaca 4 R CR Oxypoda vittata 4.25 G CR Oxytelus laqueatus 4.4 R PS-C Paederus littoralis 8 G CR Pella cognata 5.25 G CR Philonthus addendus 10.75 R CR Philonthus decorus 12 R CR Philonthus intermedius 9.5 R CR Philonthus laminatus 9 R CR Philonthus politus 11.75 R CR Philonthus sanguinolentus 7.5 R CR Philonthus succicola 12 R CR Philonthus tenuicornis 12.5 R CR Philonthus varians 6.5 R CR Phloeocharis subtilissima 1.75 G CR Platydacus chalcoccephalus 16 R CR Platystethus arenarius 3.9 R PS-C Platystethus nitens 2.85 R PS-C Proteinus ovalis 2 R CR Quedius cinctus 8 R CR Quedius curtippennis 12.5 R CR Quedius invreae 9.5 R CR Quedius lateralis 12.5 R CR Quedius picipes 9.5 R CR

135 species size feeding mode feeding Rugilus orbiculatus 4.5 R CR Staphylinus erythropterus 16 R CR Stenus ochropus 3.25 G CR Tachinus humeralis 7.5 R CR Tachinus rufipes 5.75 R CR Tachyporus atriceps 2.65 R CR Tachyporus hypnorum 3.5 R CR Tachyporus nitidulus 2.5 R CR Tasgius winkleri 16.5 R CR Tinotus morion 2.25 R P

136 Table S3: List of species and specimens recorded respectively in each treatment. Family Species Topsoil removed Coppice Forest Geotrupidae Anoplotrupes stercorosus (Scriba, 1791) 6 3 33 Scarabaeidae Acrossus depressus (Kugelann, 1792) 7 6 26 Acrossus rufipes (Linné, 1758) 1 1 Agrilinus ater (DeGeer, 1774) 3 2 Aphodius pedellus (DeGeer, 1774) 2 4 Bodilopsis rufa (Moll, 1782) 9 5 7 Calamosternus granarius (Linné, 1767) 7 31 43 Colobopterus erraticus (Linné, 1758) 5 Esymus pusillus (Herbst, 1789) 14 7 1 Euorodalus paracoenosus Balthasar & Hrubant, 1960 381 156 9 Chilo thorax distinctus (O. F. Müller, 1776) 21 1 Limarus maculatus (Sturm, 1800) 14 18 243 Melinopterus prodromus (Brahm, 1790) 360 211 92 Melinopterus sphacelatus (Panzer, 1798) 1 Nimbus contaminatus (Herbst, 1783) 1 1

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MATCHING BLOCK 203/238

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Onthophagus coenobita (Herbst, 1783) 251 294 462 Onthophagus fracticornis (Preyssler, 1790) 201 215 46 Onthophagus illyricus (Scopoli, 1763) 3 2 Onthophagus medius (Kugelann, 1792) 1 Onthophagus ovatus (Linné, 1758) 5510 3440 281 Onthophagus similis (Scriba, 1790) 1 Onthophagus verticicornis (Laicharting, 1781) 8022 10506 16356

Otophorus haemorrhoidalis (Linné, 1758) 1 1 Oxyomus sylvestris (Scopoli, 1763) 2 Parammoecius corvinus (Erichson, 1848) 1 Planolinus fasciatus (A. G. Olivier, 1789) 2 3 2 Sisyphus schaefferi (Linné, 1758) 106 62 3

137 Family Species Topsoil removed Coppice Forest *Volinus sticticus* (Panzer, 1798) 176 82 1684 *Staphylinidae* *Acrolocha amabilis* (Heer, 1841) 3 15 130 *Acrolocha pliginskii* (Bernhauer, 1912) 23 9 5 *Acrolocha sulcula* (Stephens, 1834) 13 12 5 *Acrotona benicki* (Allen, 1940) 28 6 0 *Acrotona muscorum* (C. N. F. Brisout de Barneville, 1860) 1 7 1 *Acrotona parvula* (Mannerheim, 1830) 12 35 35 *Aleochara bipustulata* (Linné, 1760) 9 0 0 *Aleochara curtula* (Goeze, 1777) 49 13 12 *Aleochara intricata* Mannerheim, 1830 21 18 12 *Aleochara lanuginosa* Gravenhorst, 1802 0 2 1 *Amischa nigrofusca* (Stephens, 1832) 1 0 0 *Anotylus hamatus* (Fairmaire & Laboulbène, 1856) 18 26 0 *Anotylus inustus* (Gravenhorst, 1806) 253 109 93 *Anotylus mutator* (Lohse, 1963) 3 7 26 *Anotylus sculpturatus* (Gravenhorst, 1806) 249 253 409 *Anotylus tetracarlinatus* (Block, 1799) 16 17 14 *Anthobium unicolor* (Marsham, 1802) 0 2 0 *Astenus gracilis* (Paykull, 1789) 1 0 0 *Atheta cadaverina* (C. N. F. Brisout de Barneville, 1860) 0 2 2 *Atheta cauta* (Erichson, 1837) 1 0 0 *Atheta cinnamoptera* (C. G. Thomson, 1856) 0 0 3 *Atheta crassicornis* (Fabricius, 1792) 0 1 0 *Atheta episcopalis* Bernhauer, 1910 27 16 43 *Atheta fimorum* (C. N. F. Brisout de Barneville, 1860) 7 36 47 *Atheta fungicola* (C. G. Thomson, 1852) 0 0 1

138 Family Species Topsoil removed Coppice Forest *Atheta fungivora* (C. G. Thomson, 1867) 5 11 9 *Atheta gagatina* (Baudi di Selve, 1848) 0 4 34 *Atheta indubia* (Sharp, 1869) 1 0 0 *Atheta intermedia* (C. G. Thomson, 1852) 0 0 2 *Atheta laevana* (Mulsant & Rey, 1852) 2 6 42 *Atheta laticollis* (Stephens, 1832) 0 0 1 *Atheta liliputana* (C. N. F. Brisout de Barneville, 1860) 0 0 1 *Atheta longicornis* (Gravenhorst, 1802) 8 12 1 *Atheta marcida* (Erichson, 1837) 0 2 4 *Atheta nigripes* (C. G. Thomson, 1856) 4 7 1 *Atheta oblita* (Erichson, 1839) 1 0 1 *Atheta puberula* (Sharp, 1869) 0 3 0 *Atheta putrida* (Kraatz, 1856) 0 6 4 *Atheta ravilla* (Erichson, 1839) 0 0 3 *Atheta sodalis* (Erichson, 1837) 0 0 1 *Atheta sordidula* (Erichson, 1837) 1 2 1 *Atheta triangulum* (Kraatz, 1856) 0 0 1 *Autalia longicornis* Scheerpeltz, 1947 1 16 38 *Autalia rivularis* (Gravenhorst, 1802) 2 4 0 *Bisnius fimetarius* (Gravenhorst, 1802) 5 11 259 *Dinaraea angustula* (Gyllenhal, 1810) 1 0 0 *Drusilla canaliculata* (Fabricius, 1787) 2 0 0 *Eurodotina inquinula* (Gravenhorst, 1802) 16 15 1 *Gabrieus piliger* Mulsant & Rey, 1876 1 0 0 *Gabrieus splendidulus* (Gravenhorst, 1802) 0 0 1 *Gyrophypnus fracticornis* (O. Müller, 1776) 0 1 2 *Ilyobates nigricollis* (Paykull, 1800) 1 0 1 *Ischnosoma longicorne* (Mäklin, 1847) 0 0 1 *Leptacinus sulcifrons* (Stephens, 1833) 3 0 0

139 Family Species Topsoil removed Coppice Forest *Lesteva longoelytrata* (Goeze, 1777) 0 0 1 *Liogluta alpestris* (Heer, 1839) 6 1 0 *Liogluta granigera* (Kiesenwetter, 1850) 0 1 8 *Nehemitropia lividipennis* (Mannerheim, 1830) 2 0 1 *Ocalea badia* Erichson, 1837 0 0 2 *Ocyopus nitens* (Schränk, 1781) 5 4 3 *Olophrum assimile* (Paykull, 1800) 5 4 0 *Omalium rivulare* (Paykull, 1789) 27 27 338 *Ontholestes murinus* (Linné, 1758) 5 4 0 *Oxypoda acuminata* (Stephens, 1832) 275 299 1624 *Oxypoda brevicornis* (Stephens, 1832) 0 0 1 *Oxypoda opaca* (Gravenhorst, 1802) 1 1 17 *Oxypoda vittata* Märkel, 1842 0 0 1 *Oxytelus laqueatus* (Marsham, 1802) 2 3 3 *Paederus littoralis* Gravenhorst, 1802 1 0 0 *Pella cognata* (Märkel, 1842) 0 1 0 *Philonthus addendus* Sharp, 1867 1 4 7 *Philonthus decorus* (Gravenhorst, 1802) 0 1 3 *Philonthus intermedius* (Lacordaire, 1835) 1 1 1 *Philonthus laminatus* (Creutzer, 1799) 1 0 0 *Philonthus politus* (Linné, 1758) 0 1 0 *Philonthus sanguinolentus* (Gravenhorst, 1802) 1 0 0 *Philonthus succicola* C. G. Thomson, 1860 10 11 6 *Philonthus tenuicornis* Mulsant & Rey, 1853 0 1 2 *Philonthus varians* (Paykull, 1789) 12 17 0 *Phloeocharis subtilissima* Mannerheim, 1830 0 0 2 *Platydracus chalconcephalus* (Fabricius, 1801) 13 75 441 *Platystethus arenarius* (Geoffroy, 1785) 4 3 7

140 Family Species Topsoil removed Coppice Forest *Platystethus nitens* (C. R. Sahlberg, 1832) 1 0 0 *Proteinus ovalis* Stephens, 1834 24 90 178 *Quedius cinctus* (Paykull, 1790) 0 1 6 *Quedius curtippennis* Bernhauer, 1908 1 3 0 *Quedius invreae* Gridelli, 1924 1 0 1 *Quedius lateralis* (Gravenhorst, 1802) 0 0 55 *Quedius picipes* (Mannerheim, 1830) 1 1 1 *Rugilus orbiculatus* (Paykull, 1789) 1 1 0 *Staphylinus erythropterus* Linné, 1758 0 5 1 *Stenus ochropus* Kiesenwetter, 1858 0 0 1 *Tachinus humeralis* Gravenhorst, 1802 39 142 886 *Tachinus rufipes* (Linné, 1758) 3 1 0 *Tachyporus atriceps* Stephens, 1832 0 1 0 *Tachyporus hypnorum* (Fabricius, 1775) 3 1 1 *Tachyporus nitidulus* (Fabricius, 1781) 1 0 0 *Tasgius winkleri* (Bernhauer, 1906) 0 2 1 *Tinotus morion* (Gravenhorst, 1802) 16 75 6

141 Table S4: Results of multiple comparisons for parametric models with simultaneous adjustment of p-values for dung beetle species, dwellers, relocating beetles, and rove beetles species among treatments. Species group Comparison Estimate Std. error z-value p-value Dung beetles Coppice vs. Topsoil removed -0.137 0.135 -1.013 0.311 Forest vs. Topsoil removed -0.230 0.139 -1.653 0.098 Forest vs. Coppice -0.092 0.143 -0.644 0.519 Dwellers Coppice vs. Topsoil removed -0.170 0.185 -0.919 0.358 Forest vs. Topsoil removed -0.208 0.187 -1.112 0.266 Forest vs. Coppice -0.038 0.194 -0.194 0.846 Relocating beetles Coppice vs. Topsoil removed -0.099 0.199 -0.497 0.619 Forest vs. Topsoil removed -0.257 0.208 -1.234 0.217 Forest vs. Coppice -0.158 0.213 -0.741 0.459 Rove beetles Coppice vs. Topsoil removed 0.169 0.095 1.790 0.074 Forest vs. Topsoil removed 0.144 0.095 1.518 0.129 Forest vs. Coppice -0.025 0.091 -0.273 0.785

142 Table S5: Results of multiple comparisons for parametric models with simultaneous adjustment of p-values for the global site factor (univariate p values reported). Comparison Estimate Std. error z-value p-value Coppice vs. Topsoil removed -0.197 0.052 -3.812 >0.001 Forest vs. Topsoil removed -0.597 0.052 -11.534 >0.001 Forest vs. Coppice -0.400 0.052 -7.723 >0.001

Table S6: Results of multiple comparisons for parametric models with simultaneous adjustment of p-values for the total vegetation cover (univariate p values reported). Comparison Estimate Std. error z-value p-value Coppice vs. Topsoil removed 30.56 9.18 3.329 >0.001 Forest vs. Topsoil removed 16.67 9.18 1.816 0.069 Forest vs. Coppice -13.89 9.18 -1.513 -0.130

143 Figure S2. Observed sample coverage (solid lines) and extrapolated sample coverage (dotted lines, up to twice the sample size taken) of a) dung beetles and b) rove beetles sampled in baited pitfall traps on topsoil-removed plots, coppices, and forest plots. Transparent shading indicates 95% confidence intervals based on 200 bootstrap replicates.

144 Figure S3: Mean number of species of dung beetle and rove beetles species among treatments.

145 Figure S4: Response of abundances of single dung beetle species to topsoil removal, coppicing, and forest control. Uppercase letters indicate statistically significant differences.

146 Figure S5 (part I): Response of abundances of single rove beetle species to topsoil removal, coppicing, and forest control. Uppercase letters indicate statistically significant differences.

147 Figure S5 (part II): Response of abundances of single rove beetle species to topsoil removal, coppicing, and forest control. Uppercase letters indicate statistically significant differences.

148 Table S7: Results of multiple comparisons for parametric models with simultaneous adjustment of p-values for dung and rove beetle species among treatments. Family, species Comparison Estimate Std. Error z-value p-value Geotrupidae Anoplotrupes stercorosus Coppice vs. Topsoil removed -0.706 0.802 -0.881 0.379 Forest vs. Topsoil removed 1.689 0.578 2.922 0.003 Forest vs. Coppice 2.395 0.711 3.370 >0.001 Scarabaeidae Acrossus depressus Coppice vs. Topsoil removed -0.154 0.555 -0.278 0.781 Forest vs. Topsoil removed 1.312 0.425 3.087 0.002 Forest vs. Coppice 1.466 0.452 3.243 0.001 Euorodalus paracoenosus Coppice vs. Topsoil removed -0.824 0.246 -3.355 >0.001 Forest vs. Topsoil removed -3.692 0.425 -8.697 >0.001 Forest vs. Coppice -2.868 0.431 -6.659 >0.001 Limarus maculatus Coppice vs. Topsoil removed 0.243 0.446 0.546 0.585 Forest vs. Topsoil removed 2.909 0.387 7.523 >0.001 Forest vs. Coppice 2.666 0.364 7.316 >0.001 Melinopterus prodromus Coppice vs. Topsoil removed -0.309 0.431 -0.718 0.473 Forest vs. Topsoil removed -1.258 0.443 -2.841 0.004 Forest vs. Coppice -0.949 0.444 -2.137 0.033 Onthophagus coenobita Coppice vs. Topsoil removed 0.121 0.163 0.741 0.459 Forest vs. Topsoil removed 0.615 0.159 3.875 >0.001 Forest vs. Coppice 0.494 0.158 3.132 0.002 Onthophagus fracticornis Coppice vs. Topsoil removed 0.108 0.235 0.459 0.646 Forest vs. Topsoil removed -1.421 0.269 -5.278 >0.001 Forest vs. Coppice -1.529 0.268 -5.702 >0.001 Onthophagus ovatus Coppice vs. Topsoil removed -0.228 0.386 -0.590 0.555 Forest vs. Topsoil removed -3.668 0.459 -8.000 >0.001 Forest vs. Coppice -3.440 0.459 -7.496 >0.001

149 Family, species Comparison Estimate Std. Error z-value p-value Onthophagus verticicornis Coppice vs. Topsoil removed 0.304 0.187 1.627 0.104 Forest vs. Topsoil removed 0.722 0.187 3.866 >0.001 Forest vs. Coppice 0.418 0.187 2.239 0.025 Sisyphus schaefferi Coppice vs. Topsoil removed -0.384 0.330 -1.163 0.245 Forest vs. Topsoil removed -3.370 0.664 -5.075 >0.001 Forest vs. Coppice -2.986 0.668 -4.473 >0.001 Volinus sticticus Coppice vs. Topsoil removed -0.753 0.347 -2.172 0.030 Forest vs. Topsoil removed 2.181 0.324 6.725 >0.001 Forest vs. Coppice 2.934 0.337 8.703 >0.001 Staphylinidae Acrolocha amabilis Coppice vs. Topsoil removed 1.496 0.776 1.927 0.054 Forest vs. Topsoil removed 4.059 0.745 5.447 >0.001 Forest vs. Coppice 2.563 0.529 4.847 >0.001 Acrotona parvula Coppice vs. Topsoil removed 1.034 0.387 2.670 0.007 Forest vs. Topsoil removed 1.028 0.388 2.640 0.008 Forest vs. Coppice -0.007 0.313 -0.020 0.983 Aleochara curtula Coppice vs. Topsoil removed -1.365 0.455 -3.000 0.003 Forest vs. Topsoil removed -1.616 0.495 -3.262 0.001 Forest vs. Coppice -0.251 0.544 -0.461 0.645 Anotylus inustus Coppice vs. Topsoil removed -0.887 0.256 -3.465 >0.001 Forest vs. Topsoil removed -1.108 0.262 -4.227 >0.001 Forest vs. Coppice -0.221 0.272 -0.811 0.417 Anotylus mutator Coppice vs. Topsoil removed 0.772 0.932 0.828 0.408 Forest vs. Topsoil removed 2.428 0.870 2.791 0.005 Forest vs. Coppice 1.656 0.745 2.224 0.026 Anotylus sculpturatus Coppice vs. Topsoil removed -0.031 0.199 -0.156 0.876 Forest vs. Topsoil removed 0.436 0.195 2.235 0.025 Forest vs. Coppice 0.467 0.196 2.388 0.017 Anotylus tetracaratus Coppice vs. Topsoil removed 0.258 0.003 90.100 >0.001 Forest vs. Topsoil removed 0.116 0.003 40.600 >0.001

150 Family, species Comparison Estimate Std. Error z-value p-value Forest vs. Coppice -0.142 0.004 -35.000 >0.001 Atheta fimorum Coppice vs. Topsoil removed 1.632 0.473 3.455 >0.001 Forest vs. Topsoil removed 1.958 0.466 4.198 >0.001 Forest vs. Coppice 0.326 0.325 1.002 0.316 Atheta gagatina Coppice vs. Topsoil removed 23.251 0.003 6835.000 >0.001 Forest vs. Topsoil removed 25.515 0.003 7502.000 >0.001 Forest vs. Coppice 2.264 0.005 470.000 >0.001 Atheta laevana Coppice vs. Topsoil removed 1.099 0.808 1.359 0.174 Forest vs. Topsoil removed 3.045 0.717 4.249 >0.001 Forest vs. Coppice 1.946 0.432 4.503 >0.001 Atheta longicornis Coppice vs. Topsoil removed 0.424 0.567 0.749 0.454 Forest vs. Topsoil removed -2.086 1.115 -1.871 0.061 Forest vs. Coppice -2.510 1.097 -2.288 0.022 Autalia longicornis Coppice vs. Topsoil removed 2.800 1.111 2.520 0.012 Forest vs. Topsoil removed 3.632 1.095 3.317 >0.001 Forest vs. Coppice 0.832 0.499 1.669 0.095 Bisnius fimetarius Coppice vs. Topsoil removed 0.776 0.592 1.311 0.190 Forest vs. Topsoil removed 3.927 0.512 7.667 >0.001 Forest vs. Coppice 3.151 0.393 8.016 >0.001 Eurodotina inquinula Coppice vs. Topsoil removed 0.872 0.997 0.875 0.3816 Forest vs. Topsoil removed -2.434 1.410 -1.727 0.084 Forest vs. Coppice -3.307 1.431 -2.310 0.021 Omalium rivulare Coppice vs. Topsoil removed 0.024 0.416 0.057 0.954 Forest vs. Topsoil removed 2.662 0.371 7.176 >0.001 Forest vs. Coppice 2.638 0.368 7.173 >0.001 Oxypoda acuminata Coppice vs. Topsoil removed 0.010 0.291 0.036 0.971 Forest vs. Topsoil removed 1.714 0.285 6.022 >0.001 Forest vs. Coppice 1.704 0.284 5.988 >0.001

