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

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

This thesis originated from a partnership of **Faculty of Science, University of South Bohemia**, and **Institute of Entomology, Biology Centre CAS**, supporting doctoral studies in the **Entomology** study program.

Přírodovědecká
fakulta
Faculty
of Science

BIOLOGY
CENTRE
CAS

Financial support

The projects presented in this thesis were supported by the Czech Academy of Sciences, Program AV 21, the Regional Cooperation of the Regions and Institutes of the Czech Academy of Sciences (R200961701), Institute of Entomology, Biology Centre, Czech Academy of Sciences (RVO//:60077344), MSM200961902 (Czech Academy of Sciences), LIFE15 NAT/CZ/001028, and GACR (22-27166S), and by the Operational Program Integrated Infrastructure within the project: Sustainable smart farming systems taking into account the future challenges 313011W112, co-financed by the European Regional Development Fund.

Cover photo: Lucie Ambrožová

Acknowledgements

First of all, I would like to thank Lukáš Čížek, who has been my supervisor throughout my studies, for always being patient with me and adding his incredible insight to various topics. I specially thank him for introducing me to the amazing world of insects, a discipline that I certainly would not have thought I would love some ten years ago.

I would like to thank František Sládeček, Tomáš Zítek and Aleš Bezděk who adopted me in their dung beetle gang and guided my first steps as a dung-beetle newbie. Special thanks go to Franta, who constantly tried to improve my writing.

Also, I thank my Czech colleagues Michal Perlík, Petr Kozel and Lukáš Drag, not only for accompanying me during my dirty fieldworks, but mostly for their friendly support during my frequent PhD crises.

Further thanks belong to the German crew in Fabrikschleichach where I spent the internship. First, I would like to thank Simon Thorn who taught me a lot (not only) about science, for his incredible statistical skills that brought our papers to another level, but mainly for his friendship. I also thank to Lea, Peter, Steff, Jana, Annika, Dominik, Giorgi, and Marvin, who made the lockdown times in the middle of Steigerwald a great fun.

Last but not least, I would like to thank my family and friends for their endless support, even though they may never understand why I chose this particular topic.

List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

I. **Ambrožová, L.**, Sládeček, F. X. J., Zítek, T., Perlík, M., Kozel, P., Jirků, M. & Čížek, L. (2021). 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). Understanding the drivers of ß-diversity improves conservation prioritization for Central European dung beetles. *Biological Conservation*, 273, p. 109682. doi: 10.1016/j.biocon.2022.109682. (IF = 7.499)
LA led the field sampling, determined the sampled material, and was responsible for the manuscript writing. Her contribution was 45 %.

Co-author agreement

Lukáš Čížek, the supervisor of this Ph.D. thesis and co-author of papers „Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities“ and „Understanding the drivers of ß-diversity improves conservation prioritization for Central European dung beetles“, fully acknowledges the stated contribution of Lucie Ambrožová to these manuscripts.

………………………………………………

Mgr. Lukáš Čížek, Ph.D.

Simon Thorn, lead author of papers „Coppicing and topsoil removal promote diversity of dung-inhabiting beetles (Coleoptera: Scarabaeidae, Geotrupidae, Staphylinidae) in forests“ and „Understanding the drivers of ß-diversity improves conservation prioritization for Central European dung beetles“ acknowledges the stated contribution of Lucie Ambrožová to these manuscripts.

………………………………………………

Dr. Simon Thorn

František J.X. Sládeček, co-author of papers „Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities“ and „Understanding the drivers of ß-diversity improves conservation prioritization for Central European dung beetles“, acknowledges the stated contribution of Lucie Ambrožová to these manuscripts.

………………………………………………

RNDr. František X. J. Sládeček, Ph.D.

Contents

Introduction

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

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).

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 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.

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; Milotić *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. thirouxi, 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 (Milotić *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;

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 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).

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.

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 *Chilothorax* (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; Trible 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 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.

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; Õmura, 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; Õmura, 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; Õmura, 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. 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 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. 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.

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 CO_2 and CH_4, 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 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, Rhoadphodius 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* *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 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 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.

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 (Doube, 2018) and dung-breeding flies (*Musca vetustissima, Haematobia irritans exigua*), a 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; Doube, 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.

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.

7. References

Agoglitta, R., Moreno, C.E., Zunino, M., Bonsignori, G., Dellacasa, M., 2012. Cumulative annual dung beetle diversity in Mediterranean seasonal environments. Ecol. Res. 27, 387–395. https://doi.org/10.1007/s11284-011-0910-8

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 Biol. Sci. 281, 20141470. https://doi.org/10.1098/rspb.2014.1470

Andresen, E., 2002. Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. Ecol. Entomol. 27, 257–270. https://doi.org/10.1046/j.1365-2311.2002.00408.x

Andriuzzi, W.S., Wall, D.H., 2018. Soil biological responses to, and feedbacks on, trophic rewilding. Philos. Trans. R. Soc. B Biol. Sci. 373, 20170448. https://doi.org/10.1098/rstb.2017.0448

Anonymous, 2018. Research, Farm & Conservation [WWW Document]. Bug Farm. URL https://www.thebugfarm.co.uk/research-farm/

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/10.1080/00222930802105130

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 Ecol. 132, 53–59. https://doi.org/10.1016/j.apsoil.2018.08.011

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

Barbero, E., Palestrini, C., Rolando, A., 1999. Dung beetle conservation: Effects of habitat and resource selection (Coleoptera: Scarabaeoidea). J. Insect Conserv. 3, 75–84. https://doi.org/10.1023/A:1009609826831

Barragán, F., Moreno, C.E., Escobar, F., Bueno-Villegas, J., Halffter, G., 2014. The impact of grazing on dung beetle diversity depends on both biogeographical and ecological context. J. Biogeogr. 41, 1991–2002. https://doi.org/10.1111/jbi.12351

Bellis, J., Bourke, D., Williams, C., Dalrymple, S., 2019. Identifying factors associated with the success and failure of terrestrial insect translocations. Biol. Conserv. 236, 29–36. https://doi.org/10.1016/j.biocon.2019.05.008

Benton, T.G., Bryant, D.M., Cole, L., Crick, H.Q.P., 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. J. Appl. Ecol. 39, 673–687. 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. Forage & Grazinglands 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. J. Appl. Ecol. 49, 1365–1372. https://doi.org/10.1111/j.1365-2664.2012.02210.x

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. Agric. Ecosyst. Environ. 162, 36–44. 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. Ecol. Entomol. 40, 124–135. https://doi.org/10.1111/een.12240

Bezák, P., Mitchley, J., 2014. Drivers of change in mountain farming in Slovakia: from socialist collectivisation to the Common Agricultural Policy. Reg. Environ. Chang. 14, 1343–1356. https://doi.org/10.1007/s10113-013-0580-x

Bičík, I., Jančák, V., 2005. Transformační procesy v českém zemědělství po roce 1990.