151 Family, species Comparison Estimate Std. Error z-value p-value Platydacus chalcocephalus Coppice vs. Topsoil removed 1.689 0.431 3.915 >0.001 Forest vs. Topsoil removed 3.707 0.420 8.834 >0.001 Forest vs. Coppice 2.018 0.322 6.271 >0.001 Proteinus ovalis Coppice vs. Topsoil removed 1.323 0.004 373.400 >0.001 Forest vs. Topsoil removed 2.085 0.004 588.000 >0.001 Forest vs. Coppice 0.762 0.005 151.900 >0.001 Tachinus humeralis Coppice vs. Topsoil removed 1.188 0.392 3.029 0.002 Forest vs. Topsoil removed 3.456 0.382 9.042 >0.001 Forest vs. Coppice 2.268 0.341 6.650 >0.001 Tinotus morion Coppice vs. Topsoil removed 1.394 0.555 2.512 0.012 Forest vs. Topsoil removed -0.978 0.687 -1.424 0.154 Forest vs. Coppice -2.372 0.646 -3.674 >0.001 Table S8: Results of as standardized mean pairwise distances in the functional space between treatments. Species group Comparison Estimate Std. error z-value p-value Dung beetles Coppice vs. Topsoil removed -0.263 0.124 -2.126 0.033 Forest vs. Topsoil removed 0.269 0.124 2.173 0.029 Forest vs. Coppice 0.532 0.124 4.299 >0.001 Rove beetles Coppice vs. Topsoil removed -0.090 0.146 -0.616 0.538 Forest vs. Topsoil removed -0.995 0.146 -6.794 >0.001 Forest vs. Coppice -0.904 0.146 -0.617 >0.001

152 Table S9: Results of permutational multivariate analysis of variance based on Bray- Curtis distance matrices. Species group Comparison R² F-value p-value Dung beetles Topsoil removed vs. Coppice 0.056 0.945 1.000 Topsoil removed vs. Forest 0.308 7.132 0.003 Coppice vs. Forest 0.249 5.306 0.012 Rove beetles Topsoil removed vs. Coppice 0.140 2.610 0.036 Topsoil removed vs. Forest 0.546 19.223 0.003 Coppice vs. Forest 0.408 11.021 0.003 Table S10: Results of multivariate homogeneity of dispersions between treatments. Species group Comparison Difference Lower Upper p adj. Dung beetles Coppice vs. Topsoil removed -0.052 -0.182 0.078 0.584 Forest vs. Topsoil removed -0.088 -0.217 0.042 0.231 Forest vs. Coppice -0.036 -0.165 0.094 0.774 Rove beetles Coppice vs. Topsoil removed 0.055 -0.017 0.126 0.162 Forest vs. Topsoil removed -0.017 -0.089 0.054 0.819 Forest vs. Coppice -0.072 -0.144 0.000 0.050

153 Chapter III

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Understanding the drivers of β -diversity improves conservation prioritization for Central European dung beetles

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156 Abstract

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The conversion and degradation of natural habitats has caused global declines in terrestrial insect diversity. Conserving insect diversity has therefore gained increasing attention in international conservation agendas. Dung beetles (Geotrupidae, Scarabaeidae) are diverse and abundant coprophagous insects who remove dung and enhance nutrient cycling. Today, half of Central European dung beetle species are threatened. While past research has concentrated on local (α - diversity) of dung beetles, the compositional differences between sites (β -diversity) have been largely neglected. However, maximizing the overall outcome of conservation measures requires a detailed understanding of the factors determining compositional differences between sites. We separated β -diversity of dung beetle communities, sampled across the Czech Republic, into independent components of spatial turnover and nestedness. We tested the relative importance of space, temperature, precipitation, elevation, season, grazing herbivore and antiparasitic treatment via multiple regressions for distance matrices to reveal which factors drive the β -diversity of dung beetle communities. Our results show that β -diversity of dung beetle communities is mostly driven by spatial distance, followed by similarly strong effects of season and mean temperature. Herbivore type and antiparasitic treatment had lesser influence than environment but can be influenced by conservation management. Nevertheless, antiparasitic treatment increased nestedness and resulted in an overall lower γ -diversity. Based on the principle of complementarity, we recommend – in order of decreasing importance – giving (1) conservation priority to the most distant sites, under (2) the largest differences in mean annual temperature, ensure (3) year-round grazing by (4) multiple herbivore species, and (5) avoid using antiparasitics. 157

Keywords Antiparasitics, Biodiversity protection, Coprophagous insects, Ivermectin, Multiple regression, Principle of complementarity

1. Introduction The conversion and degradation of natural habitats and land use change has been causing worldwide biodiversity decline (Newbold et al., 2015). Terrestrial insect abundance has declined by ~1 % a year since 1960 (van Klink et al., 2020). This decline is particularly strong in landscapes dominated by agriculture (Seibold et al., 2019). Maintaining species-rich insect communities has hence become a major goal in global nature conservation agendas (Samways et al., 2020). Declining species richness of local assemblages (α -diversity) threatens their functionality and the ecosystem services they provide (Verdú et al., 2020). Local α -diversity multiplies with compositional differences among sites (β -diversity) to the overall number of species (γ -diversity) in a region (Whittaker, 1960). There is growing evidence that the increasing land-use intensity and climate change reduce the β -diversity of biological communities (reviewed in Mori et al., 2018). β -diversity has thus attracted increasing attention in ecology and conservation biology (Socolar et al., 2016a). Systematic conservation planning utilizes β -diversity to maximize the outcome of conservation efforts via the “principle of complementarity” (Bush et al., 2016; Socolar et al., 2016a, Socolar et al., 2016). Here, the overall species number across heterogeneous landscapes (γ -diversity) is maximized by selecting sites that host complementary species assemblages (Moilanen et al., 2009). The principle of complementarity has been used in assessing the conservation priority of tropical forest reserves (Howard et al., 1998), reserve networks for various terrestrial and Mediterranean freshwater taxa (Kati et al.,

158 2004), boreal mammals (Wiersma and Urban, 2005), or for groundwater biodiversity protection (Michel et al., 2009). β -diversity can be separated into turnover and nestedness components (Baselga, 2010). Nestedness occurs when species-poor assemblages host subsets of species-rich ones (Wright et al., 1992). Nestedness mainly reflects the exclusion of species from local communities by environmental filtering (Gaston and Blackburn, 2000). By contrast, turnover implies species replacement due to environmental sorting or spatial and historical constraints (Qian et al., 2004). In conservation planning, it is important to distinguish between turnover and nestedness in order to maximize the overall γ -diversity by the protection of complementary communities, rather than nested species assemblages (Moilanen et al., 2009). In an extreme case, a species-poor site may host a completely different species assemblage than a species-rich one (turnover), which would encourage the conservation of the species-poor site to maximize γ -diversity. Vice versa, if the species-poor site only contains species that already occur in the species-rich site (nestedness), then priority should be given to the most species-rich site (Jacquemyn et al., 2007). Dung beetles (Geotrupidae, Scarabaeidae) are diverse, abundant, and often specialized coprophagous insects, making them widely used bioindicators (Nichols et al., 2008; Spector, 2006). Owing to their feeding and nesting behavior, dung beetles play a main role in dung removal and thus provide important ecosystem services, such as suppressing livestock parasites and enhancing nutrient cycling (Milotić et al., 2019; Nichols et al., 2008). Today, dung beetles are increasingly under threat by habitat loss (Roslin, 2001), land use changes (Frank et al., 2017b; Sánchez-Bayo and Wyckhuys, 2019; Tonelli et al., 2019), and the widespread use of antiparasitics (Ambrožová et al., 2021; Lumaret et al., 2012). Some antiparasitics, mainly macrocyclic lactones (e.g., ivermectin), are excreted in faeces in doses which are lethal or sublethal for dung beetle larvae up to several weeks post-treatment

159 (Jacobs and Scholtz, 2015). Nearly half of dung beetle species are currently threatened or locally extinct in Central Europe (Buse et al., 2015; Král and Bezděk, 2017). α -diversity of dung beetle assemblages decreases with elevation (Errouissi and Jay-Robert, 2019; Gebert et al., 2020), increases with temperature (Ferreira et al., 2019), increases with precipitation (Righi et al., 2018). Dung beetle α -diversity has a bimodal pattern across the season, peaking in spring and autumn (Palestrini et al., 1995). Preference for dung of certain herbivore is usually not species-specific but largely depends on habitat context (Barbero et al., 1999), e.g., species richness in sheep dung was higher than in cattle dung in Brazilian savanna (Correa et al., 2020), while cattle dung was preferred by Scarabaeinae in Italian open landscape and deer lumps by Aphodiinae in forest (Barbero et al., 1999). The use of certain antiparasitics disrupts dung beetle α -diversity (Verdú et al., 2018). Yet, the contribution of individual environmental variables in determining β -diversity of dung beetles remains unclear, thus hampering systematic conservation planning. We hypothesized that geographical and climatic variables (space, temperature, elevation, precipitation) will have greater effect on the dung beetle β -diversity than management (grazing herbivore, antiparasitic treatment, grazing season). We also expect that species turnover will play more important role than nestedness. Finally, we simulated which combination of herbivores and seasons would yield the highest γ -diversity across the study area.

160 **2. Methods**

2.1. Study area and beetle surveys We sampled 83 sites distributed in three regions across the Czech Republic, plus one site close to the border in Austria (Fig. 1). The study regions cover a large variability in temperature, precipitation, and elevation (Table 1, Fig. 1). Study sites were located on pastures grazed by horse (*Equus caballus* f. *caballus*), cattle (*Bos primigenius* f. *taurus*) and European bison (*Bison bonasus*, hereafter included in cattle), and sheep (*Ovis aries*). Study sites were grazed by animals that were either all treated by antiparasitics (macrocyclic lactones, praziquantel, benzimidazoles, pyrantel, closantel) at once, or all untreated. We sampled dung beetles (Coleoptera: Geotrupidae, Scarabaeidae) three times a year to cover seasonal changes in dung beetle communities (Sladecek et al., 2013). Surveys were conducted from 2018 to 2020 in spring (April – early June), summer (July – August), and autumn (September – October). In each sampling campaign, we sampled 10 dung pats from large herbivores (horse and cattle), and 20 dung pats from sheep (to account for their smaller dung pat sizes) per site, to obtain a representative sample of a local community. This procedure ensured a high sample completeness as confirmed by coverage-based rarefaction. Sampled dung pats were 1–5 days old, hosting the highest number of species (Sladecek et al., 2013). Beetles were floated out of the dung of large herbivores in a bucket with water or collected directly from sheep droppings. We also collected dung beetles found in the upper soil layer and large tunnellers (Geotrupidae) in visible tunnels under each pat. All collected individuals were identified to species level. Nomenclature follows Löbl and Löbl (2016) and conservation status follows the Czech Red List (Král and Bezděk, 2017). Collected specimens were aggregated from all sampled dung pats for each sampling date, site, and herbivore species to represent the local community at a

161 given site in each season for the following analyses (α -diversity). As the distribution of dung beetle species may be limited by their larval survival under variable environmental conditions (Halffter and Edmonds, 1982), we classified the recorded species according to their larval development as dwellers (most Aphodiinae who develop in the dung pat itself) and relocators (traditionally referred as rollers and tunnelers; Geotrupidae, Scarabaeinae and Colobopterus erraticus, whose larvae develop in underground nest provisioned by the parents). All specimen of the two species protected by the Czech law (Act No.114/1992 Sb.; Sisyphus schaefferi and Copris lunaris) were recorded in situ and released, therefore our study did not require ethical approval. Fig. 1. Study sites across the Czech Republic and one site at the border in Austria. The upper right inset depicts a principal components analysis including mean annual temperature, altitude, and total annual precipitation; bottom right inset indicates the position of the Czech Republic in Central Europe.

162 Table 1. Summary of environmental conditions and total number of samples obtained in the study regions. Region Mean annual temperature [°C] Mean annual precipitation [mm] Altitude [m a.s.l.] Number of observations Bohemian Forest 5.4 ± 0.5 1024 ± 53 861 ± 143 72 Central Bohemia 8.7 ± 0.2 514 ± 11 244 ± 36 48 South Moravia 8.9 ± 0.5 608 ± 26 280 ± 89 37

163 2.2. Data analysis Data analyses were performed using R 4.1.1. (R Core Team, 2021). Compositional dissimilarities of dung beetle communities (β -diversity) were modelled in dependence of environmental dissimilarities. Therefore, we calculated pairwise dissimilarities for beetle communities and environmental variables. Following Schmera et al. (2020), we separated the pairwise dissimilarities, measured as Sørensen pairwise dissimilarity, into components of turnover (i.e. relative complement of nestedness in β -diversity) and nestedness (i.e. intersection of nestedness and β -diversity) (Baselga, 2010). This procedure was performed for all species, relocators, dwellers, and red-listed species separately. We selected the spatial distance between sites, season, herbivore species, and antiparasitic treatment as predictor variables. Furthermore, we extracted the mean annual temperature and the total annual precipitation from the WorldClim database (Fick and Hijmans, 2017) and the altitude from a digital elevation model. Afterwards, we conducted a principal components analysis, provided by the R- function 'princomp', to select only non-co-linear environmental variables, i.e., temperature (Fig. 1), for further analyses (Venables and Ripley, 2002). Geographic coordinates were used to calculate spatial distances by means of great-circle distances between sites (Harrison et al., 1992). We used the Euclidean distance between the Julian dates within each year as seasonal dissimilarity, and the Euclidean distances between mean annual temperatures as temperature dissimilarities. Dissimilarities between herbivore species were calculated using their patristic distances derived from an ultrametric phylogenetic tree of mammals (Upham et al., 2019). Finally, we used Gower's distance between treated and not treated sites as the treatment dissimilarity (Gower, 1971). All resulting pair-wise dissimilarities among environmental variables were standardized to a range between 0 and 1 to yield comparable coefficients in subsequent statistical modelling.

164 Prior to statistical analyses, we confirmed sample completeness by coverage- based rarefaction-extrapolation curves (Appendix, Fig. A1). We used nonmetric multidimensional scaling based on Bray-Curtis distances to visualize dissimilarities in communities (Faith et al., 1987). Second, we tested the effect of environmental dissimilarity matrices on community dissimilarities using multiple regression on distance matrices (MRM) (Lichstein, 2007). Therefore, we selected community dissimilarity matrices as a response variable, and geographical distance, seasonal distance, temperature distance, treatment distance, and herbivore distances as explanatory matrices. The MRM was calculated using the function 'MRM' ('ecodist' package; Goslee and Urban, 2007). Despite that the use of MRM and regularized discriminant analysis (Friedman, 1989) for analyzing dissimilarity data in general is debated with mixed support (Anderson et al., 2011; Legendre et al., 2015), MRM offers a straightforward and unique chance to compare multiple distance-matrices without interposing any ordination procedure (Legendre and Fortin, 2010). Furthermore, the underlying permutation test uses a pseudo-t-test to assess significance, rather than using the regression coefficients directly (Legendre et al., 1994). We used incidence-based rarefaction/extrapolation, provided by the R- package 'iNEXT' to estimate γ -diversity of dung beetles in different categories (Fig. 2). Therefore, we estimated the total number of species per 50 sites sampled for each category (e.g., for each herbivore species within herbivores). Furthermore, we applied the conceptual framework provided by Schall et al. (2020) to link the complementary dung beetle assemblages among different seasons and herbivore types (Fig. 4). This approach allows estimation of the combination of different herbivores and different seasons for maximizing γ -diversity. Therefore, we varied the proportion of herbivores and respective seasons in steps of 5 % to obtain 219 hypothetical landscapes, each represented by 60 randomly drawn sites. We pooled

165 our data across all seasons on the site level, but kept years, seasons, herbivores, and treatment separately, resulting in a total of 158 observations. Afterwards, we repeated the procedure 1000 times for each of the 219 hypothetical landscapes and extracted the mean number of species, i.e., γ -diversity, for each landscape. To account for the slightly unbalanced representation of herbivores in the study regions, we adjusted the selection probability of each sample according to the region. Therefore, the selection probability within a region summed up to 1/3, i.e., the higher the number of potential samples in a region, the lower the selection probability. This approach allowed us to show the effects of landscape composition corrected for the effect of region. The effect of landscape composition on dung beetle γ -diversity was then modelled by generalized additive models (package 'mgcv'; Wood, 2011) with three factorial full tensor product spline smoothers (Wood, 2006). The response surfaces, i.e., dung beetle γ -diversity in dependence of herbivore type resp. season, were visualized by Ternary diagrams by means of the package 'Ternary' (Smith, 2017).

166 3. Results In total, we analyzed 82,699 specimens belonging to four species of Geotrupidae and 56 species of Scarabaeidae. Out of the 60 species, 26 are red-listed (Appendix, Table A1). The study regions were separated along a temperature and precipitation/altitude gradient (Fig. 1). The NMDS depicted the separation of dung beetle communities among regions (Fig. 2a), seasons (Fig. 2b), herbivores (Fig. 2c), and between treated and untreated sites (Fig. 2d). South Moravia had the highest estimated γ -diversity and Bohemian Forest the lowest (Fig. 2a). Spring and autumn communities greatly overlapped in species composition, while summer communities diverged (Fig. 2b). Spring yielded the highest estimated γ -diversity, while autumn the lowest (Fig. 2b). Communities from horse dung pats were the most different from those in cattle dung; sheep communities overlapped with both, but more with cattle. Sheep yielded the highest estimated γ -diversity, while cattle the lowest (Fig. 2c). Antiparasitic treatment separated communities with only a slight overlap between them, with treated sites yielding lower γ -diversity (Fig. 2d).

167 Fig. 2. Non-metric multidimensional scaling of dung beetle communities separated into a) study regions, b) seasons, c) herbivores, and d) sites treated and not treated by antiparasitics. Stress value = 0.2073449. Insets show species richness of 50 samples based on incidence-based rarefaction/extrapolation.

168 Multiple regression on distance matrices revealed an increase in overall β -diversity of all species with increasing dissimilarity in space, season, mean temperature, herbivore, and treatment (Fig. 3a). In most cases, increasing turnover component and decreasing nestedness were driving the overall β -diversity. β -diversity of red-listed species increased most with increasing dissimilarity in space and season (Fig. 3d). β -diversity of relocating beetles increased most with temperature, followed by space and season (Fig. 3g). β -diversity of dwellers increased most with season, space, and herbivore (Fig. 3j). Antiparasitic treatment slightly increased nestedness of all species, red-listed species and relocators (Fig. 3c, f, i).

169 Fig. 3. Regression coefficients of multiple regression on distance matrices are given for the significant predictors. Results are given for overall β -diversity, turnover, and nestedness component separately. Statistical details may be found in the Appendix, Table A2.

170 To reach the maximum γ -diversity, it is best to combine 30–50 % of spring, 40–60 % of summer, and 0–30 % of autumn grazing, pointing towards year-round grazing (Fig. 4a). On the other hand, only one-season grazing can reduce the γ -diversity to 20 (only summer), 16 (only spring), or down to 15 species (only autumn). Highest γ -diversity can be obtained by combining grazing of 40–50 % horse with 30 % sheep, and 20–30 % cattle (Fig. 4b). For red-listed species, combination of 65 % of summer, 25 % of autumn and 5 % of spring grazing, and 30 % of sheep, 15 % of cattle and 55 % of horse grazing yields the highest diversity (Fig. 4).

171 Fig. 4. Ternary plots depicting γ -diversity of dung beetles along compositional gradients of a) season and b) herbivore.

172 4. Discussion Spatial turnover, not nestedness, determined the β -diversity of dung beetles on a country-wide scale. Here, geographic distances between sites, followed by season and temperature, were the main drivers of turnover (Fig. 3). The importance of geographic distance and temperature points to the need of a conservation management that selects distant localities, covering large gradients in mean annual temperatures. The effect of season encourages year-round grazing. The effect of herbivore was relatively low, but it supports the combination of grazing of all three herbivore species (Fig. 3, Fig. 4b). Sites with antiparasitic treatment had lower γ -diversity as treated communities were nested in untreated ones (Figs. 2d, 3c, i).

4.1. Spatial distance drives turnover Spatial distance was the most important predictor of overall and red-listed beetles' β -diversity, mainly driven by turnover (Fig. 3). Thus, our results corroborate the findings of Soinenen et al. (2018), who highlighted species turnover as the main driver of β -diversity across various taxa, ranging from bacteria, fungi, and plants to invertebrates and vertebrates. Our findings are also in line with the concept of distance decay, indicating decreasing similarity of biological communities with increasing spatial distance (Nekola and White, 1999). High spatial turnover in dung beetle communities reflects a large heterogeneity, indicating differences in environmental variables including land-use. Land-use might be particularly important in the Czech Republic, where agriculture from around 1950s underwent intensive collectivization. In the interest of intensive production, livestock was preferably fed on grain and concentrated feed, rather than allowed to graze in natural pastures (Lerman et al., 2004). As outdoor animal grazing nearly disappeared, the amount of dung sources in the open landscape dramatically declined for nearly 40 years and dung beetles became largely dependent on smaller dung of deer, mouflon,

173 and wild boar. This is the likely reason behind the high share of red-listed dung beetle species in the Czech Republic, where out of 100 species, 59 are red-listed including 15 regionally extinct species (Král and Bezděk, 2017). Since about the 1990s, the amount of outdoor animal grazing has increased, but mostly in colder uplands and mountain regions (Mládek et al., 2006). Our results demonstrate that regional γ -diversity of dung beetles in warm lowlands almost doubles that in colder regions (Fig. 2a), and the warm regions hosted many more red-listed species than colder ones (Fig. 2a, Appendix, Table A1). This might underline the importance of space in our study, indicating that conservation priority should be given to selecting spatially distant sites hosting different species to reach highest γ -diversity, e.g., combining sites from the Bohemian Forest and South Moravia (Fig. 2a).

4.2. Importance of temperature We found that temperature is the strongest positive driver of β -diversity for relocating beetles via high turnover – in this case, even more important than spatial distance (Fig. 3g). This finding indicates that relocating species are more limited by temperature than by spatial distances, e.g., dispersal limitations. This assumption is in line with Lobo et al. (2002) and Hortal et al. (2011), who consider Scarabaeinae a thermophilous group adapted to warmer climate and not limited by their dispersal capabilities. Scarabaeinae thermal sensitivity can be an evolutionary constraint, as they originated under a warm tropical climate (Davis et al., 2002). The proximate limiting factor could be Scarabaeinae sensitivity to long periods of freezing conditions in the soil (Hanski and Cambefort, 1991), which is related to their reproductive behavior, e.g., the depth of their tunnels (Mamantov and Sheldon, 2021). In our study area, only a few species such as *Anoplotrupes stercorosus* and *Geotrupes stercorarius* occurred in cold regions, while the majority, such as *Onthophagus vacca*, *O. medius*, *O. verticicornis*, *O. lemuri*, *O. furcatus*, *Copris*

174 *lunaris*, *Euoniticellus fulvus*, *Sisyphus schaefferi*, were associated with warm areas (Fig. 2a). We did not observe any effect of temperature on the β -diversity on dwellers (Fig. 3j). Spatial diversity patterns of Scarabaeinae (relocators) and Aphodiinae (mostly dwellers) distribution do not overlap, as Aphodiinae can better tolerate lower temperatures than Scarabaeinae species, with Aphodiinae diversity peaking in colder regions than Scarabaeinae (reviewed in Cabrero-Sanudo and Lobo, 2006). 4.3. Year-round grazing promotes diversity The effect of the season was comparably important for β -diversity as was the spatial distance (Fig. 3). Therefore, seasonally fluctuating environmental conditions favor niche partitioning based on species' thermal constraints (Albrecht and Gotelli, 2001; Chesson and Huntly, 1997). Indeed, many dung beetle species (including red-listed ones) are largely seasonal, such as *Euorodalus coenosus* peaking in spring, *Onthophagus illyricus* or *O. furcatus* peaking in summer, *Sigorus porcus* peaking in autumn, or *Melinopterus consputus* having two peaks in early spring and late autumn. Grazing in spring and summer were similarly important, while grazing in autumn added fewer species (Fig. 4a), indicating the importance of year-round grazing. Our results also indicate that turnover between seasons is a major driver behind the importance of year-round grazing (Fig. 3). A positive effect of year-round grazing was documented also for other taxa, such as butterflies, orchids, and birds (Köhler et al., 2016; Konvička et al., 2021; WallisDeVries et al., 2016). Therefore, we emphasize that conservation priority should be given to the seasonal extension of grazing rather than establishing new sites close by.

175 4.4. Importance of herbivores Increasing nestedness of relocators indicate that relocators discriminate between types of herbivore dung less than dwellers. Based on the findings of Edwards (1991), Sowig (1996), and Gittings and Giller (1998), we assume that relocating beetles might be less specialized on herbivore dung types than dwellers, as they develop in more stable underground conditions, compared to weather-exposed dung pats on the surface where dwellers develop. Compared to the abiotic factors (space, season, temperature), the overall effect of herbivore identity on β -diversity was smaller, yet significant (Fig. 3). Nevertheless, a combination of herbivore species, preferably from distantly related lineages, can ensure higher turnover among dung types and result in higher dung beetle diversity. This is because herbivore dung differs in quality (e.g., water content, nutrient content, size of fiber particles), size and quantity (Finn and Giller, 2002; Holter, 2016). Dung beetles are generally attracted to all types of herbivore dung and are relatively flexible in diet (Frank et al., 2017a; Martín-Piera and Lobo, 1996). Most dung beetle species, however, have preferences for certain dung types (Finn and Giller, 2002), although the preference is usually rather context-dependent (e.g., biotope, microclimate, herbivore's diet; Barbero et al., 1999). Therefore, different dung types can be more suitable under varying environmental conditions, e.g., dry conditions may increase attractivity of more humid or larger cattle dung pats less prone to rapid desiccation. Our ternary plot (Fig. 4b) revealed that the highest γ -diversity was obtained by the combination of all three herbivores, which can increase the γ -diversity up to 37 % (Fig. 4b). However, multiple herbivore species are rarely kept on one pasture. Therefore, combining different herbivores can be a simple way to increase dung beetle diversity. This is particularly relevant, since we statistically accounted for the unbalanced grazing across our study area, i.e., cattle grazing is more common in

176 cold higher elevations, while warm lowlands are usually grazed by sheep, and our findings are independent of the study regions. 4.5. Antiparasitic treatment Compared to the environmental conditions, the effect of antiparasitic treatment on β -diversity of dung beetles was rather small. It, however, increased nestedness (Fig. 3). Increased nestedness coupled to decreasing γ -diversity (Fig. 2d) indicates that dung beetle communities first lose their characteristic species, ultimately leading to more homogenous communities. Given the common sensitivity of dung-inhabiting arthropods to some widely used antiparasitics, e.g., ivermectin (Puniamoorthy et al., 2014), antiparasitic treatment likely affects populations of specialized or locally restricted biota more than widely distributed generalists (Davies et al., 2004). Consequently, treated sites tend to host widely distributed non-specialized generalists, often recruited from dwellers (Fig. 3l), for instance *Melinopterus prodromus*, *Volinus sticticus*, *Aphodius pedellus*, or *Calamosternus granarius*. Tonelli et al. (2017) reported the same process of less common species disappearing first, while more common and dominant species were not significantly affected in treated sites. This process, called subtractive homogenization (Socolar et al., 2016a), has the most negative consequences for biodiversity. Not only diversity, but also ecosystem functioning is negatively affected by using antiparasitics (Verdú et al., 2018). We showed that antiparasitic treatment increased nestedness of relocating beetles (Fig. 3d). As relocating beetles are important agents in dung removal (Milotić et al., 2019), their reduced diversity can even lead to the disruption of dung removal through lesser resiliency of the relocating beetles' community (Ambrožová et al., 2021; Beynon et al., 2012). We conclude that the use of antiparasitic agents should be spared, at least in areas dedicated to conservation of biodiversity and natural ecological processes.

177 5. Conclusions To protect high γ -diversity of dung beetles on a landscape scale, priority should be given to the sites with complementary communities, i.e., the sites with high species turnover. The highest turnover can be ensured by selecting spatially distant sites covering a wide range of temperatures. Moreover, we identified several management actions which can significantly increase diversity – year-round grazing, followed by grazing of multiple herbivore species, and the avoidance of antiparasitics are simple. These tools can increase overall dung beetle diversity by ensuring the conservation of complementary communities.

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190 Appendix A. Supplementary data Figure A1: Observed sample coverage for all underlying observations, i.e., dung beetle species aggregated on sites, seasons, herbivore, and treatment type.

191 Table A1: Complete list of species with corresponding abundances and red-list status. Species Count Red-listed Geotrupidae Anoplotrupes stercorosus (Scriba, 1791) 1125 no Geotrupes spiniger (Marsham, 1802) 276 yes Geotrupes stercorarius (Linnaeus, 1758) 238 yes Trypocopris vernalis (Linnaeus, 1758) 235 no Scarabaeidae Acanthobodilus immundus (Creutzer, 1799) 3 yes Acrossus depressus (Kugelann, 1792) 646 no Acrossus luridus (Fabricius, 1775) 1409 no Acrossus rufipes (Linnaeus, 1758) 705 no Agrilinus ater (De Geer, 1774) 399 no Agrilinus convexus (Erichson, 1848) 5 yes Ammoecius brevis Erichson, 1848 1 yes Aphodius pedellus (Degeer, 1774) 2760 no Bodilopsis rufa (Moll, 1782) 1061 no Bodilus ictericus (Laicharting, 1781) 48 yes Bodilus lugens (Creutzer, 1799) 20 yes Calamosternus granarius (Linnaeus, 1767) 888 no Chilo thorax distinctus (Müller, 1776) 9451 no Colobopterus erraticus (Linnaeus, 1758) 2549 no Coprimorphus scrutator (Herbst, 1789) 280 yes Copris lunaris (Linnaeus, 1758) 2 yes Esymus pusillus (Herbst, 1789) 3367 no Euheptaulacus porcellus (Fruvaldszky, 1879) 3 yes Euoniticellus fulvus (Goeze, 1777) 1303 yes Euorodalus coenosus (Panzer, 1798) 47 yes Euorodalus paracoenosus (Balthasar & Hrubant, 1960) 26 yes Eupleurus subterraneus (Linnaeus, 1758) 39 no Labarrus lividus (Olivier, 1789) 2 yes Limarus maculatus (Sturm, 1800) 1 no Melinopterus consputus (Creutzer, 1799) 12746 yes Melinopterus prodromus (Brahm, 1790) 8073 no Melinopterus sphacelatus (Panzer, 1798) 12512 yes Nimbus contaminatus (Herbst, 1783) 1948 yes Nimbus obliterated (Panzer, 1823) 89 yes

192 Species Count Red-listed Onthophagus coenobita (Herbst, 1783) 209 no Onthophagus fracticornis (Preyssler, 1790) 1725 no Onthophagus furcatus (Fabricius, 1781) 69 yes Onthophagus illyricus (Scopoli, 1763) 248 yes Onthophagus joannae Goljan, 1953 1602 no Onthophagus lemur (Fabricius, 1781) 1 yes Onthophagus medius (Kugelann, 1792) 39 no Onthophagus nuchicornis (Linnaeus, 1758) 549 no Onthophagus ovatus (Linnaeus, 1767) 4497 no Onthophagus ruficapillus Brullé, 1832 249 yes Onthophagus semicornis (Panzer, 1798) 9 yes Onthophagus similis (Scriba, 1790) 203 no Onthophagus taurus (Schreber, 1759) 1 yes Onthophagus vacca (Linnaeus, 1767) 301 yes Onthophagus verticicornis (Laicharting, 1781) 431 no Otophorus haemorrhoidalis (Linnaeus, 1758) 6460 no Oxyomus sylvestris (Scopoli, 1763) 48 no Parammoecius corvinus (Erichson, 1848) 1 no Plagiogonus arenarius (Olivier, 1789) 15 yes Planolinus fasciatus (Olivier, 1789) 66 no Rhodaphodius foetens (Fabricius, 1787) 705 yes Sigorus porcus (Fabricius, 1792) 55 yes Sisyphus schaefferi (Linnaeus, 1758) 242 yes Subrinus sturmi (Harold, 1870) 54 yes Teuchestes fossor (Linnaeus, 1758) 1505 no Trichonotulus scrofa (Fabricius, 1787) 2 yes Volinus sticticus (Panzer, 1798) 1156 no

193 Table A2: Results of multiple regression on distance matrices. Variable Distance p R² p F p All species overall beta intercept 0.410 1 0.402 0.001 1643.666 0.001 herbivore 0.047 0.001 season 0.185 0.001 treatment 0.012 0.004 space 0.226 0.001 temperature 0.153 0.001 All species turnover intercept 0.265 1 0.380 0.001 1501.846 0.001 herbivore 0.058 0.001 season 0.181 0.001 treatment 0.005 0.256 space 0.297 0.001 temperature 0.194 0.001 All species nestedness intercept 0.145 0.001 0.079 0.001 210.053 0.001 herbivore -0.011 0.022 season 0.004 0.619 treatment 0.007 0.014 space -0.070 0.001 temperature -0.041 0.007 Red-listed overall beta intercept 0.449 1 0.275 0.001 771.077 0.001 herbivore 0.032 0.002 season 0.214 0.001 treatment 0.040 0.001 space 0.376 0.001 temperature 0.086 0.003

194 Variable Distance p R² p F p Red-listed turnover intercept 0.263 1 0.248 0.001 69667.959 0.001 herbivore 0.036 0.01 season 0.284 0.001 treatment 0.035 0.002 space 0.490 0.001 temperature 0.128 0.003 Red-listed nestedness intercept 0.186 0.001 0.083 0.001 184.463 0.001 herbivore -0.004 0.31 season -0.070 0.001 treatment 0.006 0.092 space -0.114 0.001 temperature -0.043 0.006 Relocators overall beta intercept 0.373 1 0.442 0.001 1705.242 0.001 herbivore 0.034 0.002 season 0.133 0.001 treatment 0.010 0.021 space 0.203 0.001 temperature 0.426 0.001 Relocators turnover intercept 0.123 1 0.392 0.001 1382.200 0.001 herbivore 0.009 0.328 season 0.176 0.001 treatment -0.003 0.621 space 0.218 0.001 temperature 0.660 0.001 Relocators nestedness intercept 0.250 0.001 0.111 0.001 321.314 0.001 herbivore 0.025 0.002 season -0.043 0.004

195 Variable Distance p R2 p F p treatment 0.013 0.008 space -0.015 0.431 temperature -0.234 0.001 Dwellers overall beta intercept 0.399 1 0.280 0.001 927.783 0.001 herbivore 0.080 0.001 season 0.345 0.001 treatment 0.008 0.125 space 0.221 0.001 temperature 0.010 0.731 Dwellers turnover intercept 0.177 1 0.184 0.001 536.257 0.001 herbivore 0.067 0.001 season 0.369 0.001 treatment 0.022 0.013 space 0.285 0.001 temperature 0.057 0.215 Dwellers nestedness intercept 0.222 0.001 0.023 0.001 55.266 0.001 herbivore 0.014 0.177 season -0.024 0.149 treatment -0.014 0.019 space -0.064 0.021 temperature -0.047 0.132 Visitors overall beta intercept 0.427 1 0.034 0.001 81.833 0.001 herbivore -0.029 0.034 season 0.032 0.064 treatment 0.022 0.015 space 0.208 0.001 temperature 0.073 0.221

196 Variable Distance p R2 p F p Visitors turnover intercept 0.246 1 0.066 0.001 85.120 0.001 herbivore -0.046 0.016 season 0.034 0.091 treatment 0.022 0.044 space 0.267 0.001 temperature 0.109 0.113 Visitors nestedness intercept 0.182 0.001 0.019 0.001 22.777 0.001 herbivore 0.017 0.01 season -0.002 0.817 treatment -0.0003 0.946 space -0.059 0.012 temperature -0.036 0.176

197 Summary

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199 Summary The aim of the thesis was to evaluate the environmental and management-related factors influencing the diversity of Central European dung beetles with a special focus on their threats and conservation. Since dung beetles are one of the most affected taxa by modern agricultural practices and land-use changes, understanding what drives their diversity is crucial for efficient conservation. In the first chapter, I studied the effects of routine antiparasitic treatment with ivermectin on dung beetle communities and their potential to threaten ecosystem functioning. Second chapter dealt with alternative forest managements leading to forest opening (renewed coppice and additional removal of topsoil layer) and its effect on diversity of dung- dwelling beetles. In the third chapter, I tested the relative importance of several environmental and management factors driving turnover or nestedness of dung beetle communities to provide scientific evidence for systematic conservation planning. Chapter I focused on ivermectin, one of the world's most often used broad- spectrum antiparasitics. It is well known that herbivore dung containing ivermectin residues is harmful for dung beetles for several weeks following treatment. However, little was known about whether routine treatment can alter dung beetle communities on regularly treated sites. This study revealed that routinely treated sites had significantly lower species richness and abundances than sites without treatment, even if ivermectin residues were not present. This finding suggests that dung beetle communities on routinely treated sites were already impoverished. When ivermectin residues were present in dung, the biomass of dung relocating beetles decreased by 64 %, suggesting that the community was less capable of removing dung. In a long run, reduction of functionally most efficient taxa can pose a serious threat to the provided ecosystem services.

200 In the Chapter II, we studied the effect of alternative forest management on forest dung and rove beetles. Traditional forest managements, such as pollarding, coppicing or wood pasture, were largely abandoned in most parts of Europe during the last century, which resulted in significant loss of open-forest specialists. By our manipulative experiment, we tested whether small-scale measures (ca. 20 x 20 m plots) can increase diversity of dung-inhabiting beetles. We found that each of the experimental treatments supported different communities of dung and rove beetles compared to the forest plots. Moreover, we recorded several species considered as "open habitat specialists" in relatively high numbers, suggesting that even small scale interventions can provide suitable habitat for them. We concluded that the mosaic of coppice and patches of bare soil can promote landscape-level γ -diversity of dung-inhabiting beetles within forests. In the Chapter III, we tested the relative strength of environmental and management-related variables that determine dung beetle β -diversity (i.e., turnover and nestedness). The aim was to reveal which variables should be given the conservation priority to yield the highest γ -diversity of dung beetles on a country- wide scale. Our results revealed that geographical distance, mean annual temperature and sampling season were the major factors driving turnover in dung beetle communities. Management-related factors, grazing herbivore and antiparasitic treatment, had also significant, yet lesser effect than environment. On the other hand, it is relatively easier to support dung beetle diversity by changing management on established sites, rather than setting new sites under ideal environmental conditions. Hence, we simulated which grazing regime is optimal to yield highest γ -diversity, and our results supported the combination of grazing of three major herbivore species, as well as year-round grazing. The only variable resulting in higher nestedness was antiparasitic treatment, suggesting that communities on treated sites are subset of communities from untreated sites. Based

201 on our results, we recommended that conservation priority should be given (in decreasing order) to the grazing which covers large spatial distance and temperature gradient, is year-round and done by multiple herbivore species without antiparasitic treatment. The studies presented in this thesis broadens the existing knowledge on dung beetle conservation biology. My findings confirm that the management alone can have significant impact on dung beetle diversity. Here, I demonstrated that especially traditional or extensive management brings many positives for dung beetle communities, such as small-scale forest openings, no antiparasitic treatment, combination of grazing herbivores or year-round grazing. Besides, I demonstrated that modern forestry or agricultural practices can pose a risk to dung beetle communities and provided ecosystem services, as they often favor widespread generalist species over specialists. Finally, I believe that the management recommendations coming out from my dissertation are widely useable for nature conservation.

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203 Author's Curriculum Vitae

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205 Author's Curriculum Vitae Name: Lucie Ambrožová Date of birth: 21. 1. 1992 Nationality: Czech Address: Biology Centre CAS, Branišovská 1160/31, 370 05 České Budějovice, Czech Republic Telephone: +420 734 306 051 E-mail: L.Ambrozova@seznam.cz ORCID: 0000-0002-3258-2661 Education 2017–2022 Ph.D. candidate in Entomology, University of South Bohemia in České Budějovice, Faculty of Science. 2015–2017 Mgr. in Zoology, University of South Bohemia in České Budějovice, Faculty of Science. 2011–2015 Bc. in Biology, University of South Bohemia in České Budějovice, Faculty of Science. Work experience 2017–now Ph.D. student, Biology Centre CAS, Institute of Entomology

206 Internship November 2021 – Field Station Fabrikschleichach, Biozentrum, Julius-Maximilians Universität Würzburg, Germany Supervisor: Dr. Simon Thorn September – December 2020 – Field Station Fabrikschleichach, Biozentrum, Julius-Maximilians Universität Würzburg, Germany Supervisor: Dr. Simon Thorn Field experience Steppe beetles in former military areas after rewilding (2015–2021), dung beetle surveys in Podyjí National park (Military LIFE for Nature; 2019–2021), entomological expedition to southern Ural, RU (2019), mark-recapture study on *Rosalia alpina* (2017, 2020), dung beetle surveys in Prague (2018–2019), dung beetle inventory in Cerová upland, SK (2021–2022), leadership of field surveys on dung beetles in Šumava National park (2018–2022). Teaching University of South Bohemia in České Budějovice, Faculty of Science: Entomological excursion (2020–2022) Field-work courses for first year students (2017–2021) Interdisciplinary excursion (2017–2019) Vertebratological excursion (2017) Julius-Maximilians-Universität Würzburg, Faculty of Biology: Zoological excursion to Georgia (2022)

207 Publications with impact factor (IF) Ambrožová, L., Sládeček, F. X. J., Zítek, T., Perlík, M., Kozel, P., Jirků, M. & Čížek, L. (2021).

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Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities.

Agriculture, Ecosystems & Environment, 321, p. 107634. doi: 10.1016/j.agee.2021.107634. (IF = 6.576) Ambrožová, L., Finnberg, S., Feldmann, B., Buse, J., Preuss, H., Ewald, J. & Thorn, S. (2021). Coppicing and topsoil removal promote diversity of dung-inhabiting beetles (Coleoptera: Scarabaeidae, Geotrupidae, Staphylinidae) in forests. *Agricultural and Forest Entomology*, 24, p. 104–113. doi: 10.1111/afe.12472. (IF = 2.126) Ambrožová, L., Čížek, L., Sládeček, F.X.J. & Thorn, S. (2022).