Bičík, I., Jeleček, L., Štěpánek, V., 2001. Land-use changes and their social driving forces in Czechia in the 19th and 20th centuries. Land use policy 18, 65–73. https://doi.org/10.1016/S0264-8377(00)00047-8

Birkett, A.J., Blackburn, G.A., Menéndez, R., 2018. Linking species thermal tolerance to elevational range shifts in upland dung beetles. Ecography (Cop.). 41, 1510–1519. https://doi.org/10.1111/ecog.03458

Blacksell, M., 2010. Agriculture and landscape in the 21st century Europe: the post-communist transition. Eur. Countrys. 2. https://doi.org/10.2478/v10091-010-0002-8

Blackwell, M., Malloch, D., 1991. Life History and Arthropod Dispersal of a Coprophilous Stylopage . Mycologia 83, 360–366. https://doi.org/10.1080/00275514.1991.12026020

Bogoni, J.A., da Silva, P.G., Peres, C.A., 2019. Co-declining mammal–dung beetle faunas throughout the Atlantic Forest biome of South America. Ecography (Cop.). 42, 1803–1818. https://doi.org/10.1111/ecog.04670

Bogoni, J.A., Graipel, M.E., de Castilho, P.V., Fantacini, F.M., Kuhnen, V.V., Luiz, M.R., Maccarini, T.B., Marcon, C.B., de Souza Pimentel Teixeira, C., Tortato, M.A., Vaz-de-Mello, F.Z., Hernández, M.I.M., 2016. Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodivers. Conserv. 25, 1661–1675. https://doi.org/10.1007/s10531-016-1147-1

Bornemissza, G.F., 1976. The Australian dung beetle project 1965–1975. Aust.

Meat Res. Comm. Rev. 30, 1–30.

Bornemissza, G.F., Williams, C.H., 1970. An effect of dung beetle activity on plant yield. Pedobiologia (Jena). 10, 1–7.

Brompton, S.L., 2018. Does rewilding benefit dung beetle biodiversity? University of the West of England, Bristol.

Brown, J., Scholtz, C.H., Janeau, J.-L., Grellier, S., Podwojewski, P., 2010. Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. Appl. Soil Ecol. 46, 9–16. https://doi.org/10.1016/j.apsoil.2010.05.010

Buse, J., Šlachta, M., Sladecek, F.X.J., Carpaneto, G.M., 2018. Summary of the morphological and ecological traits of Central European dung beetles. Entomol. Sci. 21, 315–323. https://doi.org/10.1111/ens.12313

Buse, J., Šlachta, M., Sladecek, F.X.J., Pung, M., Wagner, T., Entling, M.H., 2015. Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles. Biol. Conserv. 187, 112–119. https://doi.org/10.1016/j.biocon.2015.04.011

Byrne, M.J., Watkins, B., Bouwer, G., 2013. Do dung beetle larvae need microbial symbionts from their parents to feed on dung? Ecol. Entomol. 38, 250–257. https://doi.org/10.1111/een.12011

Cabrero-Sanudo, F.J., Lobo, J.M., 2006. Determinant variables of Iberian Peninsula Aphodiinae diversity (Coleoptera, Scarabaeoidea, Aphodiidae). J. Biogeogr. 33, 1021–1043. https://doi.org/10.1111/j.1365-2699.2006.01485.x

Carpaneto, G.M., 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

Chirico, J., Wiktelius, S., Waller, P.J., 2003. Dung beetle activity and the development of trichostrongylid eggs into infective larvae in cattle faeces. Vet.

Parasitol. 118, 157–163. https://doi.org/10.1016/j.vetpar.2003.09.013

Coldham, J., 2011. Dung Beetles and Internal Parasites of Sheep. Sydney.

Corwin, R.M., 1997. Economics of gastrointestinal parasitism of cattle. Vet. Parasitol. 72, 451–460. https://doi.org/10.1016/S0304-4017(97)00110-6

Da Cruz, L., Dadour, I.R., McAllister, I.L., Jackson, A., Isaacs, T., 2002. Seasonal variation in trachoma and bush flies in north-western Australian Aboriginal communities. Clin. Experiment. Ophthalmol. 30, 80–83. https://doi.org/10.1046/j.1442-6404.2002.00491.x

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., Scholtz, C.H., 2001. Historical vs. ecological factors influencing global patterns of scarabaeine dung beetle diversity. Divers. Distrib. 7, 161–174. https://doi.org/10.1111/j.1472-4642.2001.00102.x

Davis, A.L. V., Scholtz, C.H., Philips, T.K., 2002. Historical biogeography of scarabaeine dung beetles. J. Biogeogr. 29, 1217–1256. https://doi.org/10.1046/j.1365-2699.2002.00776.x

Díaz, S., Lavorel, S., Chapin, F.S., Tecco, P.A., Gurvich, D.E., Grigulis, K., 2007. Functional Diversity — at the Crossroads between Ecosystem Functioning and Environmental Filters, in: Canadell, J., Pataki, D., Pitelka, L. (Eds.), Terrestrial Ecosystems in a Changing World. Springer, Berlin, pp. 81–91. https://doi.org/10.1007/978-3-540-32730-1_7

Dirnböck, T., Essl, F., Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob. Chang. Biol. 17, 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

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 Onthophagus gazella (F.) (Coleoptera: Scarabaeidae) and Haematobia irritans exigua De Meijere (Diptera: Muscidae). Aust. J. Entomol. 33, 71–74. https://doi.org/10.1111/j.1440-6055.1994.tb00924.x

Dortel, E., Thuiller, W., Lobo, J.M., Bohbot, H., Lumaret, J.P., Jay-Robert, P., 2013. Potential effects of climate change on the distribution of Scarabaeidae dung beetles in Western Europe. J. Insect Conserv. 17, 1059–1070. https://doi.org/10.1007/s10841-013-9590-8

Doube, B., 2008. The pasture growth and environmental benefits of dung beetles to the southern Australian cattle industry.

Doube, B.M., 2018. Ecosystem services provided by dung beetles in Australia. Basic Appl. Ecol. 26, 35–49. https://doi.org/10.1016/j.baae.2017.09.008

Doube, B.M., 1990. A functional classification for analysis of the structure of dung beetle assemblages. Ecol. Entomol. 15, 371–383. https://doi.org/10.1111/j.1365-2311.1990.tb00820.x

Durie, P., 1975. Some possible effects of dung beetle activity on the infestation of pastures by intestinal worm larvae of cattle. J. Appl. Ecol. 12, 827–831.

Edwards, P., 2007. Introduced Dung Beetles in Australia 1967-2007. Current status and future directions.

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. https://doi.org/10.1051/vetres:2001134

Errouissi, F., Jay-Robert, P., 2019. Consequences of habitat change in euromediterranean landscapes on the composition and diversity of dung beetle assemblages (Coleoptera, Scarabaeoidea). J. Insect Conserv. 23, 15–28. https://doi.org/10.1007/s10841-018-0110-8

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. https://doi.org/10.1603/0013-8746(2004)097[0701:CASODB]2.0.CO;2

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.1365-2915.2010.00891.x

Escobar, F., Halffter, G., Solís, Á., Halffter, V., Navarrete, D., 2008. Temporal shifts in dung beetle community structure within a protected area of tropical wet forest: a 35-year study and its implications for long-term conservation. J. Appl. Ecol. 45, 1584–1592. https://doi.org/10.1111/j.1365-2664.2008.01551.x

Fedrigo, J.K., Ataide, P.F., Filho, J.A., Oliveira, L. V., Jaurena, M., Laca, E.A., Overbeck, G.E., Nabinger, C., 2018. Temporary grazing exclusion promotes rapid recovery of species richness and productivity in a long-term overgrazed Campos grassland. Restor. Ecol. 26, 677–685. https://doi.org/10.1111/rec.12635

Finch, D., Schofield, H., Floate, K.D., Kubasiewicz, L.M., Mathews, F., 2020. 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

Floate, K.D., 2021. Chilothorax distinctus (Coleoptera : Scarabaeidae): an occasional pest in agro-ecosystems on the Canadian Prairies? J. Entomol. Soc. Br. Columbia 118, 57–64.