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Understanding the drivers of β -diversity improves conservation prioritization for Central European dung beetles. *Biological Conservation*, 273,

p. 109682. doi: 10.1016/j.biocon.2022.109682. (IF = 7.499). Non-IF publications Ambrožová, L., Sládeček, F. X. J. & Čížek, L. (2019). Koprofágní vrubounovití (Scarabaeidae) a chrobákovití (Geotrupidae) brouci na vybraných lokalitách Šumavy a jejich odpověď na aplikaci antiparazitik u hospodářských zvířat. *Silva Gabreta* 25, p. 15–24. Ambrožová, L., Sládeček, F. X. J. & Čížek, L. (2019): O „hovniválech“ a odčervování. *Šumava léto*, p. 16–17. Ambrožová, L., Sládeček, F. X. J., Roučková, R., Dvořák, V. & Čížek, L. (2020). Koprofágní vrubounovití (Scarabaeidae) a chrobákovití (Geotrupidae) brouci na vybraných lokalitách Šumavy a jejich odpověď na aplikaci antiparazitik u hospodářských zvířat II. *Silva Gabreta* 26, p. 1–14.

208 Ambrožová L., Perlík M., Kozel P., Zítek T., Bezděk A. & Čížek L. (2020). Výsledky faunistického průzkumu koprofágních brouků (Coleoptera: Geotrupidae, Scarabaeidae) na vybraných lokalitách na území Národního parku Podyjí v letech 2018–2020. *Thayensia* 17, p. 31–41. Ambrožová, L., Sládeček, F. X. J., Roučková, R., Dvořák, V. & Čížek, L. (2021). Výsledky faunistického průzkumu koprofágních brouků (Coleoptera: Geotrupidae, Scarabaeidae) na vybraných lokalitách na území Národního parku Šumava v roce 2020. *Silva Gabreta* 27, p.121–132. International conferences: Ambrožová, L., Sládeček, F. X. J., Zítek, T., Perlík, M., Kozel, P., Jirků, M. & Čížek, L. (2021).

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Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities [

poster]. In: Schröder-Esselbach, B., Dauber, J., Richter, D., Borchert, V. & Hogueve, J. V. C. (Eds.): 50th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland. Book of Abstracts. 30 th August to 1 st September 2021. Braunschweig, Germany.

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	Understanding the drivers of β -diversity improves conservation prioritization for Central European dung beetles. Biological Conservation, 273,		Understanding the drivers of β -diversity improves conservation prioritization for Central European dung beetles 2022, Biological Conservation	
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11/238	SUBMITTED TEXT	25 WORDS	47% MATCHING TEXT	25 WORDS
	O'Hea et al., 2010; Rodríguez-Vivas et al., 2020; Verdú et al., 2018a; Weaving et al., 2020). Floate et al. (Floate et al., 2005, 2002)		O'Hea et al., 2010, Martínez et al., 2017, Rodríguez-Vivas et al., 2020), foraging, olfactory and locomotor abilities (Verdú et al., 2015), and mobility (Martínez et al., 2017, Pérez-Cogollo et al., 2017, Weaving et al., 2020).	
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12/238	SUBMITTED TEXT	11 WORDS	100% MATCHING TEXT	11 WORDS
	eprinomectin and ivermectin, but no effect was observed for moxidectin.		eprinomectin and ivermectin, but no effect was observed for moxidectin.	
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13/238	SUBMITTED TEXT	93 WORDS	48% MATCHING TEXT	93 WORDS
	O’Hea et al., 2010; Rodríguez-Vivas et al., 2020), olfactory and locomotor abilities (Verdú et al., 2015) and mobility of adult beetles (Martínez et al., 2017; Pérez-Cogollo et al., 2017; Weaving et al., 2020), while it usually does not kill them. Ivermectin residues, however, substantially reduce larval survival (Martínez et al., 2017; Norma M. O’Hea et al., 2010; Pérez-Cogollo et al., 2017), decrease number and body size of newly emerged beetles (S. A. Beynon et al., 2012; González-Tokman et al., 2017), and change offspring sex-ratio in favor of males (González-Tokman et al., 2017). O’Hea et al., 2010, Martínez et al., 2017, Rodríguez-Vivas et al., 2020), foraging, olfactory and locomotor abilities (Verdú et al., 2015), and mobility (Martínez et al., 2017, Pérez-Cogollo et al., 2017, Weaving et al., 2020). Larvae are even more affected, as ivermectin residues substantially reduce their survival (O’Hea et al., 2010, Martínez et al., 2017, Pérez-Cogollo et al., 2017, Finch et al., 2020), decrease the number and body size of newly emerged beetles (González-Tokman et al., 2017), and change the offspring sex-ratio in favor of males (González-Tokman et al., 2017).			
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	large pastures (< 130 ha) or a coherent network of small pastures to ensure large pastures (<130 ha) or a coherent network of small pastures are required to ensure			
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15/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Cumulative annual dung beetle diversity in Mediterranean seasonal environments. Ecol. Res. 27, 387–395. https://doi.org/10.1007/s11284-011-0910-8 Cumulative annual dung beetle diversity in Mediterranean seasonal environments. Ecol Res 27:387–395. https://doi.org/10.1007/s11284-011-0910-8			
	W https://link.springer.com/article/10.1007/s11056-022-09922-0			
16/238	SUBMITTED TEXT	25 WORDS	100% MATCHING TEXT	25 WORDS
	Ahrens, D., Schwarzer, J., Vogler, A.P., 2014. The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. Proc. R. Soc. B Ahrens D., Schwarzer J., Vogler A.P. The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. Proc. R. Soc. B. 2014;281:20141470.			
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
17/238	SUBMITTED TEXT	20 WORDS	92% MATCHING TEXT	20 WORDS
	Andriuzzi, W.S., Wall, D.H., 2018. Soil biological responses to, and feedbacks on, trophic rewilding. Philos. Trans. R. Soc. B			
	SA Biologisk_Projekt.pdf (D157118788)			

18/238	SUBMITTED TEXT	22 WORDS	79% MATCHING TEXT	22 WORDS
	Arillo, A., Ortuño, V.M., 2008. Did dinosaurs have any relation with dung-beetles? (The origin of coprophagy). J. Nat. Hist. 42, 1405–1408. https://doi.org/10.1098/rspb.2014.1470		Arillo A& Ortuño VM. 2008Did dinosaurs have any relation with dung-beetles? (The origin of coprophagy). J. Nat. Hist. 42, 1405–1408. (doi:10.1080/00222930802105130).	
	W https://doi.org/10.1098/rspb.2014.1470			
19/238	SUBMITTED TEXT	31 WORDS	95% MATCHING TEXT	31 WORDS
	Badenhorst, J., Dabrowski, J., Scholtz, C.H., Truter, W.F., 2018. Dung beetle activity improves herbaceous plant growth and soil properties on confinements simulating reclaimed mined land in South Africa. Appl. Soil		Badenhorst, J.; Dabrowski, J.; Scholtz, C. H.; Truter, W. F. (2018). "Dung beetle activity improves herbaceous plant growth and soil properties on confinements simulating reclaimed mined land in South Africa". Applied Soil	
	W https://en.wikipedia.org/wiki/Dung_beetle			
20/238	SUBMITTED TEXT	41 WORDS	93% MATCHING TEXT	41 WORDS
	Bang, H.S., Lee, J.-H., Kwon, O.S., Na, Y.E., Jang, Y.S., Kim, W.H., 2005. Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Appl. Soil Ecol. 29, 165–171. https://doi.org/10.1016/j.apsoil.2004.11.001 26		Bang, H. S. , Lee, J.-H. , Kwon, O. S. , Na, Y. E. , Jang, Y. S. , & Kim, W. H. (2005). Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Applied Soil https://doi.org/10.1016/j.apsoil.2004.11.001 [	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5838066/			
21/238	SUBMITTED TEXT	24 WORDS	100% MATCHING TEXT	24 WORDS
	Barbero, E., Palestrini, C., Rolando, A., 1999. Dung beetle conservation: Effects of habitat and resource selection (Coleoptera: Scarabaeoidea). J. Insect Conserv. 3, 75–84.		Barbero E., Palestrini C., Rolando A. Dung beetle conservation: Effects of habitat and resource selection (Coleoptera: Scarabaeoidea) J. Insect Conserv. 1999;3:75–84.	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
22/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Linking agricultural practice to insect and bird populations: a historical study over three decades.		Linking agricultural practice to insect and bird populations: a historical study over three decades.	
	W https://doi.org/10.1371/journal.pone.0185809			

23/238	SUBMITTED TEXT	49 WORDS	86% MATCHING TEXT	49 WORDS
	https://doi.org/10.1046/j.1365-2664.2002.00745.x Bertone, M.A., Green, J.T., Washburn, S.P., Poore, M.H., Watson, D.W., 2006. The Contribution of Tunneling Dung Beetles to Pasture Soil Nutrition. <i>Forage & Grazinglands</i> 4, 1–12. https://doi.org/10.1094/FG-2006-0711-02-RS Beynon, Sarah A., Mann, D.J., Slade, E.M., Lewis, O.T., 2012. Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems.		https://doi.org/10.1016/0304-4017(93)90157-I [PubMed] [Google Scholar] • Bertone, M. A. , Green, J. T. , Washburn, S. P. , Poore, M. H. , & Watson, D. W. (2006). The contribution of tunnelling dung beetles to pasture soil nutrition. <i>Forage and Grazinglands</i>,, 4(1). https://doi.org/10.1094/FG-2006-0711-02-RS [Google Scholar] • Beynon, S. A. , Mann, D. J. , Slade, E. M. , & Lewis, O. T. (2012). Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems.	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5838066/			
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	Beynon, S. A., Peck, M., Mann, D.J., Lewis, O.T., 2012. Consequences of alternative and conventional endoparasite control in cattle for dung-associated invertebrates and ecosystem functioning.			
	SA VET344s2_15_uid_32399946_fname_3865_1443947883_64155.docx (D18779734)			
25/238	SUBMITTED TEXT	37 WORDS	86% MATCHING TEXT	37 WORDS
	https://doi.org/10.1016/j.agee.2012.08.010 Beynon, S.A., Wainwright, W.A., Christie, M., 2015. The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry. <i>Ecol. Entomol.</i> 40, 124–135. https://doi.org/10.1111/een.12240 27		https://doi.org/10.1111/j.1365-2664.2012.02210.x [Google Scholar] • Beynon, S. A. , Wainwright, W. A. , & Christie, M. (2015). The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry. <i>Ecological</i> https://doi.org/10.1111/een.12240 [	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5838066/			
26/238	SUBMITTED TEXT	14 WORDS	100% MATCHING TEXT	14 WORDS
	Life History and Arthropod Dispersal of a Coprophilous Stylopage . <i>Mycologia</i> 83, 360–366.		Life history and arthropod dispersal of a coprophilous Stylopage <i>Mycologia</i> (1991) •	
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27/238	SUBMITTED TEXT	20 WORDS	100% MATCHING TEXT	20 WORDS
	Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. <i>Biodivers. Conserv.</i> 25, 1661–1675.		Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. <i>Biodivers. Conserv.</i> 25, 1661–1675. (10.1007/	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6408906/			

28/238	SUBMITTED TEXT	11 WORDS	100% MATCHING TEXT	11 WORDS
	An effect of dung beetle activity on plant yield. Pedobiologia (		An effect of dung beetle activity on plant yield. Pedobiologia 10: 1–7.	
	W https://www.researchgate.net/publication/216850237_Effect_of_tunneler_dung_beetles_on_cattle_dung ...			
29/238	SUBMITTED TEXT	21 WORDS	100% MATCHING TEXT	21 WORDS
	Brown, J., Scholtz, C.H., Janeau, J.-L., Grellier, S., Podwojewski, P., 2010. Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties.		Brown, J.; Scholtz, C. H.; Janeau, J. L.; Grellier, S.; Podwojewski, P. (2010). "Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties" (	
	W https://en.wikipedia.org/wiki/Dung_beetle			
30/238	SUBMITTED TEXT	17 WORDS	100% MATCHING TEXT	17 WORDS
	Summary of the morphological and ecological traits of Central European dung beetles. Entomol. Sci. 21, 315–323.		Summary of the morphological and ecological traits of Central European dung beetles Entomol. Sci. (2018) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
31/238	SUBMITTED TEXT	21 WORDS	100% MATCHING TEXT	21 WORDS
	Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles. Biol. Conserv. 187, 112–119.		Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles Biol. Conserv. (2015) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
32/238	SUBMITTED TEXT	24 WORDS	100% MATCHING TEXT	24 WORDS
	Mazziotta, A., Valerio, L., 2007. Inferring species decline from collection records: Roller dung beetles in Italy (Coleoptera, Scarabaeidae). Divers. Distrib. 13, 903–919. https://doi.org/10.1111/j.1472-4642.2007.00397.x		Mazziotta A, Valerio L (2007) Inferring species decline from collection records: roller dung beetles in Italy (Coleoptera, Scarabaeidae). Divers Distrib 13:903–919. https://doi.org/10.1111/j.1472-4642.2007.00397.x	
	W https://link.springer.com/article/10.1007/s11056-022-09922-0			
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	Davis, A., 2002. Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies and survey design. African Entomol. 10, 53–65. Davis, A.L. V.,		Davis, A. L. V. 2002. Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies and survey design. African entomology 10(1): 53-65. Davis, A. L. V.,	
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34/238	SUBMITTED TEXT	37 WORDS	91% MATCHING TEXT	37 WORDS
	Doherty, W.M., Stewart, N.P., Obb, R.M., Keiran, P.J., 1994. In-Vitro Comparison of the Larvicidal Activity of Moxidectin and Abamectin Against <i>Onthophagus 30 gazella</i> (F.) (Coleoptera: Scarabaeidae) and <i>Haematobia irritans exigua</i> De Meijere (Diptera: Muscidae).		Doherty, W.M., Stewart, N.P., Cobb, R.M. & Keiran, P.J. (1994) In-vitro comparisons of the larvicidal activity of moxidectin and abamectin against <i>Onthophagus gazella</i> (F.) (Coleoptera: Scarabaeidae) and <i>Haematobia irritans exigua</i> De Meijere (Diptera: Muscidae).	
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	Doube, B.M., 2018. Ecosystem services provided by dung beetles in Australia. <i>Basic Appl. Ecol.</i> 26, 35–49.		Doube, B.M. Ecosystem services provided by dung beetles in Australia. <i>Basic Appl. Ecol.</i> 2018, 26, 35–49. [	
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	Doube, B.M., 1990. A functional classification for analysis of the structure of dung beetle assemblages. <i>Ecol. Entomol.</i> 15, 371–383.		Doube, B.M. A functional classification for analysis of the structure of dung beetle assemblages. <i>Ecol. Entomol.</i> 1990, 15, 371–383. [	
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	Edwards, P., 2007. Introduced Dung Beetles in Australia 1967–2007. Current status and future directions.		Edwards, P. 2007. Introduced dung beetles in Australia 1967–2007. Current status and future directions.	
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	Errouissi, F., Alvinerie, M., Galtier, P., Kerboeuf, D., Lumaret, J.-P., 2001. The negative effects of the residues of ivermectin in cattle dung using a sustained- release bolus on <i>Aphodius constans</i> (Duft.) (Coleoptera: Aphodiidae). <i>Vet. Res.</i> 32, 421–427.		Errouissi F, Alvinerie M, Galtier P, Kerboeuf D, Lumaret J-P. The negative effects of the residues of ivermectin in cattle dung using a sustained-release bolus on <i>Aphodius constans</i> (Duft.) (Coleoptera: Aphodiidae). <i>Vet Res.</i> 2001;32: 421–427.	
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	Errouissi, F., Jay-Robert, P., Lumaret, J.P., Piau, O., 2004. Composition and structure of Dung Beetle (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) assemblages in mountain grasslands of the Southern Alps. Ann. Entomol. Soc. Am. 97, 701–709. W https://doi.org/10.3390/insects12090781		Errouissi, F.; Jay-Robert, P.; Lumaret, J.P.; Piau, O. Composition and structure of dung beetle (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) assemblages in mountain grasslands of the Southern Alps. Ann. Entomol. Soc. Am. 2004, 97, 701–709. [	
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	Errouissi, F., Lumaret, J.P., 2010. Field effects of faecal residues from ivermectin slow-release boluses on the attractiveness of cattle dung to dung beetles. Med. Vet. Entomol. 24, 433–440. https://doi.org/10.1111/ W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/		Errouissi F., Lumaret J.P. Field effects of faecal residues from ivermectin slow-release boluses on the attractiveness of cattle dung to dung beetles. Med Vet. Entomol. 2010;24:433–440. doi: 10.1111/	
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	Implications of Endectocide Residues on the Survival of Aphodiine Dung Beetles: A Meta-Analysis. Environ. Toxicol. Chem. 39, 863–872. W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388		Implications of endectocide residues on the survival of aphodiine dung beetles: a meta-analysis Environ. Toxicol. Chem. (2020) •	
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	K.D., 1998. Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada. Bull. Entomol. Res. 88, 25–35. W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388		K.D. Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada Bull. Entomol. Res. (1998) •	
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	Floate, K.D., Colwell, D.D., Fox, A.S., 2002. Reductions of non-pest insects in dung of cattle treated with endectocides: a comparison of four products. Bull. Entomol. Res. 92, 471–481. https://doi.org/10.1079/BER2002201 Floate, K.D., Wardhaugh, K.G., Boxall, A.B.A., Sherratt, T.N., 2005. Fecal residues of veterinary parasiticides: Nontarget effects in the pasture environment. W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...		Floate, K.D., Colwell, D.D. & Fox, A.S. (2002) Reductions of non-pest insects in dung of cattle treated with endectocides: a comparison of four products. Bulletin of Research 92, 471–481. CrossRefGoogle ScholarPubMed D., Wardhaugh, K.G., Boxall, A.B.A. & Sherratt, T.N. (2005) Fecal residues of veterinary pesticides: Nontarget effects in the pasture environment.	

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	Forgie, S.A., Paynter, Q., Zhao, Z., Flowers, C., Fowler, S. V., 2018. Newly released non-native dung beetle species provide enhanced ecosystem services in New Zealand pastures. Ecol. Entomol. 43, 431–439. W https://www.mdpi.com/1424-2818/15/1/91		Forgie, S.A.; Paynter, Q.; Zhao, Z.; Flowers, C.; Fowler, S.V. Newly released non-native dung beetle species provide enhanced ecosystem services in New Zealand pastures. Ecol. Entomol. 2018, 43, 431–439. [	
45/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Land use affects dung beetle communities and their ecosystem service in forests and grasslands. W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388		Land use affects dung beetle communities and their ecosystem service in forests and grasslands	
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	Ivermectin alters reproductive success, body condition and sexual trait expression in dung beetles. Chemosphere 178, 129–135. 33 W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388		Ivermectin alters reproductive success, body condition and sexual trait expression in dung beetles Chemosphere (2017) •	
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	Environmentally-realistic concentrations of anthelmintic drugs affect survival and motility in the cosmopolitan earthworm <i>Lumbricus terrestris</i> (Linnaeus, 1758). Appl. Soil Ecol. 137, 87–95. W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388		Environmentally-realistic concentrations of anthelmintic drugs affect survival and motility in the cosmopolitan earthworm <i>Lumbricus terrestris</i> (Linnaeus, 1758) Appl. Soil. Ecol. (2019) •	
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	Halfpeter, G., Edmonds, W.D., 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae). An Ecological and Evolutive Approach. SA Fascinating behaviors of <i>Aphodius elegans</i>-07170351.docx (D70108613)			
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	Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., W https://doi.org/10.1371/journal.pone.0185809		Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H,	
50/238	SUBMITTED TEXT	21 WORDS	97% MATCHING TEXT	21 WORDS
	More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12. https://doi.org/10.1371/journal.pone.0185809 W https://doi.org/10.1371/journal.pone.0185809		More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12(10): e0185809. https://doi.org/10.1371/journal.pone.0185809	

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	Hanski, I., 1991. North temperate dung beetles, in: Hanski, I., Cambefort, Y. (Eds.), <i>Dung Beetle Ecology</i>. Princeton University Press, Princeton, pp. 75–96. Hanski, I., Cambefort, Y., 1991. <i>Dung beetle ecology</i>. Princeton University Press, New Jersey. SA 950614P226_int15fis_Researchproject_2015-10-26144128.pdf (D15864877)			
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	Hata, K., Edmonds, W.D., 1983. Structure and function of the mandibles of adult dung beetles (Coleoptera : Scarabaeidae). <i>Int. J. Insect Morphol. Embryol.</i> 12, 1–12. W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
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	J., 2006. Toxicity of four veterinary parasiticides on larvae of the dung beetle 34 <i>Aphodius constans</i> in the laboratory. SA VET344s2_14_uid_31866453_fname_2244_1409830371_44840.docx (D18779600)			
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	Herd, R.P., Sams, R.A., Ashcraft, S.M., 1996. Persistence of ivermectin in plasma and faeces following treatment of cows with ivermectin sustained-release, pour-on or injectable formulations. W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...			
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	Hirschberger, P., 1998. Spatial distribution, resource utilisation and intraspecific competition in the dung beetle <i>Aphodius ater</i>. <i>Oecologia</i> 116, 136–142. W https://www.mdpi.com/1424-2818/15/1/91			
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	Holter, P., 2016. Herbivore dung as food for dung beetles: elementary coprology for entomologists. <i>Ecol. Entomol.</i> 41, 367–377. https://doi.org/10.1111/ W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			

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	https://doi.org/10.14411/eje.2004.051 Holter, P., 1979. Effect of Dung-Beetles (Aphodius spp.) and Earthworms on the Disappearance of Cattle Dung. Oikos 32, 393. https://doi.org/10.2307/3544751 W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5838066/		https://doi.org/10.2307/3543332 [Google Scholar] Effect of dung-beetles (Aphodius spp.) and earthworms on the disappearance of cattle dung. Oikos, 32, 393–402. https://doi.org/10.2307/3544751 [	
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	Holter, P., Scholtz, C.H., 2007. What do dung beetles eat? Ecol. Entomol. 32, 690– 697. W https://www.mdpi.com/1424-2818/15/1/91		Holter, P.; Scholtz, C.H. What do dung beetles eat? Ecol. Entomol. 2007, 32, 690–697. [	
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	Horgan, F.G., 2007. Dung beetles in pasture landscapes of Central America: proliferation of synanthropic species and decline of forest specialists. Biodivers. Conserv. 16, 2149–2165. https://doi.org/10.1007/s10531-006-9145-3 W https://doi.org/10.1007/s10531-006-9145-3		Horgan, F.G. Dung beetles in pasture landscapes of Central America: proliferation of synanthropic species and decline of forest specialists. Biodivers Conserv 16, 2149–2165 (2007). https://doi.org/10.1007/s10531-006-9145-3	
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	Hutton, S. a, Giller, P.S., 2003. The effects of the intensification of agriculture on northern temperate dung beetle communities. J. Appl. Ecol. 40, 994–1007. W https://kids.frontiersin.org/articles/10.3389/frym.2021.583675		Hutton, S. A., and Giller, P. S. 2003. The effects of the intensification of agriculture on northern temperate dung beetle communities. J. Appl. Ecol. 40:994–1007.	
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	T., Scholtz, C.H., 2015. A review on the effect of macrocyclic lactones on dung-dwelling insects: Toxicity of macrocyclic lactones to dung beetles. Onderstepoort J Vet Res 82, 1–8. W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...		T. and Scholtz, Clarke H. 2015. A review on the effect of macrocyclic lactones on dung-dwelling insects: Toxicity of macrocyclic lactones to dung beetles. Onderstepoort J Vet Res,	
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	https://doi.org/10.4102/ojvr.v82i1.858 Jay-Robert, P., Niogret, J., Errouissi, F., Labarussias, M., Paoletti, É., Luis, M.V., Lumaret, J.-P., 2008. Relative efficiency of extensive grazing vs. wild ungulates management for dung beetle conservation in a heterogeneous landscape from Southern Europe (Scarabaeinae, Aphodiinae, Geotrupinae). Biol. Conserv. 141, 2879–2887. https://doi.org/10.1016/j.biocon.2008.09.001 SA Case+study+4+-+group+3+%281%29.docx (D153209478)			

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	Junco, M., Iglesias, L.E., Sagués, M.F., Guerrero, I., Zegbi, S., Saumell, C.A., 2021. Effect of macrocyclic lactones on nontarget coprophilic organisms: a review.		Junco, M. Iglesias, L. E. Sagués, M. F. Guerrero, I. Zegbi, S. and Saumell, C. A. 2021. Effect of macrocyclic lactones on nontarget coprophilic organisms: a review.	
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	Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. Bioscience 56, 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:		Losey, J. E.; Vaughan, M. (2006). "The Economic Value of Ecological Services Provided by Insects" (BioScience. 56 (4): 311–23. doi:10.1641/0006-3568(2006)56[311:	
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	F., 2002. Use of anthelmintics in herbivores and evaluation of risks for the non target fauna of pastures.			
	SA VET347s2_14_uid_31553123_fname_2074_1411114188_23209.docx (D18779824)			
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	temperate dung beetles, in: Hanski, I., Cambefort, Y. (Eds.), Dung Beetle Ecology. Princeton University Press, Princeton, pp. 97–115.			
	SA 950614P226_int15fis_Researchproject_2015-10-26144128.pdf (D15864877)			

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	Quantifying immediate and delayed effects of anthelmintic exposure on ecosystem functioning supported by a common dung beetle species. PLoS One 12, 1–15. https://doi.org/10.1371/journal.pone.0182730		Quantifying immediate and delayed effects of anthelmintic exposure on ecosystem functioning supported by a common dung beetle species. PLoS ONE 12(8): e0182730. https://doi.org/10.1371/journal.pone.0182730	
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	Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness. Agric. Ecosyst. Environ. 264, 9–14.		Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness Agric. Ecosyst. Environ. (2018) •	
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	j.agee.2018.05.002 Manning, P., Slade, E.M., Beynon, S.A., Lewis, O.T., 2017		j.1365-2664.2003.00863.x [6] ↑ Manning, P., Slade, E. M., Beynon, S. A., and Lewis, O. T. 2017.	
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	Effect of dung beetle species richness and chemical perturbation on multiple ecosystem functions. Ecol. Entomol. 42, 577–586. https://doi.org/10.1111/een.12421 Manning, P., Slade, E.		Effect of dung beetle species richness and chemical perturbation on multiple ecosystem functions. Ecol. Entomol. 42:577–86. een.12421 Article information Citation Manning P, Ong X and Slade E (2021)	
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74/238	SUBMITTED TEXT	19 WORDS	100% MATCHING TEXT	19 WORDS
	Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. Agric. Ecosyst. Environ. 218, 87–94. https://doi.org/10.1016/j.agee.2015.11.007		Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. Agric Ecosyst Environ 218:87–94. https://doi.org/10.1016/j.agee.2015.11.007	
	W https://link.springer.com/article/10.1007/s11056-022-09922-0			
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	Mantoni, C., Tsafack, N., Palusci, E., Di Pietro, S., Fattorini, S., 2021. Diversity Patterns of Dung Beetles along a Mediterranean Elevational Gradient. Insects 12, 781. https://doi.org/10.3390/insects12090781		Mantoni, C.; Tsafack, N.; Palusci, E.; Di Pietro, S.; Fattorini, S. Diversity Patterns of Dung Beetles along a Mediterranean Elevational Gradient. Insects 2021, 12, 781. https://doi.org/10.3390/insects12090781	
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	Martínez, I.M., Lumaret, J.-P., Ortiz Zayas, R., Kadiri, N., 2017. The effects of sublethal and lethal doses of ivermectin on the reproductive physiology and larval development of the dung beetle <i>Euoniticellus intermedius</i> (Coleoptera: Scarabaeidae). <i>Can. Entomol.</i> 149, 461–472. W https://doi.org/10.1371/journal.pone.0182730			
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	Milotić, T., Baltzinger, C., Eichberg, C., Eycott, A.E., Heurich, M., Müller, J., Noriega, J.A., Menendez, R., Stadler, J., Ádám, R., W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
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	Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the 40 Western Palaearctic. <i>J. Biogeogr.</i> 46, 70–82. https://doi.org/10.1111/ W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
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	Nervo, B., Tocco, C., Caprio, E., Palestini, C., Rolando, A., 2014. The effects of body mass on dung removal efficiency in dung beetles. <i>PLoS One</i> 9. W https://www.mdpi.com/1424-2818/15/1/91			
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	Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S., Favila, M.E., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. <i>Biol. Conserv.</i> 141, 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011 W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5838066/			
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	Kirwan, L., Finn, J.A., 2010. Experimental mixtures of dung fauna 41 affect dung decomposition through complex effects of species interactions. <i>Oikos</i> 119, 1081–1088. Kirwan L, Finn J a. Experimental mixtures of dung fauna affect dung decomposition through complex effects of species interactions. <i>Oikos</i>. 2010;119: 1081–1088. • W https://doi.org/10.1371/journal.pone.0182730			
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	doi.org/10.1111/j.1752-4598.2009.00068.x Ömura, S., 2008. Ivermectin: 25 years and still going strong. SA VET344s2_15_uid_32482087_fname_3865_1444019363_69223.docx (D18779746)			
84/238	SUBMITTED TEXT	29 WORDS	100% MATCHING TEXT	29 WORDS
	Ortega-Martínez, I.J., Moreno, C.E., Escobar, F., 2016. A dirty job: manure removal by dung beetles in both a cattle ranch and laboratory setting. <i>Entomol. Exp. Appl.</i> 161, 70–78. Ortega-Martínez, I.J.; Moreno, C.E.; Escobar, F. A dirty job: Manure removal by dung beetles in both a cattle ranch and laboratory setting. <i>Entomol. Exp. Appl.</i> 2016, 161, 70–78. [W https://www.mdpi.com/1424-2818/15/1/91			
85/238	SUBMITTED TEXT	21 WORDS	100% MATCHING TEXT	21 WORDS
	Effects of herd management and the use of ivermectin on dung arthropod communities in grasslands. <i>Basic Appl. Ecol.</i> 40, 19–29. Effects of herd management and the use of ivermectin on dung arthropod communities in grasslands <i>Appl. Ecol.</i> (2019) • W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
86/238	SUBMITTED TEXT	26 WORDS	92% MATCHING TEXT	26 WORDS
	Penttilä, A., Slade, E.M., Simojoki, A., Riutta, T., Minkkinen, K., Roslin, T., 2013. Quantifying Beetle-Mediated Effects on Gas Fluxes from Dung Pats. <i>PLoS One</i> 8. https://doi.org/10.1371/journal.pone.0061454. Penttilä, A., Slade, E. M., Simojoki, A., Riutta, T., Minkkinen, K., and Roslin, T. (2013). Quantifying beetle-mediated effects on gas fluxes from dung pats. <i>PLoS One</i> 8:e71454. doi: 10.1371/journal.pone.0061454 W https://www.frontiersin.org/articles/863669			
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	Perrin, W., Fontana, S., Coq, S., Berlioz, L., Jay-Robert, P., Moretti, M., 2021. The 42 Influence of Fine-Scale Grazing Heterogeneity on Dung Beetle Assemblages: What Trait Analysis Teaches Us. SA Biologisk_Projekt.pdf (D157118788)			

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	Piccini, I., Nervo, B., Forshage, M., Celi, L., Palestrini, C., Rolando, A., Roslin, T., 2018. Dung beetles as drivers of ecosystem multifunctionality: Are response and effect traits interwoven? Sci. Total Environ. 616–617, 1440–1448. https://doi.org/10.1016/j.scitotenv.2018.06.069		Piccini, I., Nervo, B., Forshage, M., Celi, L., Palestrini, C., Rolando, A., et al. Dung beetles as drivers of ecosystem multifunctionality: Are response and effect traits interwoven? Sci. Total Environ. 616, 1440–1448. doi: 10.1016/j.scitotenv.2018.06.069	
	W https://www.frontiersin.org/articles/863669			
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	Arcila-Fuentes, W.R., Ojeda-Chi, M.M., Martínez-M, I., 2020. Evaluation of the attraction, lethal and sublethal effects of the faeces of ivermectin-treated cattle on the dung beetle <i>Digitonthophagus gazella</i> (Coleoptera: Scarabaeidae). Austral		Arcila-Fuentes, William R Ojeda-Chi, Melina M and Martínez-M, Imelda 2020. Evaluation of the attraction, lethal and sublethal effects of the faeces of ivermectin-treated cattle on the dung beetle <i>Digitonthophagus gazella</i> (Coleoptera: Scarabaeidae). Austral	
	W https://doi.org/10.4039/tce.2017.11			
90/238	SUBMITTED TEXT	43 WORDS	81% MATCHING TEXT	43 WORDS
	Römbke, J., Coors, A., Fernández, Á.A., Förster, B., Fernández, C., Jensen, J., Lumaret, J.P., Cots, M.Á.P., Liebig, M., 2010. Effects of the parasiticide ivermectin on the structure and function of dung and soil invertebrate communities in the field (Madrid, Spain). Appl. Soil			
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	Rosenlew, H., Roslin, T., 2008. Habitat fragmentation and the functional efficiency of temperate dung beetles. Oikos 117, 1659–1666.		Rosenlew H, Roslin T. Habitat fragmentation and the functional efficiency of temperate dung beetles. Oikos. 2008;117: 1659–1666. •	
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	Roslin, T., 2000. Dung beetle movements at two spatial scales. Oikos 91, 323–335.		Roslin, T. (2000) Dung beetle movements at two spatial scales. Oikos 91, 323–335.	
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	Worldwide decline of the entomofauna: A review of its drivers. Biol. Conserv. 232, 8–27.		Worldwide decline of the entomofauna: a review of its drivers Biol. Conserv. (2019) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			

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	Sands, B., Wall, R., 2017. Dung beetles reduce livestock gastrointestinal parasite availability on pasture. J. Appl. Ecol. 54, 1180–1189.		Sands B, Wall R. Dung beetles reduce livestock gastrointestinal parasite availability on pasture. J Appl Ecol. 2016; •	
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	Sommer, C., Steffansen, B., Nielsen, B.O., Grønvold, J., Vagn Jensen, K.M., Brøchner Jespersen, J., Springborg, J., Nansen, P., 1992. Ivermectin excreted 45 in cattle dung after subcutaneous injection or pour-on treatment: Concentrations and impact on dung fauna. Bull. Entomol. Res. 82, 257–264.		Sommer C, Steffansen B, Nielsen BO, Grønvold J, Vagn Jensen K-M, Brøchner Jespersen J, et al. Ivermectin excreted in cattle dung after subcutaneous injection or pour-on treatment: concentrations and impact on dung fauna. Bull Entomol Res. 1992;82: 257. •	
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	Stanbrook, R., Wheeler, C.P., Harris, W.E., Jones, M., 2021. Habitat type and altitude work in tandem to drive the community structure of dung beetles in Afromontane forest. J. Insect Conserv. 25, 159–173.		Stanbrook, R.; Wheeler, C.P.; Harris, W.E.; Jones, M. Habitat type and altitude work in tandem to drive the community structure of dung beetles in Afromontane forest. J. Insect Conserv. 2021, 25, 159–173. [	
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	Strong, L., Wall, R., 1994. Effects of ivermectin and moxidectin on the insects of cattle dung.		Strong, L. & Wall, R. (1994) Effects of ivermectin and moxidectin on the insects of cattle dung.	
	W https://doi.org/10.1017/S0007485300041523			
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	Suarez, V.H., Lifschitz, A.L., Sallovitz, J.M., Lanusse, C.E., 2003. Effects of ivermectin and doramectin faecal residues on the invertebrate colonization of cattle dung.		Suarez, V.H., Lifschitz, A.L., Sallovitz, J.M. & Lanusse, C.E. (2003) Effects of ivermectin and doramectin faecal residues on the invertebrate colonisation of cattle dung.	
	W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...			
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	M., Lanusse, C.E., 2009. Effects of faecal residues of moxidectin and doramectin on the activity of arthropods in cattle dung.		M. and Lanusse, Carlos E. 2009. Effects of faecal residues of moxidectin and doramectin on the activity of arthropods in cattle dung.	
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	Tonelli, M., 2021. Some considerations on the terminology applied to dung beetle functional groups. <i>Ecol. Entomol.</i> 46, 772–776. https://doi. Tonelli M. Some considerations on the terminology applied to dung beetle functional groups. <i>Ecol. Entomol.</i> 2021;46:772–776. doi: 10.1111/ W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
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	Tonelli, M., Verdú, J.R., Morelli, F., Zunino, M., 2020. Dung beetles: functional 46 identity, not functional diversity, accounts for ecological process disruption caused by the use of veterinary medical products. <i>J. Insect Conserv.</i> 24, 643–654. https://doi. Tonelli M., Verdú J.R., Morelli F., Zunino M. Dung beetles: Functional identity, not functional diversity, accounts for ecological process disruption caused by the use of veterinary medical products. <i>J. Insect Conserv.</i> 2020;24:643–654. doi: 10.1007/ W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
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	Tonelli, M., Verdú, J.R., Zunino, M., 2019. Grazing abandonment and dung beetle assemblage composition: Reproductive behaviour has something to say. <i>Ecol. Indic.</i> 96, 361–367. https://doi. Tonelli M., Verdú J.R., Zunino M. Grazing abandonment and dung beetle assemblage composition: Reproductive behaviour has something to say. <i>Ecol. Indic.</i> 2019;96:361–367. doi: 10.1016/ W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
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	Tonelli, M., Verdú, J.R., Zunino, M., 2018. Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. <i>Biodivers. Conserv.</i> 27, 189–204. https://doi.org/10.1007/s10531-017-1428-3 Tonelli, M., Verdú, J.R., Zunino, M. Tonelli M., Verdú J.R., Zunino M. Effects of the progressive abandonment of grazing on dung beetle biodiversity: Body size matters. <i>Biodivers. Conserv.</i> 2018;27:189–204. doi: 10.1007/s10531-017-1428-3. [CrossRef] [Google Scholar] 39. Tonelli M., Verdú J.R., Zunino M. W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
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	Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub- mountainous landscape of Central Italy. <i>PeerJ</i> 5, e2780. Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub-mountainous landscape of Central Italy. <i>PeerJ.</i> 2017;5:e2780. W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			

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	Lobo, J.M., 47 Sánchez-Piñero, F., Numa, C., 2018a. First assessment of the comparative toxicity of ivermectin and moxidectin in adult dung beetles: Sub-lethal symptoms and pre-lethal consequences.		Lobo, Jorge M. Sánchez-Piñero, Francisco and Numa, Catherine 2018. First assessment of the comparative toxicity of ivermectin and moxidectin in adult dung beetles: Sub-lethal symptoms and pre-lethal consequences.	
	W https://doi.org/10.4039/tce.2017.11			
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	Verdú, J.R., Cortez, V., Ortiz, A.J., González-Rodríguez, E., Martínez-Pinna, J., Lumaret, J.-P., Lobo, J.M., Numa, C., Sánchez-Piñero, F., 2015. Low doses of ivermectin cause sensory and locomotor disorders in dung beetles. Sci. Rep. 5, 13912. https://doi.org/10.1038/srep13912		Verdú, J.R., Cortez, V., Ortiz, A.J., González-Rodríguez, E., Pinna, J.M., Lumaret, J.-P, et Low doses of ivermectin cause sensory and locomotor disorders in dung beetles. Scientific https://doi.org/10.1038/srep13912 .	
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	Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: An interdisciplinary field study. Sci. Total Environ. 618, 219–228.		Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study Sci. Total. Environ. (2018) •	
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	Vitner, J., 1998. Reproductive biology of the Central European Aphodius species with largescutellum (Coleoptera: Scarabaeidae: Aphodiidae). Acta			
	SA 2009-12-28_0203238.pdf (D2248363)			
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	Weaving, H., Sands, B., Wall, R., 2020. Reproductive sublethal effects of macrocyclic lactones and synthetic pyrethroids on the dung beetle Onthophagus similis.		Weaving, H. Sands, B. and Wall, R. 2020. Reproductive sublethal effects of macrocyclic lactones and synthetic pyrethroids on the dung beetle Onthophagus similis.	
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	Wratten, S.D., Forbes, A.B., 1996. Environmental assessment of veterinary avermectins in temperate pastoral ecosystems.		Wratten, S.D. & Forbes, A.B. (1996) Environmental assessment of veterinary avermectins in temperate pastoral ecosystems.	
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	Yamada, D., Imura, O., Shi, K., Shibuya, T., 2007. Effect of tunneler dung beetles on cattle dung decomposition, soil nutrients and herbage growth. Grassl. Sci. 53, 121–129.		Yamada, D.; Imura, O.; Shi, K.; Shibuya, T. Effect of tunneller dung beetles on cattle dung decomposition, soil nutrients and herbage growth. Grassl. Sci. 2007, 53, 121–129. [	
	W https://www.mdpi.com/1424-2818/15/1/91			
112/238	SUBMITTED TEXT	17 WORDS	100% MATCHING TEXT	17 WORDS
	Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities		Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities -	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
113/238	SUBMITTED TEXT	69 WORDS	77% MATCHING TEXT	69 WORDS
	Agriculture, Ecosystems & Environment (2021) 321, 107634 DOI: 10.1016/j.agee.2021.107634 50 51 Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities		Agriculture, Ecosystems & Environment Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			

114/238

SUBMITTED TEXT

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Abstract Use of ivermectin in agro-ecosystems negatively affects non-target dung beetles, which provide keystone ecosystem services for pasture functioning. While the direct effects of ivermectin on dung beetles are at the center of scientific attention, its long-lasting effects on routinely treated pastures have not yet been studied on real communities and under field conditions. We focused on basic characteristics (species richness, abundance, biomass) and functionality (dung removal ability represented by guild composition) of dung beetle communities in response to ivermectin treatment. We selected 15 sites with routine ivermectin treatment and 11 without any treatment, both for at least five consecutive years prior to our sampling. We covered wide range of climatic conditions in the Czech Republic, seasonal variability, and sampled the dung of four main herbivore dung types. Additionally, we separated the samples from ivermectin treated sites into two categories, i) recently treated representing immediate effects (treated >8 weeks prior to sampling, expected lethal or sublethal levels of residues), and ii) long-ago treated representing lasting effects (treated <8 weeks, expected sublethal or inconsequential levels of residues). Ivermectin treated sites had ca. 35% lower species richness and 44% lower abundance per pat. Per pat biomass did not change. However, from a functional perspective, ivermectin use significantly decreased the biomass of beetles with high contribution to dung removal (relocating and dwelling beetles), while the biomass of beetles with low contribution (dung visiting adults with saprophagous larvae) was not affected. This was accomplished with decrease in per pat functionality at treated sites, i.e., the dung removal ability of the community. Our results highlight that the effects of ivermectin use can last far beyond its physical presence in the grazing system. Via its effects on dung beetles, routine antiparasitic treatment by ivermectin has negative consequences for both pasture biodiversity and ecosystem functioning. Therefore, all alternatives should be carefully considered to ensure that the positives of any antiparasitic treatment outweigh the damages. In areas where biodiversity is of concern, as well as in organic farming systems, all precautions should be taken to avoid excretion of toxic residues on-site.