Floate, K.D., 1998. Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada. Bull. Entomol. Res. 88, 25–35. https://doi.org/10.1017/S0007485300041523

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. Annu. Rev. Entomol. 50, 153–179. https://doi.org/10.1146/annurev.ento.50.071803.130341

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. https://doi.org/10.1111/een.12513

Frank, K., Hülsmann, M., Assmann, T., Schmitt, T., Blüthgen, N., 2017. Land use affects dung beetle communities and their ecosystem service in forests and grasslands. Agric. Ecosyst. Environ. 243, 114–122. https://doi.org/10.1016/j.agee.2017.04.010

Gebert, F., Steffan-Dewenter, I., Moretto, P., Peters, M.K., 2020. Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. J. Biogeogr. 47, 371–381. https://doi.org/10.1111/jbi.13710

Gittings, T., Giller, P.S., Stakelum, G., 1994. Dung decomposition in contrasting temperate pastures in relation to dung beetle and earthworm activity. Pedobiologia (Jena). 38, 455–474.

Głowaciński, Z., 2002. Coleoptera, in: Pawłowski, J., Kubisz, D., Mazur, M. (Eds.), Red List of Threatened Animals in Poland. p. 155.

González-Tokman, D., Martínez M., I., Villalobos-Ávalos, Y., Munguía-Steyer, R., Ortiz-Zayas, M. del R., Cruz-Rosales, M., Lumaret, J.-P., 2017. Ivermectin alters reproductive success, body condition and sexual trait expression in dung beetles. Chemosphere 178, 129–135.

https://doi.org/10.1016/j.chemosphere.2017.03.013

Goodenough, A.E., Webb, J.C., Yardley, J., 2019. Environmentally-realistic concentrations of anthelmintic drugs affect survival and motility in the cosmopolitan earthworm Lumbricus terrestris (Linnaeus, 1758). Appl. Soil Ecol. 137, 87–95. https://doi.org/10.1016/j.apsoil.2019.02.001

Habel, J.C., Samways, M.J., Schmitt, T., 2019. Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. Biodivers. Conserv. 28, 1343–1360. https://doi.org/10.1007/s10531-019-01741-8

Habel, J.C., Segerer, A., Ulrich, W., Torchyk, O., Weisser, W.W., Schmitt, T., 2016. Butterfly community shifts over two centuries. Conserv. Biol. 30, 754–762. https://doi.org/10.1111/cobi.12656

Halffter, G., Edmonds, W.D., 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae). An Ecological and Evolutive Approach. Institúto de Ecología, México.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., De Kroon, H., 2017. 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

Hanski, I., 1991. North temperate dung beetles, in: Hanski, I., Cambefort, Y. (Eds.), Dung Beetle Ecology. Princeton University Press, Princeton, pp. 75–96.

Hanski, I., Cambefort, Y., 1991. Dung beetle ecology. Princeton University Press, New Jersey.

Hata, K., Edmonds, W.D., 1983. Structure and function of the mandibles of adult dung beetles (Coleoptera : Scarabaeidae). Int. J. Insect Morphol. Embryol. 12, 1–12. https://doi.org/10.1016/0020-7322(83)90031-4

Hempel, H., Scheffczyk, A., Schallnaß, H.J., Lumaret, J.P., Alvinerie, M., Römbke, J., 2006. Toxicity of four veterinary parasiticides on larvae of the dung beetle

Aphodius constans in the laboratory. Environ. Toxicol. Chem. 25, 3155–3163. https://doi.org/10.1897/06-022R2.1

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. Int. J. Parasitol. 26, 1087–1093. https://doi.org/10.1016/S0020-7519(96)80007-5

Hirschberger, P., 1998. Spatial distribution, resource utilisation and intraspecific competition in the dung beetle Aphodius ater. Oecologia 116, 136–142. https://doi.org/10.1007/s004420050572

Hirschberger, P., Bauer, T., 1994. Influence of earthworms on the disappearance of sheep dung. Pedobiologia (Jena). 38, 475–480.

Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. J. Appl. Ecol. 48, 148–152. https://doi.org/10.1111/j.1365-2664.2010.01919.x

Holecová, M., Franc, V., 2001. Červený zoznam rastlín a živočíchov Slovenska, in: Baláž, D., Marhold, K., Urban, P. (Eds.), Ochrana Prírody. Banská Bystrica, pp. 111–128.

Holter, P., 2016. Herbivore dung as food for dung beetles: elementary coprology for entomologists. Ecol. Entomol. 41, 367–377. https://doi.org/10.1111/een.12316

Holter, P., 2004. Dung feeding in hydrophilid, geotrupid and scarabaeid beetles: Examples of parallel evolution. Eur. J. Entomol. 101, 365–372. 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

Holter, P., Scholtz, C.H., 2007. What do dung beetles eat? Ecol. Entomol. 32, 690–697. https://doi.org/10.1111/j.1365-2311.2007.00915.x

Holter, P., Scholtz, C.H., 2005. Are ball-rolling (Scarabaeini, Gymnopleurini, Sisyphini) and tunnelling scarabaeine dung beetles equally choosy about the size of ingested dung particles? Ecol. Entomol. 30, 700–705. https://doi.org/10.1111/j.0307-6946.2005.00746.x

Horgan, F.G., 2007. Dung beetles in pasture landscapes of Central America: proliferation of synanthropogenic species and decline of forest specialists. Biodivers. Conserv. 16, 2149–2165. https://doi.org/10.1007/s10531-006-9145-3

Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A., Lobo, J.M., 2011. Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. Ecol. Lett. 14, 741–748. https://doi.org/10.1111/j.1461-0248.2011.01634.x

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. https://doi.org/10.1111/j.1365-2664.2003.00863.x

Jacobs, C.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. 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

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. Parasitol. Res. 120, 773–783. https://doi.org/10.1007/s00436-021-07064-4

Juřena, D., Týr, V., 2008. Checklist of Scarabaeoidea (Coleoptera) of the Czech Republic and Slovakia. Klapalekiana 44 (Suppl., 3–15.

Kabir, S.M.H., Howlader, A.J., Begum, J., 1985. Effect of dung beetle activities on the growth and yield of wheat plants. Bangladesh J. Agric. 10, 49–55.

Král, D., Bezděk, A., 2017. Scarabaeoidea (vrubounovití), in: Hejda, R., Farkač, J., Chobot, K. (Eds.), Červený Seznam Ohrožených Druhů České Republiky. Bezobratlí. [Red List of Threatened Species of the Czech Republic. Invertebrates.]. Agentura ochrany přírody a krajiny ČR, Praha, pp. 409–413.