Abstract Use of ivermectin in agro-ecosystems negatively affects non-target dung beetles, which provide keystone ecosystem services for pasture functioning. While the direct effects of ivermectin on dung beetles are at the center of scientific attention, its long-lasting effects on routinely treated pastures have not yet been studied on real communities and under field conditions. We focused on basic characteristics (species richness, abundance, biomass) and functionality (dung removal ability represented by guild composition) of dung beetle communities in response to ivermectin treatment. We selected 15 sites with routine ivermectin treatment and 11 without any treatment, both for at least five consecutive years prior to our sampling. We covered wide range of climatic conditions in the Czech Republic, seasonal variability, and sampled the dung of four main herbivore dung types. Additionally, we separated the samples from ivermectin treated sites into two categories, i) recently treated representing immediate effects (treated >8 weeks prior to sampling, expected lethal or sublethal levels of residues), and ii) long-ago treated representing lasting effects (treated <8 weeks, expected sublethal or inconsequential levels of residues). Ivermectin treated sites had ca. 35% lower species richness and 44% lower abundance per pat. Per pat biomass did not change. However, from a functional perspective, ivermectin use significantly decreased the biomass of beetles with high contribution to dung removal (relocating and dwelling beetles), while the biomass of beetles with low contribution (dung visiting adults with saprophagous larvae) was not affected. This was accomplished with decrease in per pat functionality at treated sites, i.e., the dung removal ability of the community. Our results highlight that the effects of ivermectin use can last far beyond its physical presence in the grazing system. Via its effects on dung beetles, routine antiparasitic treatment by ivermectin has negative consequences for both pasture biodiversity and ecosystem functioning. Therefore, all alternatives should be carefully considered to ensure that the positives of any antiparasitic treatment outweigh the damages. In areas where biodiversity is of concern, as well as in organic farming systems, all precautions should be taken to avoid excretion of toxic residues on-site.

Introduction Changes in agricultural practices are among the primary causes of the recent loss of biodiversity and ecosystem services (Foley et al., 2005, Tscharnkte et al., 2005, Newbold et al., 2015). Animal grazing, especially in biomes where large herbivores have always been prominent, could represent a profitable agricultural activity that also sustains biologically diverse, natural, or semi-natural ecosystems (Metera et al., 2010). Intensification of livestock production, however, has resulted in widespread use of antiparasitics, mostly macrocyclic lactones, that harm non-target organisms involved in pasture functioning (Hutton and Giller, 2003, Tonelli et al., 2017, Verdú et al., 2018). Use of antiparasitics could thus lead to loss of biodiversity as well as ecosystem services (Emmerson et al., 2016). Residues in dung of animals treated with antiparasitics have the potential to adversely affect dung-breeding insects, including dung beetles that accelerate dung removal, an ecosystem service crucial to pasture functioning (Sommer et al., 1992, Lumaret and Errouissi, 2002, Nichols et al., 2008). Dung removal involves rich communities of bacteria, fungi, annelids, and arthropods (Holter, 1977, Holter, 1979). Among them, dung beetles contribute most to the initial phases of dung removal (Lumaret and Kadir, 1995, Tixier et al., 2015). They remove dung directly and/or their activity in dung pats enables the activity of other dung decomposing organisms such as earthworms, soil bacteria, and coprophilous fungi (Holter, 1979, 54 Blackwell and Malloch, 1991). Via dung removal, dung beetles decrease the survival of dung-inhabiting larvae of various pests, blood-sucking flies, and endoparasites (Edwards and Aschenborn, 1987, Sands and Wall, 2017), aerate the soil, thus allowing aerobic bacteria to reduce emission of methane from decomposing dung (Penttilä et al., 2013), affect plant fitness by dispersing seeds from dung (Milotić et al., 2019, DeCastro-Arrazola et al., 2020), and enhance soil fertility (Bang et al., 2005). Dung beetles thus promote resource cycling between plants and animals (Maldonado et al., 2019), and prevent dung accumulation on pastures (Beynon et al., 2015). Dung beetles are, however, among the terrestrial insects most affected by habitat loss, including agriculture intensification, accompanied by high usage of inadvertently harmful antiparasitics, such as ivermectin (Sánchez-Bayo and Wyckhuys, 2019). Due to its low cost and high efficiency against a broad spectrum of parasites, ivermectin is one of the most widely used antiparasitics (Guichon et al., 2000). It causes neural paralysis to Ecdysozoa (Puniamoorthy et al., 2014), making it effective against gastro-intestinal nematodes as well as both internal and external arthropod parasites (Campbell et al., 1983, Sutherland, 1990). Ivermectin is not fully metabolized by animals and is therefore excreted in its active form in dung (Campbell et al., 1983). This is a problem, since ivermectin residues are harmful to dung-feeding arthropods, including dung beetles (Floate, 2007, Lumaret et al., 2012). Depending on the treated herbivore species and the way of administration, the residues can affect dung beetles up to several weeks post-treatment (Sommer et al., 1992, Errouissi et al., 2001, Suarez et al., 2003). Ivermectin can be administered by several routes with different excretion times (in increasing order: oral, intramuscular, subcutaneous, topical, sustained release bolus) (Floate et al., 2005, Canga et

Introduction Changes in agricultural practices are among the primary causes of the recent loss of biodiversity and ecosystem services (Foley et al., 2005, Tscharnkte et al., 2005, Newbold et al., 2015). Animal grazing, especially in biomes where large herbivores have always been prominent, could represent a profitable agricultural activity that also sustains biologically diverse, natural, or semi-natural ecosystems (Metera et al., 2010). Intensification of livestock production, however, has resulted in widespread use of antiparasitics, mostly macrocyclic lactones, that harm non-target organisms involved in pasture functioning (Hutton and Giller, 2003, Tonelli et al., 2017, Verdú et al., 2018). Use of antiparasitics could thus lead to loss of biodiversity as well as ecosystem services (Emmerson et al., 2016). Residues in dung of animals treated with antiparasitics have the potential to adversely affect dung-breeding insects, including dung beetles that accelerate dung removal, an ecosystem service crucial to pasture functioning (Sommer et al., 1992, Lumaret and Errouissi, 2002, Nichols et al., 2008). Dung removal involves rich communities of bacteria, fungi, annelids, and arthropods (Holter, 1977, Holter, 1979). Among them, dung beetles contribute most to the initial phases of dung removal (Lumaret and Kadir, 1995, Tixier et al., 2015). They remove dung directly and/or their activity in dung pats enables the activity of other dung decomposing organisms such as earthworms, soil bacteria, and coprophilous fungi (Holter, 1979, Blackwell and Malloch, 1991). Via dung removal, dung beetles decrease the survival of dung-inhabiting larvae of various pests, blood-sucking flies, and endoparasites (Edwards and Aschenborn, 1987, Sands and Wall, 2017), aerate the soil, thus allowing aerobic bacteria to reduce emission of methane from decomposing dung (Penttilä et al., 2013), affect plant fitness by dispersing seeds from dung (Milotić et al., 2019, DeCastro-Arrazola et al., 2020), and enhance soil fertility (Bang et al., 2005). Dung beetles thus promote resource cycling between plants and animals (Maldonado et al., 2019), and prevent dung accumulation on pastures (Beynon et al., 2015). Dung beetles are, however, among the terrestrial insects most affected by habitat loss, including agriculture intensification, accompanied by high usage of inadvertently harmful antiparasitics, such as ivermectin (Sánchez-Bayo and Wyckhuys, 2019). Due to its low cost and high efficiency against a broad spectrum of parasites, ivermectin is one of the most widely used antiparasitics (Guichon et al., 2000). It causes neural paralysis to Ecdysozoa (Puniamoorthy et al., 2014), making it effective against gastro-intestinal nematodes as well as both internal and external arthropod parasites (Campbell et al., 1983, Sutherland, 1990). Ivermectin is not fully metabolized by animals and is therefore excreted in its active form in dung (Campbell et al., 1983). This is a problem, since ivermectin residues are harmful to dung-feeding arthropods, including dung beetles (Floate, 2007, Lumaret et al., 2012). Depending on the treated herbivore species and the way of administration, the residues can affect dung beetles up to several weeks post-treatment (Sommer et al., 1992, Errouissi et al., 2001, Suarez et al., 2003). Ivermectin can be administered by several routes with different excretion times (in increasing order: oral, intramuscular, subcutaneous, topical, sustained release bolus) (Floate et al., 2005, Canga et

al., 2009). 55 In adult beetles, ivermectin affects their reproduction (O’Hea et al., 2010, Martínez et al., 2017, Rodríguez-Vivas et al., 2020), foraging, olfactory and locomotor abilities (Verdú et al., 2015), and mobility (Martínez et al., 2017, Pérez-Cogollo et al., 2017, Weaving et al., 2020). Larvae are even more affected, as ivermectin residues substantially reduce their survival (O’Hea et al., 2010, Martínez et al., 2017, Pérez-Cogollo et al., 2017, Finch et al., 2020), decrease the number and body size of newly emerged beetles (González-Tokman et al., 2017), and change the offspring sex-ratio in favor of males (González-Tokman et al., 2017). Such adverse effects should lead to serious large-scale alteration of dung beetle communities and hamper the ecosystem service they provide in the form of dung removal. At the community level, use of ivermectin on livestock has been associated with reduced abundance and diversity of dung beetles (Hutton and Giller, 2003, Verdú et al., 2018), and the dung removal rate (Tonelli et al., 2020). Most studies compared dung beetle communities in dung of untreated and recently treated animals (e.g. Sutton et al., 2014). They thus focused on the immediate, direct effects, while long term effects of ivermectin use were rarely investigated (but see Verdú et al., 2018). Yet, these are potentially more important to pasture health. If dung beetle communities recover rapidly, then non-target effects regarding the use of ivermectin are not a serious issue. If, however, it has a lasting effect on dung beetle communities, then ivermectin usage does have a serious, persistent negative influence on dung beetles and the ecosystem services they provide. Information on this important issue is, nevertheless, insufficient, as most relevant studies (e.g. Verdú et al., 2018, Pecenka and Lundgren, 2019) were limited by the number of sites or spatial scale. Although dung removal is the main ecosystem service provided by dung beetles, not all species contribute equally. Their contribution depends on their size, abundance and feeding/nesting strategy. Dung relocating species (i.e., tunnellers and rollers) contribute more than species who do not relocate (Beynon et al., 2012a, Nervo et al., 2014). Among non-relocating dung beetles, species with adults and larvae feeding in the dung (i.e., dwellers) contribute more to dung removal than species with mostly saprophagous larvae feeding on dung mainly as adults (i.e., visitors; genus *Melinopterus*, *Chilothorax*, *Oxyomus*) (Landin, 1961, Christensen and Dobson, 1976, Gittings and Giller, 1997, Finn and Gittings, 2003, Rössner, 2012 and references therein; Buse and Entling, 2020). Ivermectin may thus affect ecosystem services provided by dung beetles not only by decreasing overall abundance and biomass, but also by altering the functional composition of their communities. Indeed, several studies pointed to the reduced numbers of relocating beetles on ivermectin treated sites than the other guilds (Sands and Wall, 2018, Tonelli et al., 2020). However, we are not aware of any study, which would account for the difference between dwellers and visitors. Such an indiscriminate approach might systematically underestimate the effect of ivermectin on the ecosystem services provided by dung beetles. The aim of this study was to investigate how routine use of ivermectin affects dung beetle communities on a landscape scale and to assess its potential effect on ecosystem services the communities provide. Thus, we carried out an extensive, large-scale survey of dung beetles at 26 grazed sites across the Czech Republic. To quantify the effect

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of ivermectin and to distinguish the lasting from immediate effect, the samples were categorized as originating from recently treated (> 8 weeks post application), long ago treated (< 8 weeks post application) or never treated pastures. To account for the effects of herbivore species, seasonal and geographic variability, our sampling included four main herbivore dung types (horse, cattle, sheep, and fallow deer), covered elevations from 180 to 800 m a.s.l., and nearly full seasonal variability. We then compared abundance, species richness, biomass, 57 functionality, and guild composition (i.e., relocators, dwellers, visitors) of dung beetle communities among the treatments. Finally, we discuss the importance of our findings for conservation of biodiversity and ecosystem services and pasture health.

2. Materials and methods

2.1. Study sites

We sampled dung beetles at 26 livestock pastures and game reserves, 25 across the Czech Republic and one in Austria. The sampling covered four regions and an elevation range of 180–800 m a.s.l. The regions include the Bohemian Forest (average annual temperature 6 °C, average annual precipitation 1028 ± 7 mm, average altitude 801 ± 12 m), South Bohemia (8 °C, 732 ± 1 mm, 393 ± 3 m), Central Bohemia (9 °C, 523 ± 16 mm, 227 ± 19 m), and South Moravia (9 ± 1 °C, 606 ± 24 mm, 268 ± 88 m). Sites were

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Section snippets

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sampling, expected lethal or sublethal levels of residues), and (iii) long ago treated (

sampling, expected lethal or sublethal levels of residues), and ii) long-ago treated

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Melinopterus, Chilo thorax) (Landin, 1961, Christensen and Dobson, 1976, Halfpeter and Edmonds, 1982, Gittings and Giller, 1997, Rössner, 2012 and references therein; Buse

Melinopterus, Chilo thorax, Oxyomus) (Landin, 1961, Christensen and Dobson, 1976, Gittings and Giller, 1997, Finn and Gittings, 2003, Rössner, 2012 and references therein; Buse

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118/238	SUBMITTED TEXT	82 WORDS	100% MATCHING TEXT	82 WORDS
	Results In total, we sampled 31,578 individuals of 58 species of dung beetles. For the complete list of species, their abundances in all treatments and guild assignment, see Appendix, Table A2, and Tab. A3 for the list of species records per localities. Use of ivermectin did affect abundance, species richness and functionality but not total biomass of dung beetles (Table 1). Compared to never treated pastures, per pat abundance was reduced by 44% on long ago treated pastures, although only marginally		Results In total, we sampled 31,578 individuals of 58 species of dung beetles. For the complete list of species, their abundances in all treatments and guild assignment, see Appendix, Table A2, and Tab. A3 for the list of species records per localities. Use of ivermectin did affect abundance, species richness and functionality but not total biomass of dung beetles (Table 1). Compared to never treated pastures, per pat abundance was reduced by 44% on long ago treated pastures, although only marginally	
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	Discussion Our results clearly demonstrate that ivermectin use leads to serious changes in dung beetle communities. First, dung of treated animals hosted communities poorer in species than untreated ones. Second, ivermectin use decreased the dung removal potential (functionality) of affected communities. Third, there is both short- and long-term effect of ivermectin use on dung beetle communities. Our sampling included the four main herbivore dung types of the temperate Europe; it nearly fully accounted		Discussion Our results clearly demonstrate that ivermectin use leads to serious changes in dung beetle communities. First, dung of treated animals hosted communities poorer in species than untreated ones. Second, ivermectin use decreased the dung removal potential (functionality) of affected communities. Third, there is both short- and long-term effect of ivermectin use on dung beetle communities. Our sampling included the four main herbivore dung types of the temperate Europe; it nearly fully accounted	
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120/238	SUBMITTED TEXT	76 WORDS	100% MATCHING TEXT	76 WORDS
	Conclusions We have found serious differences in diversity and guild composition of dung beetle communities between sites where animals are treated with ivermectin and sites without treatment. Use of ivermectin as a veterinary drug decreases species richness and seriously affects the functionality of non-target dung beetle communities via 73 changes in guild composition. If the current practice of treating grazing animals with ivermectin continues, in addition to the isolation of grazed sites, ecosystem		Conclusions We have found serious differences in diversity and guild composition of dung beetle communities between sites where animals are treated with ivermectin and sites without treatment. Use of ivermectin as a veterinary drug decreases species richness and seriously affects the functionality of non-target dung beetle communities via changes in guild composition. If the current practice of treating grazing animals with ivermectin continues, in addition to the isolation of grazed sites, ecosystem	
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Acknowledgments We are thankful to the administrations of the Šumava National Park, Podyjí National Park, Pálava Protected Landscape Area, and all owners for their kind cooperation, to Matthew Sweney for language correction, and to Petr Šmilauer and Simon Thorn for their valuable advice regarding statistics. We are also thankful to the three reviewers for their insightful comments. This work was partially funded by the Program AV21 (Czech Academy of Sciences) and by the Regional Cooperation of the Regions and		Acknowledgments We are thankful to the administrations of the Šumava National Park, Podyjí National Park, Pálava Protected Landscape Area, and all owners for their kind cooperation, to Matthew Sweney for language correction, and to Petr Šmilauer and Simon Thorn for their valuable advice regarding statistics. We are also thankful to the three reviewers for their insightful comments. This work was partially funded by the Program AV21 (Czech Academy of Sciences) and by the Regional Cooperation of the Regions and		
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Bang, H.S., Lee, J.H., Kwon, O.S., Na, Y.E., Jang, Y.S., Kim, W.H., 2005. Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Appl. Soil. Ecol. 29, 165–171. https://doi.org/10.1016/j.apsoil.2004.11.001.		Bang, H. S. , Lee, J.-H. , Kwon, O. S. , Na, Y. E. , Jang, Y. S. , & Kim, W. H. (2005). Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Applied Soil https://doi.org/10.1016/j.apsoil.2004.11.001 [		
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Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4.		Bates D, Mächler M, Bolker B, Walker S. Fitting Linear Mixed-Effects Models Using lme4.		
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https://doi.org/10.18637/jss.v067.i01. Beynon, S.A., Mann, D.J., Slade, E.M., Lewis, O.T., 2012		https://doi.org/10.1094/FG-2006-0711-02-RS [Google Scholar] • Beynon, S. A. , Mann, D. J. , Slade, E. M. , & Lewis, O. T. (2012).		
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	Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems. J. Appl. Ecol. 49, 1365–1372.		Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems J. Appl. Ecol. (2012) •	
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	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5838066/			
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	Campbell, W.C., Fisher, M.H., Stapley, E.O., Albers-Schonberg, G., Jacob, T.A., 1983. Ivermectin: a potent new antiparasitic agent. Science 221, 823–828.		Campbell, W.C., Fisher, M.H., Stapley, E.O., Albers-Schönberg, G. & Jacob, T.A. (1983) Ivermectin: a potent new antiparasitic agent. Science 221, 823–828.	
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	Czech Statistical Office 2020. Table 5 Livestock – Czech Republic. Created 29.05.2020 (code: 270147–20). Available from		Czech Statistical Office 2020. Table 5 Livestock – Czech Republic. Created 29.05.2020 (code: 270147–20). Available from... •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
138/238	SUBMITTED TEXT	29 WORDS	92% MATCHING TEXT	29 WORDS
	DeCastro-Arrazola, I., Hortal, J., Noriega, J.A., Sánchez-Piñero, F., 2020. Assessing the functional relationship between dung beetle traits and dung removal, burial, and seedling emergence. Ecology 101 (10), 03138. https://doi.org/10.1002/ecology.10103138		deCastro-Arrazola, I., Hortal, J., Noriega, J. A., Sánchez-Piñero, F. (2020). Assessing the functional relationship between dung beetle traits and dung removal, burial, and seedling emergence. Ecology 101:e03138. doi: 10.1002/ecology.10103138	
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139/238	SUBMITTED TEXT	28 WORDS	82% MATCHING TEXT	28 WORDS
	P.B., Aschenborn, H.H., 1987. Patterns of nesting and dung burial in Onitis dung beetles - implications for pasture productivity and fly control. J. Appl. Ecol. 24, 837–851.		P.B. Edwards et al. Patterns of nesting and dung burial in Onitis dung beetles - implications for pasture productivity and fly control J. Appl. Ecol. (1987) •	
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140/238	SUBMITTED TEXT	14 WORDS	100% MATCHING TEXT	14 WORDS
	How agricultural intensification affects biodiversity and ecosystem services. Adv. Ecol. Res. 55, 43–97.		How agricultural intensification affects biodiversity and ecosystem services Adv. Ecol. Res. (2016) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
141/238	SUBMITTED TEXT	30 WORDS	94% MATCHING TEXT	30 WORDS
	Errouissi, F., Lumaret, J.P., 2010. Field effects of faecal residues from ivermectin slow- release boluses on the attractiveness of cattle dung to dung beetles. Med. Vet. Entomol. 24, 433–440. https://doi.org/10.1111/j.1365-3113.2010.04333.x		Errouissi F., Lumaret J.P. Field effects of faecal residues from ivermectin slow-release boluses on the attractiveness of cattle dung to dung beetles. Med Vet. Entomol. 2010;24:433–440. doi: 10.1111/j.1365-3113.2010.04333.x	
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142/238	SUBMITTED TEXT	37 WORDS	100% MATCHING TEXT	37 WORDS
	Errouissi, F., Alvinerie, M., Galtier, P., Kerboeuf, D., Lumaret, J.P., 2001. The negative effects of the residues of ivermectin in cattle dung using a sustained- release bolus on Aphodius constans (Duft.) (Coleoptera: Aphodiidae). Vet. Res. 32, 421–427.		Errouissi F, Alvinerie M, Galtier P, Kerboeuf D, Lumaret J-P. The negative effects of the residues of ivermectin in cattle dung using a sustained-release bolus on Aphodius constans (Duft.) (Coleoptera: Aphodiidae). Vet Res. 2001;32: 421–427.	
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143/238	SUBMITTED TEXT	39 WORDS	67% MATCHING TEXT	39 WORDS
	Implications of endectocide residues on the survival of aphodiine dung beetles: a meta-analysis. Environ. Toxicol. Chem. 39, 863–872. https://doi.org/10.1002/etc.4671 . Finn, J., Gittings, T., 2003. A review of competition in north temperate dung beetle communities. Ecol. Entomol. 28, 1–13.		Implications of endectocide residues on the survival of aphodiine dung beetles: a meta-analysis Environ. Toxicol. Chem. (2020)J. Finn et al. A review of competition in north temperate dung beetle communities Ecol. Entomol. (2003) •	
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	K.D., 1998. Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada. Bull. Entomol. Res. 88, 25–35.		K.D. Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada Bull. Entomol. Res. (1998) •	
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	K.D., 2007. Endectocide residues affect insect attraction to dung from treated cattle: implications for toxicity tests. Med. Vet. Entomol. 21, 312–322.		K.D. Floate Endectocide residues affect insect attraction to dung from treated cattle: implications for toxicity tests Med. Vet. Entomol. (2007) •	
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146/238	SUBMITTED TEXT	29 WORDS	73% MATCHING TEXT	29 WORDS
	https://doi.org/10.1111/j.1365-2915.2007.00702.x . Floate, K.D., Wardhaugh, K.G., Boxall, A.B.A., Sherratt, T.N., 2005. Fecal residues of veterinary parasiticides: nontarget effects in the pasture environment. Annu. Rev. Entomol. 50, 153–179. https://doi.org/10.1146/annurev.ento.50.071803.130341 .		https://doi.org/10.1139/z72-076 [Google Scholar] D. , Wardhaugh, K. G. , Boxall, A. B. A. , & Sherratt, T. N. (2005). Faecal residues of veterinary parasiticides: Nontarget effects in the pasture environment. Annual Review of https://doi.org/10.1146/annurev.ento.50.071803.130341 [	
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	science.1111772. Fox, J., Weisberg, S., 2019. An (R) Companion to Applied Regression. Thousand Oaks (		Science (2005) • Fox, J., Weisberg, S., 2019. An (R) Companion to Applied Regression. Thousand Oaks...	
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148/238	SUBMITTED TEXT	23 WORDS	100% MATCHING TEXT	23 WORDS
	Anthelmintic resistance to ivermectin and moxidectin in 78 gastrointestinal nematodes of cattle in Europe. Int. J. Parasitol. Drug 5, 163– 171.		Anthelmintic resistance to ivermectin and moxidectin in gastrointestinal nematodes of cattle in Europe (2015) •	
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	Gittings, T., Giller, P., 1997. Life history traits and resource utilisation in an assemblage of north temperate Aphodius dung beetles (Coleoptera: Scarabaeidae). Ecography 20, 55–66.		Gittings, T. & Giller, P.S. (1997) Life history traits and resource utilisation in an assemblage of north temperate Aphodius dung beetles (Coleoptera: Scarabaeidae). Ecography 20, 55–66.	
	W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...			
150/238	SUBMITTED TEXT	17 WORDS	100% MATCHING TEXT	17 WORDS
	Ivermectin alters reproductive success, body condition and sexual trait expression in dung beetles. Chemosphere 178, 129–135.		Ivermectin alters reproductive success, body condition and sexual trait expression in dung beetles Chemosphere (2017) •	
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151/238	SUBMITTED TEXT	23 WORDS	100% MATCHING TEXT	23 WORDS
	Environmentally-realistic concentrations of anthelmintic drugs affect survival and motility in the cosmopolitan earthworm Lumbricus terrestris (Linnaeus, 1758). Appl. Soil. Ecol. 137, 87–95.		Environmentally-realistic concentrations of anthelmintic drugs affect survival and motility in the cosmopolitan earthworm Lumbricus terrestris (Linnaeus, 1758) Appl. Soil. Ecol. (2019) •	
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152/238	SUBMITTED TEXT	22 WORDS	97% MATCHING TEXT	22 WORDS
	Halffter, G., Edmonds, W.D., 1982. The nesting behavior of dung beetles (Scarabaeinae). An Ecological and Evolutive Approach. Instituto de Ecología, Mexico.		Halffter, G. and W.D. 1982. The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutive approach. Instituto Ecología, Mexico	
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153/238	SUBMITTED TEXT	19 WORDS	100% MATCHING TEXT	19 WORDS
	J., 2006. Toxicity of four veterinary parasiticides on larvae of the dung beetle Aphodius constans in the laboratory.			
	SA VET344s2_14_uid_31866453_fname_2244_1409830371_44840.docx (D18779600)			
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	https://doi.org/10.1897/06-022r2.1 . Holter, P., 1977. An experiment on dung removal by Aphodius larvae (Scarabaeidae) and earthworms. Oikos 28, 130–136. https://doi.org/10.2307/3543332 . Holter, P., 1979. Effect of dung-beetles (Aphodius spp) and earthworms on the disappearance of cattle dung. Oikos 32, 393–402.		https://doi.org/10.1515/9781400862092 [Google Scholar] • Holter, P. (1977). An experiment on dung removal by Aphodius larvae (Scarabaeidae) and earthworms. Oikos, 28, 130–136. https://doi.org/10.2307/3543332 [Google Scholar] Effect of dung-beetles (Aphodius spp.) and earthworms on the disappearance of cattle dung. Oikos, 32, 393–402.	
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155/238	SUBMITTED TEXT	24 WORDS	97% MATCHING TEXT	24 WORDS
	Hutton, S.A., Giller, P.S., 2003. The effects of the intensification of agriculture on northern temperate dung beetle communities. J. Appl. Ecol. 40, 994–1007.		Hutton, S. A., and Giller, P. S. 2003. The effects of the intensification of agriculture on northern temperate dung beetle communities. J. Appl. Ecol. 40:994–1007.	
	W https://kids.frontiersin.org/articles/10.3389/frym.2021.583675			
156/238	SUBMITTED TEXT	17 WORDS	96% MATCHING TEXT	17 WORDS
	R.M., 2004. Drug resistance in nematodes of veterinary importance: a status report. Trends Parasitol. 20, 477–481.		R.M. Kaplan Drug resistance in nematodes of veterinary importance: a status report Trends Parasitol. (2004) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
157/238	SUBMITTED TEXT	29 WORDS	98% MATCHING TEXT	29 WORDS
	Krüger, K., Scholtz, C.H., 1998. Changes in the structure of dung insect communities after ivermectin usage in a grassland ecosystem. I. Impact of ivermectin under drought conditions. Acta		Krüger, K. & Scholtz, C.H. (1998) Changes in the structure of dung insect communities after ivermectin usage in a grassland ecosystem. I. Impact of ivermectin under drought conditions. Acta	
	W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...			
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	Kadiri, N., 1995. The influence of the first wave of colonizing insects on cattle dung dispersal. Pedobiologia 39, 506–517.		Kadiri N (1995) The influence of the first wave of colonizing insects on cattle dung dispersal. Pedobiologia 39: 506–517.	
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	F., 2002. Use of anthelmintics in herbivores and evaluation of risks for the non target fauna of pastures.			
	SA VET347s2_14_uid_31553123_fname_2074_1411114188_23209.docx (D18779824)			

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	Lumaret, J.P., Errouissi, F., Floate, K., Römbke, J., Wardhaugh, K., 2012. A review on the toxicity and non-target effects of macrocyclic lactones in terrestrial and aquatic environments.		Lumaret, J.-P., Errouissi, F., Floate, K., Römbke, J., and Wardhaugh, K. 2012. A review on the toxicity and non-target effects of macrocyclic lactones in terrestrial and aquatic environments.	
	W https://doi.org/10.4039/tce.2017.11			
161/238	SUBMITTED TEXT	17 WORDS	92% MATCHING TEXT	17 WORDS
	Maldonado, M.B., Aranibar, J.N., Serrano, A.M., Chacoff, N.P., Vázquez, D.P., 2019. Dung beetles and nutrient cycling		Maldonado, M.B.; Aranibar, J.N.; Serrano, A.M.; Chacoff, N.P.; Vázquez, D.P. Dung beetles and nutrient cycling	
	W https://www.mdpi.com/1424-2818/15/1/91			
162/238	SUBMITTED TEXT	22 WORDS	100% MATCHING TEXT	22 WORDS
	Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness. Agric. Ecosyst. Environ. 264, 9–14.		Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness Agric. Ecosyst. Environ. (2018) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
163/238	SUBMITTED TEXT	41 WORDS	94% MATCHING TEXT	41 WORDS
	Martínez, M.I., Lumaret, J.P., Zayas, R.O., Kadiri, N., 2017. The effects of sublethal and lethal doses of ivermectin on the reproductive physiology and larval development of the dung beetle <i>Euoniticellus intermedius</i> (Coleoptera: 81 Scarabaeidae). Can. Entomol. 149, 461–472.		Martínez M. I, Lumaret J-P, Ortiz Zayas R, Kadiri N. The effects of sublethal and lethal doses of ivermectin on the reproductive physiology and larval development of the dung beetle <i>Euoniticellus intermedius</i> (Coleoptera: Scarabaeidae). Can Entomol. 2017;12: 1–12. •	
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164/238	SUBMITTED TEXT	27 WORDS	94% MATCHING TEXT	27 WORDS
	Milotić, T., Quidé, S., Van Loo, T., Hoffmann, M., 2017. Linking functional group richness and ecosystem functions of dung beetles: an experimental quantification. Oecologia 183, 177–190. https://doi.org/10.1007/s00344-017-0400-0		Milotić T., Quidé S., Van Loo T., Hoffmann M. Linking functional group richness and ecosystem functions of dung beetles: An experimental quantification. Oecologia. 2017;183:177–190. doi: 10.1007/s00344-017-0400-0	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
165/238	SUBMITTED TEXT	22 WORDS	100% MATCHING TEXT	22 WORDS
	Milotić, T., Baltzinger, C., Eichberg, C., Eycott, A.E., Heurich, M., Müller, J., Noriega, J. A., Menendez, R., Stadler, J., Ádám, R., 2017. Linking functional group richness and ecosystem functions of dung beetles: an experimental quantification. Oecologia 183, 177–190. https://doi.org/10.1007/s00344-017-0400-0		Milotić T., Baltzinger C., Eichberg C., Eycott A.E., Heurich M., Müller J., Noriega J.A., Menendez R., Stadler J., Ádám R., 2017. Linking functional group richness and ecosystem functions of dung beetles: An experimental quantification. Oecologia. 2017;183:177–190. doi: 10.1007/s00344-017-0400-0	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			

166/238	SUBMITTED TEXT	24 WORDS	87% MATCHING TEXT	24 WORDS
	Functionally richer communities improve ecosystem functioning: dung removal and secondary seed dispersal by dung beetles in the Western Palearctic. J. Biogeogr. 46, 70–82. https://doi.		Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palearctic. J. Biogeogr. 2019;46:70–82. doi: 10.1111/	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
167/238	SUBMITTED TEXT	29 WORDS	100% MATCHING TEXT	29 WORDS
	Nervo, B., Tocco, C., Caprio, E., Palestini, C., Rolando, A., 2014. The effects of body mass on dung removal efficiency in dung beetles. PLoS One 9 (9), 107699.		Nervo, B.; Tocco, C.; Caprio, E.; Palestini, C.; Rolando, A. The effects of body mass on dung removal efficiency in dung beetles. PLoS ONE 2014, 9,	
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	Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E., Network, S.R., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles.		Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., and M.E. 2008. The Scarabaeinae research Ecological functions and ecosystem services provided by Scarabaeinae dung beetles.	
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169/238	SUBMITTED TEXT	21 WORDS	100% MATCHING TEXT	21 WORDS
	Effects of herd management and the use of ivermectin on dung arthropod communities in grasslands. Basic. Appl. Ecol. 40, 19–29.		Effects of herd management and the use of ivermectin on dung arthropod communities in grasslands Appl. Ecol. (2019) •	
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170/238	SUBMITTED TEXT	28 WORDS	92% MATCHING TEXT	28 WORDS
	Penttilä, A., Slade, E.M., Simojoki, A., Riutta, T., Minkkinen, K., Roslin, T., 2013. Quantifying beetle-mediated effects on gas fluxes from dung pats. PLoS One 8 (8), 71454. https://doi.		Penttilä, A., Slade, E. M., Simojoki, A., Riutta, T., Minkkinen, K., and Roslin, T. (2013). Quantifying beetle-mediated effects on gas fluxes from dung pats. PLoS One 8:e71454. doi: 10.1371/	
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171/238	SUBMITTED TEXT	34 WORDS	85% MATCHING TEXT	34 WORDS
	Piccini, I., Nervo, B., Forshage, M., Celi, L., Palestini, C., Rolando, A., Roslin, T., 2018. Dung beetles as drivers of ecosystem multifunctionality: are response and effect traits interwoven? Sci. Total Environ. 616, 1440–1448. https://doi.		Piccini, I., Nervo, B., Forshage, M., Celi, L., Palestini, C., Rolando, A., et Dung beetles as drivers of ecosystem multifunctionality: Are response and effect traits interwoven? Sci. Total Environ. 616, 1440–1448. doi: 10.1016/	
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172/238	SUBMITTED TEXT	22 WORDS	95% MATCHING TEXT	22 WORDS
	R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ .		R Core Team. R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 2021; Available https://www.R-project.org/ (	
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173/238	SUBMITTED TEXT	32 WORDS	79% MATCHING TEXT	32 WORDS
	Arcila- Fuentes, W.R., Ojeda-Chi, M.M., Martínez-M, I., 2020. Evaluation of the attraction, lethal and sublethal effects of the faeces of ivermectin- treated cattle on the dung beetle Digitonthophagus gazella (Coleoptera: Scarabaeidae). Austral		Arcila-Fuentes, William R Ojeda-Chi, Melina M and Martínez-M, Imelda 2020. Evaluation of the attraction, lethal and sublethal effects of the faeces of ivermectin-treated cattle on the dung beetle Digitonthophagus gazella (Coleoptera: Scarabaeidae). Austral	
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174/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27.		Worldwide decline of the entomofauna: a review of its drivers Biol. Conserv. (2019) •	
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175/238	SUBMITTED TEXT	20 WORDS	100% MATCHING TEXT	20 WORDS
	Sands, B., Wall, R., 2017. Dung beetles reduce livestock gastrointestinal parasite availability on pasture. J. Appl. Ecol. 54, 1180–1189.		Sands B, Wall R. Dung beetles reduce livestock gastrointestinal parasite availability on pasture. J Appl Ecol. 2016; •	
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176/238	SUBMITTED TEXT	17 WORDS	100% MATCHING TEXT	17 WORDS
	Sustained parasiticide use in cattle farming affects dung beetle functional assemblages. Agric. Ecosyst. Environ. 265, 226–235.		Sustained parasiticide use in cattle farming affects dung beetle functional assemblages Agric. Ecosyst. Environ. (2018) •	
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177/238	SUBMITTED TEXT	17 WORDS	100% MATCHING TEXT	17 WORDS
	Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat. Acta Oecol. 46, 17–24.		Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat Acta Oecol (2013) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
178/238	SUBMITTED TEXT	41 WORDS	69% MATCHING TEXT	41 WORDS
	Sommer, C., Steffansen, B., Nielsen, B.O., Grønvold, J., Jensen, K.M.V., Jespersen, J.B., Springborg, J., Nansen, P., 1992. Ivermectin excreted in cattle dung after subcutaneous injection or pour-on treatment - concentrations and impact on dung fauna. Bull. Entomol. Res. 82, 257–264.		Sommer C, Steffansen B, Nielsen BO, Grønvold J, Vagn Jensen K-M, Brøchner Jespersen J, et al. Ivermectin excreted in cattle dung after subcutaneous injection or pour-on treatment: concentrations and impact on dung fauna. Bull Entomol Res. 1992;82: 257. •	
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	Strong, L., Wall, R., 1994. Effects of ivermectin and moxidectin on the insects of cattle dung.		Strong, L. & Wall, R. (1994) Effects of ivermectin and moxidectin on the insects of cattle dung.	
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180/238	SUBMITTED TEXT	24 WORDS	94% MATCHING TEXT	24 WORDS
	Suarez, V.H., Lifschitz, A.L., Sallovitz, J.M., Lanusse, C.E., 2003. Effects of ivermectin and doramectin faecal residues on the invertebrate colonization of cattle dung.		Suarez, V.H., Lifschitz, A.L., Sallovitz, J.M. & Lanusse, C.E. (2003) Effects of ivermectin and doramectin faecal residues on the invertebrate colonisation of cattle dung.	
	W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...			
181/238	SUBMITTED TEXT	21 WORDS	97% MATCHING TEXT	21 WORDS
	G., Bennett, J., Bateman, M., 2014. Effects of ivermectin residues on dung invertebrate communities in a UK farmland habitat. Insect			
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182/238	SUBMITTED TEXT	28 WORDS	100% MATCHING TEXT	28 WORDS
	Contribution of the timing of the successive waves of insect colonisation to dung removal in a grazed agro- 85 ecosystem. Eur. J. Soil. Biol. 69, 88–93.		Contribution of the timing of the successive waves of insect colonisation to dung removal in a grazed agro-ecosystem Biol. •	
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	Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub- mountainous landscape of Central Italy. Peerj 5, 2780. https://doi.		Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub-mountainous landscape of Central Italy. PeerJ. 2017;5:e2780. doi: 10.7717/	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
184/238	SUBMITTED TEXT	35 WORDS	95% MATCHING TEXT	35 WORDS
	Tonelli, M., Verdú, J.R., Morelli, F., Zunino, M., 2020. Dung beetles: functional identity, not functional diversity, accounts for ecological process disruption caused by the use of veterinary medical products. J. Insect Conserv. 24, 643– 654. https://doi.		Tonelli M., Verdú J.R., Morelli F., Zunino M. Dung beetles: Functional identity, not functional diversity, accounts for ecological process disruption caused by the use of veterinary medical products. J. Insect Conserv. 2020;24:643–654. doi: 10.1007/	
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185/238	SUBMITTED TEXT	37 WORDS	60% MATCHING TEXT	37 WORDS
	Verdú, J.R., Cortez, V., Ortiz, A.J., González-Rodríguez, E., Martínez-Pinna, J., Lumaret, J.P., Lobo, J.M., Numa, C., Sánchez-Piñero, F., 2015. Low doses of ivermectin cause sensory and locomotor disorders in dung beetles. Sci. Rep. 5, 13912. https://doi.org/10.1038/srep13912 .		Verdú, J.R., Cortez, V., Ortiz, A.J., González-Rodríguez, E., Pinna, J.M., Lumaret, J.-P, et Low doses of ivermectin cause sensory and locomotor disorders in dung beetles. Scientific https://doi.org/10.1038/srep13912 .	
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186/238	SUBMITTED TEXT	21 WORDS	100% MATCHING TEXT	21 WORDS
	Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study. Sci. Total. Environ. 618, 219–228.		Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study Sci. Total. Environ. (2018) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
187/238	SUBMITTED TEXT	26 WORDS	97% MATCHING TEXT	26 WORDS
	Weaving, H., Sands, B., Wall, R., 2020. Reproductive sublethal effects of macrocyclic lactones and synthetic pyrethroids on the dung beetle 86 <i>Onthophagus similis</i> .		Weaving, H. Sands, B. and Wall, R. 2020. Reproductive sublethal effects of macrocyclic lactones and synthetic pyrethroids on the dung beetle <i>Onthophagus similis</i> .	
	W https://doi.org/10.4039/tce.2017.11			
188/238	SUBMITTED TEXT	26 WORDS	100% MATCHING TEXT	26 WORDS
	Webb, L., Beaumont, D.J., Nager, R.G., McCracken, D.I., 2010. Field-scale dispersal of <i>Aphodius</i> dung beetles (Coleoptera: Scarabaeidae) in response to avermectin treatments on pastured cattle.			
	SA VET344s2_14_uid_31631185_fname_2244_1411101604_21807.docx (D18779549)			