Krantz, G.W., 1998. Reflections on the biology, morphology and ecology of the Macrochelidae. Exp. Appl. Acarol. 22, 125–137. https://doi.org/10.1023/A:1006097811592

Kunz, S.E., 1978. Highlights of Veterinary Entomology - 1952-1977. Bull. Entomol. Soc. Am. 24, 401–406. https://doi.org/10.1093/besa/24.4.401

Kuskova, P., Gingrich, S., Krausmann, F., 2008. Long term changes in social metabolism and land use in Czechoslovakia, 1830–2000: An energy transition under changing political regimes. Ecol. Econ. 68, 394–407. https://doi.org/10.1016/j.ecolecon.2008.04.006

Laing, R., Gillan, V., Devaney, E., 2017. Ivermectin – Old Drug, New Tricks? Trends Parasitol. 33, 463–472. https://doi.org/10.1016/j.pt.2017.02.004

Landin, B.-O., 1961. Ecological studies on dung-beetles. Opusc. Entomol. Suppl. 19, 1–228.

Larsen, T.H., Lopera, A., Forsyth, A., 2008. Understanding Trait-Dependent Community Disassembly: Dung Beetles, Density Functions, and Forest Fragmentation. Conserv. Biol. 22, 1288–1298. https://doi.org/10.1111/j.1523-1739.2008.00969.x

Lerman, Z., Csaki, C., Feder, G., 2004. The Arena and the Common Heritage, in: Agriculture in Transition: Land Policies and Evolving Farm Structures in Post-Soviet Countries. Lexington Books, Oxford, pp. 13–54.

Lipsky, Z., 1995. The changing face of the Czech rural landscape. Landsc. Urban

Plan. 31, 39–45. https://doi.org/10.1016/0169-2046(94)01034-6

Liu, J., Isbell, F., Ma, Q., Chen, Y., Xing, F., Sun, W., Wang, L., Li, J., Wang, Y., Hou, F., Xin, X., Nan, Z., Eisenhauer, N., Wang, D., 2022. Overgrazing, not haying, decreases grassland topsoil organic carbon by decreasing plant species richness along an aridity gradient in Northern China. Agric. Ecosyst. Environ. 332, 107935. https://doi.org/10.1016/j.agee.2022.107935

Liu, L.X., Weller, P.F., 1996. Antiparasitic Drugs. N. Engl. J. Med. 334, 1178–1184. https://doi.org/10.1056/NEJM199605023341808

Löbl, I., Löbl, D., 2016. Catalogue of Palaearctic Coleoptera. Volume 3, Scarabaeoidea, Scirtoidea, Dascilloidea, Buprestoidea, Byrrhoidea. Brill, Leiden, Boston.

Lobo, J.M., 2001. Decline of roller dung beetle (Scarabaeinae) populations in the Iberian peninsula during the 20th century. Biol. Conserv. 97, 43–50. https://doi.org/10.1016/S0006-3207(00)00093-8

Lobo, J.M., Lumaret, J.-P., Jay-Robert, P., 2002. Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. Glob. Ecol. Biogeogr. 11, 265–277. https://doi.org/10.1046/j.1466-822X.2002.00291.x

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:TEVOES]2.0.CO;2

Lumaret, J.-P., Errouissi, F., 2002. Use of anthelmintics in herbivores and evaluation of risks for the non target fauna of pastures. Vet. Res. 33, 547–562. https://doi.org/10.1051/vetres:2002038

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 and aquatic environments. Curr. Pharm. Biotechnol. 13, 1004–1060.

https://doi.org/10.2174/138920112800399257

Lumaret, J.-P., Kadiri, N., Martínez-M, I., 2022. The Global Decline of Dung Beetles, in: Imperiled: The Encyclopedia of Conservation. Elsevier, pp. 553–562. https://doi.org/10.1016/B978-0-12-821139-7.00018-0

Lumaret, J.-P., Kirk, A., 1991. South temperate dung beetles, in: Hanski, I., Cambefort, Y. (Eds.), Dung Beetle Ecology. Princeton University Press, Princeton, pp. 97–115.

Lumaret, J.P., Römbke, J., Kadiri, N., Errouissi, F., Tixier, T., Floate, K., 2013. Antiparasitics and their impact on soil and dung fauna, in: International UBA Workshop "Pharmaceuticals in Soil, Sludge and Slurry". Dessau-Roßlau, Germany.

Manning, P., Beynon, S.A., Lewis, O.T., 2017a. 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

Manning, P., Cutler, G.C., 2018. Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness. Agric. Ecosyst. Environ. 264, 9–14. https://doi.org/10.1016/j.agee.2018.05.002

Manning, P., Slade, E.M., Beynon, S.A., Lewis, O.T., 2017b. 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.M., Beynon, S.A., Lewis, O.T., 2016. 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

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

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 Euoniticellus intermedius (Coleoptera: Scarabaeidae). Can. Entomol. 149, 461–472. https://doi.org/10.4039/tce.2017.11

McArthur, M.J., Reinemeyer, C.R., 2014. Herding the U.S. cattle industry toward a paradigm shift in parasite control. Vet. Parasitol. https://doi.org/10.1016/j.vetpar.2013.12.021

McKellar, Q.A., 1997. Ecotoxicology and residues of anthelmintic compounds. Vet. Parasitol. 72, 413–435. https://doi.org/10.1016/S0304-4017(97)00108-8

Menéndez, R., González-Megías, A., Jay-Robert, P., Marquéz-Ferrando, R., 2014. Climate change and elevational range shifts: evidence from dung beetles in two European mountain ranges. Glob. Ecol. Biogeogr. 23, 646–657. https://doi.org/10.1111/geb.12142

Menéndez, R., Gutiérrez, D., 2004. Shifts in habitat associations of dung beetles in northern Spain: Climate change implications. Écoscience 11, 329–337. https://doi.org/10.1080/11956860.2004.11682840

Mertlik, J., 2019. Expanzivní druhy čeledí Geotrupidae a Scarabaeidae (Coleoptera) na území východních Čech [Expansive species of Geotrupidae and Scarabaeidae (Coleoptera) from eastern Bohemia]. Elateridarium 13, 35–48.

Milotić, T., Baltzinger, C., Eichberg, C., Eycott, A.E., Heurich, M., Müller, J., Noriega, J.A., Menendez, R., Stadler, J., Ádám, R., Bargmann, T., Bilger, I., Buse, J., Calatayud, J., Ciubuc, C., Boros, G., Jay-Robert, P., Kruus, M., Merivee, E., Miessen, G., Must, A., Ardali, E., Preda, E., Rahimi, I., Rohwedder, D., Rose, R., Slade, E.M., Somay, L., Tahmasebi, P., Ziani, S., Hoffmann, M., 2019. Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the

Western Palaearctic. J. Biogeogr. 46, 70–82. https://doi.org/10.1111/jbi.13452

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/s00442-016-3756-5

Mittal, I.C., 1993. Natural manuring and soil conditioning by dung beetles. Trop. Ecol. 32, 150–159.

Mládek, J., Pavlů, V., Hejcman, M., Gaisler, J. (Eds.), 2006. Pastva jako prostředek údržby trvalých travních porostů v chráněných územích. VÚRV, Praha.

Negro, M., Palestrini, C., Giraudo, M.T., Rolando, A., 2011a. The effect of local environmental heterogeneity on species diversity of alpine dung beetles (Coleoptera: Scarabaeidae). Eur. J. Entomol. 108, 91–98. https://doi.org/10.14411/eje.2011.012

Negro, M., Rolando, A., Palestrini, C., 2011b. The impact of overgrazing on dung beetle diversity in the italian maritime alps. Environ. Entomol. 40, 1081–1092. https://doi.org/10.1603/EN11105

Nervo, B., Tocco, C., Caprio, E., Palestrini, C., Rolando, A., 2014. The effects of body mass on dung removal efficiency in dung beetles. PLoS One 9. https://doi.org/10.1371/journal.pone.0107699

Nichols, E., Gómez, A., 2014. Dung beetles and fecal helminth transmission: patterns, mechanisms and questions. Parasitology 141, 614–623. https://doi.org/10.1017/S0031182013002011

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, 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

O'Hea, N. M., Kirwan, L., Finn, J.A., 2010. Experimental mixtures of dung fauna affect dung decomposition through complex effects of species interactions. Oikos 119, 1081–1088. https://doi.org/10.1111/j.1600-0706.2009.18116.x

O'Hea, Norma M., Kirwan, L., Giller, P.S., Finn, J.A., 2010. Lethal and sub-lethal effects of ivermectin on north temperate dung beetles, Aphodius ater and Aphodius rufipes (Coleoptera: Scarabaeidae). Insect Conserv. Divers. 3, 24–33. https://doi.org/10.1111/j.1752-4598.2009.00068.x

Õmura, S., 2008. Ivermectin: 25 years and still going strong. Int. J. Antimicrob. Agents 31, 91–98. https://doi.org/10.1016/j.ijantimicag.2007.08.023

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. Entomol. Exp. Appl. 161, 70–78. https://doi.org/10.1111/eea.12488

Paill, W., Mairhuber, C., 2006. Checkliste und Rote Liste der Blatthorn- und Hirschkäfer Kärntens mit besonderer Berücksichtigung der geschützten Arten (Coleoptera: Trogidae, Geotrupidae, Scarabaeidae, Lucanidae). Carinthia II 196:116, 611–626.

Pecenka, J.R., Lundgren, J.G., 2019. Effects of herd management and the use of ivermectin on dung arthropod communities in grasslands. Basic Appl. Ecol. 40, 19–29. https://doi.org/10.1016/j.baae.2019.07.006

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. https://doi.org/10.1371/journal.pone.0071454

Pérez-Cogollo, L.C., Rodríguez-Vivas, R.I., Reyes-Novelo, E., Delfín-González, H., Muñoz-Rodríguez, D., 2017. Survival and reproduction of Onthophagus landolti (Coleoptera: Scarabaeidae) exposed to ivermectin residues in cattle dung. Bull. Entomol. Res. 107, 118–125. https://doi.org/10.1017/S0007485316000705

Perrin, W., Fontana, S., Coq, S., Berlioz, L., Jay-Robert, P., Moretti, M., 2021. The

Influence of Fine-Scale Grazing Heterogeneity on Dung Beetle Assemblages: What Trait Analysis Teaches Us. Environ. Entomol. 50, 1332–1343. https://doi.org/10.1093/ee/nvab091

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.2017.10.171

Pokhrel, M.R., Cairns, S.C., Hemmings, Z., Floate, K.D., Andrew, N.R., 2021. A Review of Dung Beetle Introductions in the Antipodes and North America: Status, Opportunities, and Challenges. Environ. Entomol. 50, 762–780. https://doi.org/10.1093/ee/nvab025

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Puniamoorthy, N., Schäfer, M.A., Römbke, J., Meier, R., Blanckenhorn, W.U., 2014. Ivermectin sensitivity is an ancient trait affecting all ecdysozoa but shows phylogenetic clustering among sepsid flies. Evol. Appl. 7, 548–554. https://doi.org/10.1111/eva.12152

Rodríguez-Vivas, R.I., Basto-Estrella, G.S., Reyes-Novelo, E., Arceo-Moran, A.A., 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 Entomol. 59, 368–374. https://doi.org/10.1111/aen.12450

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 Ecol. 45, 284–292.

https://doi.org/10.1016/j.apsoil.2010.05.004

Rosenlew, H., Roslin, T., 2008. Habitat fragmentation and the functional efficiency of temperate dung beetles. Oikos 117, 1659–1666. https://doi.org/10.1111/j.1600-0706.2008.16904.x

Roslin, T., 2000. Dung beetle movements at two spatial scales. Oikos 91, 323–335. https://doi.org/10.1034/j.1600-0706.2000.910213.x

Roslin, T., Koivunen, A., 2001. Distribution and abundance of dung beetles in fragmented landscapes. Oecologia 127, 69–77. https://doi.org/10.1007/s004420000565

Rössner, E., 2012. Die Hirschkäfer und Blatthornkäfer Ostdeutschlands (Coleoptera: Scarabaeoidea). verein der Freunde & Fôrderer des Naturkundemuseums Erfurt e.V., Erfurt.

Salomão, R.P., Pires, D. de A., Baccaro, F.B., Schietti, J., Vaz-de-Mello, F.Z., Lima, A.P., Magnusson, W.E., 2022. Water table level and soil texture are important drivers of dung beetle diversity in Amazonian lowland forests. Appl. Soil Ecol. 170, 104260. https://doi.org/10.1016/j.apsoil.2021.104260

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. Biol. Conserv. 232, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Sands, B., Wall, R., 2017. Dung beetles reduce livestock gastrointestinal parasite availability on pasture. J. Appl. Ecol. 54, 1180–1189. https://doi.org/10.1111/1365-2664.12821

Schmidl, J., Büche, B., n.d. Die Rote Liste und Gesamtartenliste der Käfer (Coleoptera, exkl. Lauf- und Wasserkäfer) Deutschlands im Überblick (Stand Sept. 2011), Naturschutz und Biologische Vielfalt. Bonn-Bad Godesberg.

Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W., Bondeau, A., Bugmann, H., Carter, T.R., Gracia, C.A., de la Vega-Leinert, A.C., Erhard, M., Ewert, F., Glendining, M., House, J.I., Kankaanpää, S., Klein, R.J.T., Lavorel, S., Lindner, M., Metzger, M.J., Meyer, J., Mitchell, T.D., Reginster, I., Rounsevell, M., Sabaté, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M.T., Thonicke, K., Thuiller, W., Tuck, G., Zaehle, S., Zierl, B., 2005. Ecosystem Service Supply and Vulnerability to Global Change in Europe. Science 310, 1333–1337. https://doi.org/10.1126/science.1115233

Schwab, D.B., Riggs, H.E., Newton, I.L.G., Moczek, A.P., 2016. Developmental and Ecological Benefits of the Maternally Transmitted Microbiota in a Dung Beetle. Am. Nat. 188, 679–692. https://doi.org/10.1086/688926

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674. https://doi.org/10.1038/s41586-019-1684-3

Shaw, S.A., Sutherland, I.A., 2006. The prevalence of Stephanofilaria sp. in buffalo fly, Haematobia irritans exigua, in Central Queensland. Aust. J. Entomol. 45, 198–201. https://doi.org/10.1111/j.1440-6055.2006.00545.x

Sherratt, T.N., Macdougall, A.D., Wratten, S.D., Forbes, A.B., 1998. Models to assist the evaluation of the impact of avermectins on dung insect populations. Ecol. Modell. 110, 165–173. https://doi.org/10.1016/S0304-3800(98)00064-7

Skokanová, H., Falťan, V., Havlíček, M., 2016. Driving forces of main landscape change processes from past 200 years in Central Europe - differences between old democratic and post-socialist countries. Ekológia (Bratislava) 35, 50–65. https://doi.org/10.1515/eko-2016-0004