189/238	SUBMITTED TEXT	23 WORDS	100% MATCHING TEXT	23 WORDS
	Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67, 1–48.		Bates D, Mächler M, Bolker B, Walker S. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software. 2015;67(1):1–48. •	
	W https://doi.org/10.1371/journal.pone.0185809			
190/238	SUBMITTED TEXT	25 WORDS	100% MATCHING TEXT	25 WORDS
	Buse, J. & Entling, M.H. (2020) Stronger dung removal in forests compared with grassland is driven by trait composition and biomass of dung beetles.		Buse, J.; Entling, M.H. Stronger dung removal in forests compared with grassland is driven by trait composition and biomass of dung beetles.	
	W https://www.mdpi.com/1424-2818/15/1/91			
191/238	SUBMITTED TEXT	24 WORDS	100% MATCHING TEXT	24 WORDS
	Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles. Biological Conservation, 187, 112–119. 119		Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles Conservation,	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
192/238	SUBMITTED TEXT	13 WORDS	100% MATCHING TEXT	13 WORDS
	Summary of the morphological and ecological traits of central European dung beetles.		Summary of the morphological and ecological traits of Central European dung beetles	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
193/238	SUBMITTED TEXT	28 WORDS	98% MATCHING TEXT	28 WORDS
	Arrazola, I., Hortal, J., Noriega, J.A. & Sánchez-Piñero, F. (2020) Assessing the functional relationship between dung beetle traits and dung removal, burial, and seedling emergence. Ecology, 101,1–7.		Arrazola, I., Hortal, J., Noriega, J. A., Sánchez-Piñero, F. (2020). Assessing the functional relationship between dung beetle traits and dung removal, burial, and seedling emergence. Ecology 101:	
	W https://www.frontiersin.org/articles/863669			
194/238	SUBMITTED TEXT	35 WORDS	90% MATCHING TEXT	35 WORDS
	Lobo, J.M., Martín-Piera, F. & Veiga, C.M. (1988) Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.). I. Características determinantes de su capacidad de captura. Revue d'		Lobo J.M., Martín-Piera F., Veiga C.M. Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.): I. Características determinantes de su capacidad de captura. Rev. D'	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			

195/238	SUBMITTED TEXT	18 WORDS	100% MATCHING TEXT	18 WORDS
	Maldonado, M.B., Aranibar, J.N., Serrano, A.M., Chacoff, N.P. & Vázquez, D.P. (2019) Dung beetles and nutrient cycling		Maldonado, M.B.; Aranibar, J.N.; Serrano, A.M.; Chacoff, N.P.; Vázquez, D.P. Dung beetles and nutrient cycling	
	W https://www.mdpi.com/1424-2818/15/1/91			
196/238	SUBMITTED TEXT	22 WORDS	100% MATCHING TEXT	22 WORDS
	et al. (2019) Functionally richer communities improve ecosystem functioning: dung removal and secondary seed dispersal by dung beetles in the Western		et al. Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
197/238	SUBMITTED TEXT	29 WORDS	100% MATCHING TEXT	29 WORDS
	Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S. & Favila, M.E. (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation, 141, 1461–1474.		Nichols, E.; Spector, S.; Louzada, J.; Larsen, T.; Amezcuita, S.; Favila, M.E. (2008). "Ecological functions and ecosystem services provided by Scarabaeinae dung beetles". Biological Conservation. 141 (6): 1461–1474.	
	W https://en.wikipedia.org/wiki/Dung_beetle			
198/238	SUBMITTED TEXT	29 WORDS	100% MATCHING TEXT	29 WORDS
	Noriega, J.A., March-Salas, M., Castillo, S., García-Q, H., Hortal, J. & Santos, A.M.C. (2021) Human perturbations reduce dung beetle diversity and dung removal ecosystem function. Biotropica, 53, 753–766.		Noriega, J.A.; March-Salas, M.; Castillo, S.; García-Q, H.; Hortal, J.; Santos, A.M.C. Human perturbations reduce dung beetle diversity and dung removal ecosystem function. Biotropica 2021, 53, 753–766. [	
	W https://www.mdpi.com/1424-2818/15/1/91			
199/238	SUBMITTED TEXT	14 WORDS	100% MATCHING TEXT	14 WORDS
	Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat. Acta		Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat Acta	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
200/238	SUBMITTED TEXT	24 WORDS	100% MATCHING TEXT	24 WORDS
	Spector, S. (2006) Scarabaeine dung beetles (coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. The Coleopterists Bulletin, 60, 71–83.		Spector, S. 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. The Coleopterists Bulletin, 60: 71–83.	
	W https://doi.org/10.4039/tce.2017.11			

201/238	SUBMITTED TEXT	31 WORDS	100% MATCHING TEXT	31 WORDS
	Tonelli, M., Verdú, J.R., Morelli, F. & Zunino, M. (2020) Dung beetles: functional identity, not functional diversity, accounts for ecological process disruption caused by the use of veterinary medical products. Tonelli M., Verdú J.R., Morelli F., Zunino M. Dung beetles: Functional identity, not functional diversity, accounts for ecological process disruption caused by the use of veterinary medical products. W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
202/238	SUBMITTED TEXT	22 WORDS	100% MATCHING TEXT	22 WORDS
	Gratton, C. (2014) Insects as drivers of ecosystem processes. Current Opinion in Insect Science, 2, 26–32. 129 Gratton C. Insects as drivers of ecosystem processes. Current Opinion in Insect Science. 2014;2:26–32. • W https://doi.org/10.1371/journal.pone.0185809			
203/238	SUBMITTED TEXT	57 WORDS	50% MATCHING TEXT	57 WORDS
	Onthophagus coenobita (Herbst, 1783) 251 294 462 Onthophagus fracticornis (Preyssler, 1790) 201 215 46 Onthophagus illyricus (Scopoli, 1763) 3 2 Onthophagus medius (Kugelann, 1792) 1 Onthophagus ovatus (Linné, 1758) 5510 3440 281 Onthophagus similis (Scriba, 1790) 1 Onthophagus verticicornis (Laicharting, 1781) 8022 10506 16356 Onthophagus coenobita (Herbst, 1783) 3 40 43 Onthophagus fracticornis (Preyssler, 1790) 41 7483 7524 Onthophagus illyricus (Scopoli, 1763) 0 7 7 Onthophagus joannae Goljan, 1953 10 980 990 Onthophagus lemur (Fabricius, 1781) 0 32 32 Onthophagus taurus (Schreber, 1759) 1 6 7 Onthophagus vacca (Linnaeus, 1767) 0 1 1 verticicornis (Laicharting, 1781) 47 1065 1112 W https://doi.org/10.3390/insects12090781			
204/238	SUBMITTED TEXT	21 WORDS	100% MATCHING TEXT	21 WORDS
	Understanding the drivers of β-diversity improves conservation prioritization for Central European dung beetles Biological Conservation (2022) 273, 109682 Understanding the drivers of β-diversity improves conservation prioritization for Central European dung beetles 2022, Biological Conservation W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
205/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Understanding the drivers of β-diversity improves conservation prioritization for Central European dung beetles Understanding the drivers of β-diversity improves conservation prioritization for Central European dung beetles 2022, W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			

206/238	SUBMITTED TEXT	256 WORDS	100% MATCHING TEXT	256 WORDS
	The conversion and degradation of natural habitats has caused global declines in terrestrial insect diversity. Conserving insect diversity has therefore gained increasing attention in international conservation agendas. Dung beetles (Geotrupidae, Scarabaeidae) are diverse and abundant coprophagous insects who remove dung and enhance nutrient cycling. Today, half of Central European dung beetle species are threatened. While past research has concentrated on local (α-diversity) of dung beetles, the compositional differences between sites (β-diversity) have been largely neglected. However, maximizing the overall outcome of conservation measures requires a detailed understanding of the factors determining compositional differences between sites. We separated β-diversity of dung beetle communities, sampled across the Czech Republic, into independent components of spatial turnover and nestedness. We tested the relative importance of space, temperature, precipitation, elevation, season, grazing herbivore and antiparasitic treatment via multiple regressions for distance matrices to reveal which factors drive the β-diversity of dung beetle communities. Our results show that β-diversity of dung beetle communities is mostly driven by spatial distance, followed by similarly strong effects of season and mean temperature. Herbivore type and antiparasitic treatment had lesser influence than environment but can be influenced by conservation management. Nevertheless, antiparasitic treatment increased nestedness and resulted in an overall lower γ-diversity. Based on the principle of complementarity, we recommend – in order of decreasing importance – giving (1) conservation priority to the most distant sites, under (2) the largest differences in mean annual temperature, ensure (3) year-round grazing by (4) multiple herbivore species, and (5) avoid using antiparasitics. 157			
	The conversion and degradation of natural habitats has caused global declines in terrestrial insect diversity. Conserving insect diversity has therefore gained increasing attention in international conservation agendas. Dung beetles (Geotrupidae, Scarabaeidae) are diverse and abundant coprophagous insects who remove dung and enhance nutrient cycling. Today, half of Central European dung beetle species are threatened. While past research has concentrated on local (α-diversity) of dung beetles, the compositional differences between sites (β-diversity) have been largely neglected. However, maximizing the overall outcome of conservation measures requires a detailed understanding of the factors determining compositional differences between sites. We separated β-diversity of dung beetle communities, sampled across the Czech Republic, into independent components of spatial turnover and nestedness. We tested the relative importance of space, temperature, precipitation, elevation, season, grazing herbivore and antiparasitic treatment via multiple regressions for distance matrices to reveal which factors drive the β-diversity of dung beetle communities. Our results show that β-diversity of dung beetle communities is mostly driven by spatial distance, followed by similarly strong effects of season and mean temperature. Herbivore type and antiparasitic treatment had lesser influence than environment but can be influenced by conservation management. Nevertheless, antiparasitic treatment increased nestedness and resulted in an overall lower γ-diversity. Based on the principle of complementarity, we recommend – in order of decreasing importance – giving (1) conservation priority to the most distant sites, under (2) the largest differences in mean annual temperature, ensure (3) year-round grazing by (4) multiple herbivore species, and (5) avoid using antiparasitics. •			
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
207/238	SUBMITTED TEXT	30 WORDS	84% MATCHING TEXT	30 WORDS
	Acknowledgments We are thankful to the administrations of the Šumava National Park, Podyjí National Park, Pálava Protected Landscape Area, Prague City Hall, and all owners for their kind cooperation,			
	Acknowledgments We are thankful to the administrations of the Šumava National Park, Podyjí National Park, Pálava Protected Landscape Area, and all owners for their kind cooperation,			
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
208/238	SUBMITTED TEXT	21 WORDS	94% MATCHING TEXT	21 WORDS
	This work was partially funded by the Program AV21 (Czech Academy of Sciences), the Regional Cooperation of the Regions and			
	This work was partially funded by the Program AV21 (Czech Academy of Sciences) and by the Regional Cooperation of the Regions and			
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			

209/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Lasting decrease in functionality and richness: effects of ivermectin use on dung beetle communities. W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388		Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities -	
210/238	SUBMITTED TEXT	24 WORDS	100% MATCHING TEXT	24 WORDS
	Barbero, E., Palestirini, C., Rolando, A., 1999. Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeoidea). J. Insect Conserv. 3, 75–84. W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/		Barbero E., Palestirini C., Rolando A. Dung beetle conservation: Effects of habitat and resource selection (Coleoptera: Scarabaeoidea) J. Insect Conserv. 1999;3:75–84.	
211/238	SUBMITTED TEXT	22 WORDS	86% MATCHING TEXT	22 WORDS
	https://doi.org/10.1111/j.1466-8238.2009.00490.x. Beynon, S.A., Mann, D.J., Slade, E.M., Lewis, O.T., 2012. Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems. W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5838066/		https://doi.org/10.1094/FG-2006-0711-02-RS [Google Scholar] • Beynon, S. A. , Mann, D. J. , Slade, E. M. , & Lewis, O. T. (2012). Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems.	
212/238	SUBMITTED TEXT	21 WORDS	100% MATCHING TEXT	21 WORDS
	Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles. Biol. Conserv. 187, 112–119. W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388		Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles Biol. Conserv. (2015) •	
213/238	SUBMITTED TEXT	25 WORDS	93% MATCHING TEXT	25 WORDS
	j.1365-2699.2002.00776.x. Edwards, P.B., 1991. Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects. Funct. Ecol. 5, 617. W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/		j.1439-0310.2006.01284.x. [CrossRef] [Google Scholar] 77. Edwards P.B. Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects. Funct. Ecol. 1991;5:617–628.	
214/238	SUBMITTED TEXT	27 WORDS	94% MATCHING TEXT	27 WORDS
	Finn, J.A., Giller, P.S., 2002. Experimental investigations of colonisation by north temperate dung beetles of different types of domestic herbivore dung. Appl. Soil Ecol. 20, 1–13. https://doi.org/10.1016/ W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/		Finn J.A., Giller P.S. Experimental investigations of colonisation by north temperate dung beetles of different types of domestic herbivore dung. Appl. Soil Ecol. 2002;20:1–13. doi: 10.1016/	

215/238	SUBMITTED TEXT	11 WORDS	100% MATCHING TEXT	11 WORDS
	Frank, K., Brückner, A., Hilpert, A., Heethoff, M., Blüthgen, N., 2017		Frank K., Brückner A., Hilpert A., Heethoff M., Blüthgen N.	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
216/238	SUBMITTED TEXT	16 WORDS	90% MATCHING TEXT	16 WORDS
	Nutrient quality of vertebrate dung as a diet for dung beetles. Sci. Rep. 7, 12141. https://doi.org/10.1038/2017.7.12141 .		Nutrient quality of vertebrate dung as a diet for dung beetles. Sci. Rep. 2017;7:12141. doi: 10.1038/	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
217/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Land use affects dung beetle communities and their ecosystem service in forests and grasslands.		Land use affects dung beetle communities and their ecosystem service in forests and grasslands	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
218/238	SUBMITTED TEXT	18 WORDS	100% MATCHING TEXT	18 WORDS
	Gittings, T., Giller, P.S., 1998. Resource quality and the colonisation and succession of coprophagous dung beetles. Ecography (		Gittings, T. & Giller, P.S. (1998) Resource quality and the colonisation and succession of coprophagous dung beetles. Ecography 21, 581–592.	
	W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...			
219/238	SUBMITTED TEXT	35 WORDS	75% MATCHING TEXT	35 WORDS
	Halfpenny, G., Edmonds, W.D., 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae). An Ecological and Evolutionary Approach. Instituto de Ecología, México. Hanski, I., Cambefort, Y., 1991. Dung Beetle Ecology. Princeton University Press, New Jersey.			
	SA Fascinating behaviors of Aphodius elegans-07170351.docx (D70108613)			
220/238	SUBMITTED TEXT	19 WORDS	91% MATCHING TEXT	19 WORDS
	Holter, P., 2016. Herbivore dung as food for dung beetles: elementary coprology for entomologists. Ecol. Entomol. 41, 367–377. https://doi.org/10.1111/2016.41.367 .		Holter P. Herbivore dung as food for dung beetles: Elementary coprology for entomologists. Ecol. Entomol. 2016;41:367–377. doi: 10.1111/	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			

221/238	SUBMITTED TEXT	30 WORDS	92% MATCHING TEXT	30 WORDS
	T., Scholtz, C.H., 2015. A review on the effect of macrocyclic lactones on dung- dwelling insects: toxicity of macrocyclic lactones to dung beetles. Onderstepoort J. Vet. Res. 82, 1–8. T. and Scholtz, Clarke H. 2015. A review on the effect of macrocyclic lactones on dung-dwelling insects: Toxicity of macrocyclic lactones to dung beetles. Onderstepoort J Vet Res, W https://www.cambridge.org/core/journals/bulletin-of-entomological-research/article/fieldscale-dis ...			
222/238	SUBMITTED TEXT	31 WORDS	98% MATCHING TEXT	31 WORDS
	Lumaret, J.-P., Errouissi, F., Floate, K., Rombke, J., Wardhaugh, K., 2012. A review on the toxicity and non-target effects of macrocyclic lactones in terrestrial 184 and aquatic environments. SA VET344s2_14_uid_31837531_fname_2244_1410960510_47146.docx (D18779582)			
223/238	SUBMITTED TEXT	20 WORDS	100% MATCHING TEXT	20 WORDS
	Martín-Piera, F., Lobo, J.M., 1996. A comparative discussion of trophic preferences in dung beetle communities. Misc. Zool. 19, 13–31. Martín-Piera F., Lobo J.M. A comparative discussion of trophic preferences in dung beetle communities. Misc. Zool. 1996;19:13–31. [W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
224/238	SUBMITTED TEXT	22 WORDS	100% MATCHING TEXT	22 WORDS
	Milotić, T., Baltzinger, C., Eichberg, C., Eycott, A.E., Heurich, M., Müller, J., Noriega, J. A., Menendez, R., Stadler, J., Ádám, R., Milotić T., Baltzinger C., Eichberg C., Eycott A.E., Heurich M., Müller J., Noriega J.A., Menendez R., Stadler J., Ádám R., W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
225/238	SUBMITTED TEXT	24 WORDS	MATCHING TEXT	24 WORDS
	Functionally richer communities improve ecosystem functioning: dung removal and secondary seed dispersal by dung beetles in the Western Palearctic. J. Biogeogr. 46, 70–82. https://doi. 87% Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palearctic. J. Biogeogr. 2019;46:70–82. doi: 10.1111/ W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
226/238	SUBMITTED TEXT	29 WORDS	90% MATCHING TEXT	29 WORDS
	Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S., Favila, M.E., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biol. Conserv. 141, 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011. Nichols, E. , Spector, S. , Louzada, J. , Larsen, T. , Amezcuita, S. , & Favila, M. E. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation, 141, 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011 [W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5838066/			

227/238	SUBMITTED TEXT	14 WORDS	100% MATCHING TEXT	14 WORDS
	R Core Team, 2021. R: A Language and Environment for Statistical Computing.		R Core Team. R: A Language and Environment for Statistical Computing;	
	W https://www.mdpi.com/1424-2818/15/1/91			
228/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27.		Worldwide decline of the entomofauna: a review of its drivers Biol. Conserv. (2019) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
229/238	SUBMITTED TEXT	17 WORDS	100% MATCHING TEXT	17 WORDS
	Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat. Acta Oecol. 46, 17–24.		Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat Acta Oecol (2013) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
230/238	SUBMITTED TEXT	11 WORDS	100% MATCHING TEXT	11 WORDS
	Brood care in the dung beetle <i>Onthophagus vacca</i> (Coleoptera: Scarabaeidae):		brood care in the dung beetle <i>Onthophagus vacca</i> (Coleoptera: Scarabaeidae).	
	W https://www.frontiersin.org/articles/863669			
231/238	SUBMITTED TEXT	19 WORDS	100% MATCHING TEXT	19 WORDS
	Spector, S., 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation.		Spector, S. 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation.	
	W https://doi.org/10.4039/tce.2017.11			
232/238	SUBMITTED TEXT	26 WORDS	100% MATCHING TEXT	26 WORDS
	Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub- mountainous landscape of Central Italy. PeerJ 5, e2780.		Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub-mountainous landscape of Central Italy. PeerJ. 2017;5:e2780.	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			
233/238	SUBMITTED TEXT	25 WORDS	93% MATCHING TEXT	25 WORDS
	Tonelli, M., Verdú, J.R., Zunino, M., 2019. Grazing abandonment and dung beetle assemblage composition: reproductive behaviour has something to say. Ecol. Indic. 96, 361–367. https://doi.org/10.1016/		Tonelli M., Verdú J.R., Zunino M. Grazing abandonment and dung beetle assemblage composition: Reproductive behaviour has something to say. Ecol. Indic. 2019;96:361–367. doi: 10.1016/	
	W https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8472632/			

234/238	SUBMITTED TEXT	21 WORDS	100% MATCHING TEXT	21 WORDS
	Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study. Sci. Total Environ. 618, 219–228.		Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study Sci. Total. Environ. (2018) •	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
235/238	SUBMITTED TEXT	24 WORDS	87% MATCHING TEXT	24 WORDS
	Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B (		Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. Roy. Stat. Soc. B	
	W https://www.frontiersin.org/articles/863669			
236/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities.		Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities -	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
237/238	SUBMITTED TEXT	17 WORDS	100% MATCHING TEXT	17 WORDS
	Understanding the drivers of β -diversity improves conservation prioritization for Central European dung beetles. Biological Conservation, 273,		Understanding the drivers of β -diversity improves conservation prioritization for Central European dung beetles 2022, Biological Conservation	
	W https://www.sciencedirect.com/science/article/abs/pii/S0167880921003388			
238/238	SUBMITTED TEXT	15 WORDS	100% MATCHING TEXT	15 WORDS
	Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities [		Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities -	
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