Sommer, C., Steffansen, B., Nielsen, B.O., Grønvold, J., Vagn Jensen, K.M., Brøchner Jespersen, J., 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. https://doi.org/10.1017/S0007485300051804

Stanbrook, R., Wheater, 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. https://doi.org/10.1007/s10841-020-00289-1

Strong, L., Wall, R., 1994. Effects of ivermectin and moxidectin on the insects of cattle dung. Bull. Entomol. Res. 84, 403–409. https://doi.org/10.1017/S0007485300032533

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. J. Appl. Entomol. 127, 481–488. https://doi.org/10.1046/j.0931-2048.2003.00780.x

Suárez, V.H., Lifschitz, A.L., Sallovitz, J.M., Lanusse, C.E., 2009. Effects of faecal residues of moxidectin and doramectin on the activity of arthropods in cattle dung. Ecotoxicol. Environ. Saf. 72, 1551–1558. https://doi.org/10.1016/j.ecoenv.2007.11.009

Tocco, C., Probo, M., Lonati, M., Lombardi, G., Negro, M., Nervo, B., Rolando, A., Palestrini, C., 2013. Pastoral Practices to Reverse Shrub Encroachment of Sub-Alpine Grasslands: Dung Beetles (Coleoptera, Scarabaeoidea) Respond More Quickly Than Vegetation. PLoS One 8, e83344. https://doi.org/10.1371/journal.pone.0083344

Tonelli, M., 2021. Some considerations on the terminology applied to dung beetle functional groups. Ecol. Entomol. 46, 772–776. https://doi.org/10.1111/een.13017

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.org/10.1007/s10841-020-00240-4

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/j.ecolind.2018.09.010

Tonelli, M., Verdú, J.R., Zunino, M., 2018. Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. Biodivers. Conserv. 27, 189–204. https://doi.org/10.1007/s10531-017-1428-3

Tonelli, M., Verdú, J.R., Zunino, M.E., 2017. 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. https://doi.org/10.7717/peerj.2780

Trible, M.L., 2021. Effects of bison, cattle, and environmental factors on grassland dung beetle abundance and community structure. Wichita State University.

Týr, V., 1999. Rozšíření druhu Aphodius (Coprimorphus) scrutator (Coleoptera: Scarabaeidae) v Čechách, na Moravě a na Slovensku. [Distribution of Aphodius (Coprimorphus) scrutator (Coleoptera: Scarabaeidae) in Bohemia, Moravia and Slovakia)]. Klapalekiana 35, 145–156.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., Chase, J.M., 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368, 417–420. https://doi.org/10.1126/science.aax9931

Vanbergen, A.J., the Insect Pollinators Initiative, 2013. Threats to an ecosystem service: pressures on pollinators. Front. Ecol. Environ. 11, 251–259. https://doi.org/10.1890/120126

Verdú, J.R., Cortez, V., Martinez-Pinna, J., Ortiz, A.J., Lumaret, J.P., Lobo, J.M., 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. Sci. Rep. 8, 1–9. https://doi.org/10.1038/s41598-018-33241-0

Verdú, J.R., Cortez, V., Ortiz, A.J., González-Rodríguez, E., Martinez-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., Lobo, J.M., Sánchez-Piñero, F., Gallego, B., Numa, C., Lumaret, J.P., Cortez, V., Ortiz, A.J., Tonelli, M., García-Teba, J.P., Rey, A., Rodríguez, A., Durán, J., 2018b. Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: An interdisciplinary field study. Sci. Total Environ. 618, 219–228. https://doi.org/10.1016/j.scitotenv.2017.10.331

Verdú, J.R., Sánchez-Piñero, F., Lobo, J.M., Cortez, V., 2020. Evaluating long-term ivermectin use and the role of dung beetles in reducing short-term CH 4 and CO 2 emissions from livestock faeces: a mesocosm design under Mediterranean conditions. Ecol. Entomol. 45, 109–120. https://doi.org/10.1111/een.12777

Vitner, J., 1998. Reproductive biology of the Central European Aphodius species with largescutellum (Coleoptera: Scarabaeidae: Aphodiidae). Acta Soc. Zool. Bohemiensis 62, 227–253.

Wagner, D.L., 2020. Insect Declines in the Anthropocene. Annu. Rev. Entomol. 65, 457–480. https://doi.org/10.1146/annurev-ento-011019-025151

Wardhaugh, K., 2000. Parasiticides registered for use in cattle in Australia - an annotated bibliography and literature guide prepared for the National Dung Beetle Planning Forum. CSIRO Entomol. Contract. Rep. Ser. 56, 1–15.

Waterhouse, D.F., 1974. The biological control of dung. Sci. Am. 230, 101–108.

Weaving, H., Sands, B., Wall, R., 2020. Reproductive sublethal effects of macrocyclic lactones and synthetic pyrethroids on the dung beetle Onthophagus similis. Bull. Entomol. Res. 110, 195–200. https://doi.org/10.1017/S0007485319000567

Wratten, S.D., Forbes, A.B., 1996. Environmental assessment of veterinary avermectins in temperate pastoral ecosystems. Ann. Appl. Biol. 128, 329–348. https://doi.org/10.1111/j.1744-7348.1996.tb07327.x

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. https://doi.org/10.1111/j.1744-697X.2007.00082.x

Zortéa, T., Segat, J.C., Maccari, A.P., Sousa, J.P., Da Silva, A.S., Baretta, D., 2017. Toxicity of four veterinary pharmaceuticals on the survival and reproduction of Folsomia candida in tropical soils. Chemosphere 173, 460–465. https://doi.org/10.1016/j.chemosphere.2017.01.06

Chapter I

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

Agriculture, Ecosystems & Environment (2021) 321, 107634
DOI: 10.1016/j.agee.2021.107634

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

Lucie AMBROŽOVÁ[1,2], František Xaver Jiří SLÁDEČEK[1,2,*], Tomáš ZÍTEK[1,2], Michal PERLÍK[1,2], Petr KOZEL[1,2], Miloslav JIRKŮ[3], Lukáš ČÍŽEK[1,2]

Affiliations:

[1] Faculty of Science, Department of Zoology, University of South Bohemia in České Budějovice, Branišovská 1760, CZ-37005 České Budějovice, Czech Republic

[2] Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 1160/31, CZ-37005 České Budějovice, Czech Republic

[3] Czech Academy of Sciences, Biology Centre, Institute of Parasitology, Branišovská 1160/31, CZ-37005 České Budějovice, Czech Republic

[*] Corresponding author:

Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 1160/31, CZ-37005 České Budějovice, Czech Republic. E-mail: franzsladecek@gmail.com

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, Tscharntke *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, 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).

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 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, 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 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 sampling, expected lethal or sublethal levels of residues), and (iii) long ago treated (antiparasitics administered more than eight weeks before the sampling; expected 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.

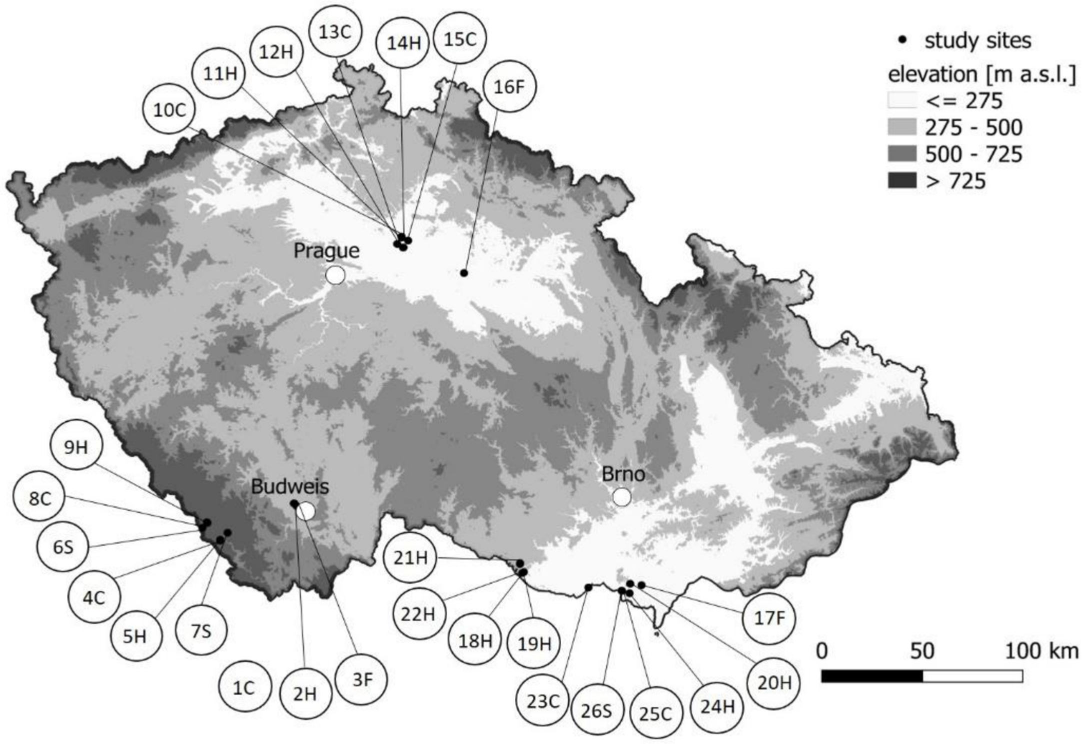

Fig. 1. Study sites. Distribution of study sites in four climatically and biogeographically distinct regions of the Czech Republic where dung beetle surveys were conducted in 2018 (Bohemian Forest: 1–6, South Bohemia: 7–9, Central Bohemia: 10–16, South Moravia: 17–26; site 23 is 0.5 km from the Czech 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 ×body length^3.316)*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).

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 *Colobopterus*), (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.*, *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 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 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. 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).

Relocators were more likely to be present ($\chi2 = 35{,}212$, $df = 2$, $p < 0.001$) 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 ($\chi2 = 18.146$, $df = 2$, $p < 0.001$) 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 ($\chi2 = 0.834$, $df = 2$, $p = 0.659$).

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).

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.

	χ2	**df**	**p**		**χ2**	**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**					

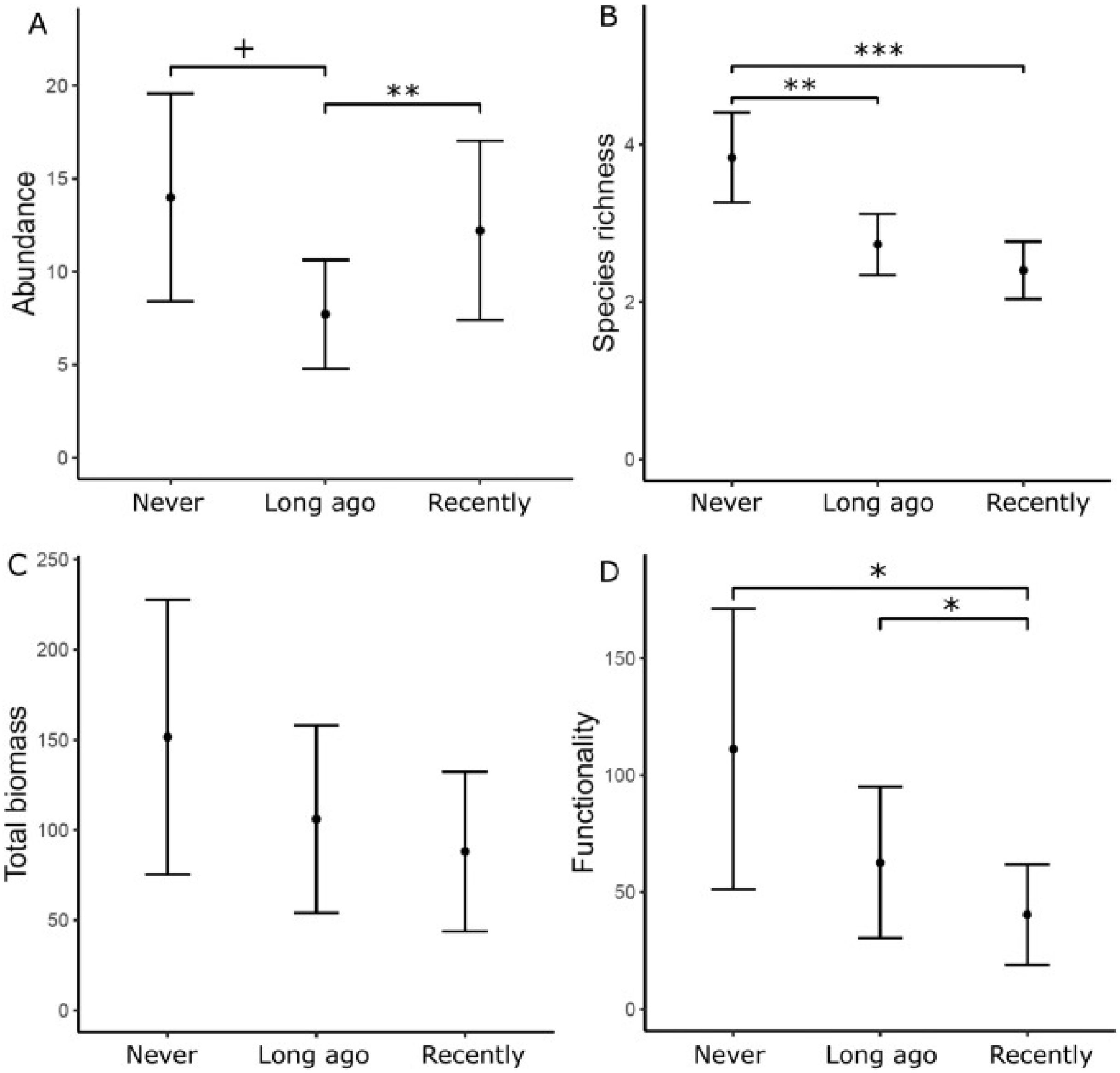

Fig. 2. Effects of ivermectin on abundance (A), species richness (B), total biomass (C), and functionality (D) of dung beetles in dung pats at sites never treated with ivermectin (Never), sites treated > 8 weeks ago (Long ago) and treated < 8 weeks ago (Recently). Functionality reflects dung removal 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 ~ 0.05, * = p < 0.05, * * = p < 0.001, * ** = p < 0.001.

4. 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 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 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.

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 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 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. 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 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.

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 Institutes of the Czech Academy of Sciences (R200961701), M.J. was supported by the Inst. of Parasitology and Inst. of Entomology, Biology Centre, Czech Academy of Sciences (RVO//:60077344), F.X.J.S. was supported by MSM200961902 (Czech Academy of Sciences), L.C. was supported by the Operational Program Integrated Infrastructure within the project: Sustainable smart farming systems taking into account the future challenges 313011W112, co-financed by the European Regional Development Fund.

References

Audino, L.D., Louzada, J., Comita, L., 2014. Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? Biol. Conserv. 169, 248–257. https://doi.org/10.1016/j.biocon.2013.11.023.

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.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–49. https://doi.org/10.18637/jss.v067.i01.

Beynon, S.A., Mann, D.J., Slade, E.M., Lewis, O.T., 2012a. Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems. J. Appl. Ecol. 49, 1365–1372. https://doi.org/10.1111/j.1365-2664.2012.02210.x.

Beynon, S.A., Peck, M., Mann, D.J., Lewis, O.T., 2012b. Consequences of alternative and conventional endoparasite control in cattle for dung-associated invertebrates and ecosystem functioning. Agr. Ecosyst. Environ. 162, 36–44. 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 UK cattle industry. Ecol. Entomol. 40, 124–135. https://doi.org/10.1111/een.12240.

Blackwell, M., Malloch, D., 1991. Life history and arthropod dispersal of a coprophilous Stylopage. Mycologia 83, 360–366. https://doi.org/10.2307/3759996.

Blüthgen, N., Menzel, F., Blüthgen, N., 2006. Measuring specialization in species interaction networks. BMC Ecol. 6, 9. https://doi.org/10.1186/1472-6785-6-9.

Buse, J., Entling, M.H., 2020. Stronger dung removal in forests compared with grassland is driven by trait composition and biomass of dung beetles. Ecol. Entomol. 45, 223–231. https://doi.org/10.1111/een.12793.

Buse, J., Šlachta, M., Sladecek, F.X.J., Pung, M., Wagner, T., Entling, M.H., 2015. Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles. Biol. Conserv. 187, 112–119. https://doi. org/10.1016/j.biocon.2015.04.011.

Buse, J., Šlachta, M., Sladecek, F.X.J., Carpaneto, G.M., 2018. Summary of the morphological and ecological traits of Central European dung beetles. Entomol. Sci. 21, 315–323. https://doi.org/10.1111/ens.12313.

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. https://doi.org/ 10.1126/science.6308762.

Canga, A.G., Prieto, A.M.S., Liébana, M.J.D., Martínez, N.F., Vega, M.S., Vieitez, J.J.G., 2009. The pharmacokinetics and metabolism of ivermectin in domestic animal species. Vet. J. 179, 25–37. https://doi.org/10.1016/j.tvjl.2007.07.011.

Christensen, C.M., Dobson, R.C., 1976. Biological and ecological studies on *Aphodius distinctus* (Mueller) (Coleoptera-Scarabaeidae). Am. Midl. Nat. 95, 242–249.

Collinge, S.K., 2000. Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology 81, 2211–2226. https://doi.org/ 10.1890/0012-9658(2000)081[2211:EOGFOI]2.0.CO;2.

Crump, A., Omura, S., 2011. Ivermectin, 'Wonder drug' from Japan: the human use perspective. P. Jpn. Acad. B Phys. 87, 13–28. https://doi.org/10.2183/pjab.87.13.

Czech Statistical Office 2020. Table 5 Livestock – Czech Republic. Created 29.05.2020 (code: 270147–20). Available from https://www.czso.cz/csu/czso/zem_ts. [accessed 26.1.2021].

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/ecy.3138.

Edwards, 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. https://doi.org/10.2307/2403984.

Emmerson, M., Morales, M.B., Oñate, J.J., Batáry, P., Berendse, F., Liira, J., Aavik, T., Guerrero, I., Bommarco, R., Eggers, S., Pärt, T., Tscharntke, T., Weisser, W., Clement, L., Bengtsson, J., 2016. How agricultural intensification affects biodiversity and ecosystem services. Adv. Ecol. Res. 55, 43–97. https://doi.org/10.1016/bs. aecr.2016.08.005.

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.1365-2915.2010.00891.x.

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. https:// doi.org/10.1051/vetres:2001134.

Finch, D., Schofield, H., Floate, K.D., Kubasiewicz, L.M., Mathews, F., 2020. 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. https://doi.org/10.1046/j.1365-2311.2002.00487.x.

Floate, K.D., 1998. Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada. Bull. Entomol. Res. 88, 25–35. https://doi.org/10.1017/ S0007485300041523.

Floate, K.D., 2007. Endectocide residues affect insect attraction to dung from treated cattle: implications for toxicity tests. Med. Vet. Entomol. 21, 312–322. 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.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574. https://doi.org/ 10.1126/science.1111772.

Fox, J., Weisberg, S., 2019. An (R) Companion to Applied Regression. Thousand Oaks (CA).

Geurden, T., Chartier, C., Fanke, J., di Regalbono, A.F., Traversa, D., von Samson-Himmelstjerna, G., Demeler, J., Vanimisetti, H.B., Bartram, D.J., Denwood, M.J., 2015. Anthelmintic resistance to ivermectin and moxidectin in gastrointestinal nematodes of cattle in Europe. Int. J. Parasitol. Drug 5, 163–171. https://doi.org/ 10.1016/j.ijpddr.2015.08.001.

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. https://doi.org/10.1111/j.1600-0587.1997.tb00347.x.

González-Tokman, D., Martínez, M.I., Villalobos-Ávalos, Y., Munguía-Steyer, R., Ortiz-Zayas, M.D., Cruz-Rosales, M., Lumaret, J.P., 2017. Ivermectin alters reproductive success, body condition and sexual trait expression in dung beetles. Chemosphere 178, 129–135. https://doi.org/10.1016/j.chemosphere.2017.03.013.

Goodenough, A.E., Webb, J.C., Yardley, J., 2019. Environmentally-realistic concentrations of anthelmintic drugs affect survival and motility in the cosmopolitan earthworm *Lumbricus terrestris* (Linnaeus, 1758). Appl. Soil. Ecol. 137, 87–95. https://doi.org/10.1016/j.apsoil.2019.02.001.

Guichon, P.T., Jim, G.K., Booker, C.W., Schunicht, O.C., Wildman, B.K., Brown, J.R., 2000. Relative cost-effectiveness of treatment of feedlot calves with ivermectin versus treatment with a combination of fenbendazole, permethrin, and fenthion, 349-349 J. Am. Vet. Med. Assoc. 217. https://doi.org/10.2460/ javma.2000.216.1965.

Halffter, G., Edmonds, W.D., 1982. The nesting behavior of dung beetles (Scarabaeinae). An Ecological and Evolutive Approach. Instituto de Ecología, Mexico.

Harrison, X.A., 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. Peerj 2. https://doi.org/10.7717/peerj.616.

Hartig, F., 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hempel, H., Scheffczyk, A., Schallnass, H.J., Lumaret, J.P., Alvinerie, M., Römbke, J., 2006. Toxicity of four veterinary parasiticides on larvae of the dung beetle *Aphodius constans* in the laboratory. Environ. Toxicol. Chem. 25, 3155–3163. 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.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.

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. https:// doi.org/10.1111/j.1365-2664.2003.00863.x.

Juřena, D., Týr, V., 2008. Seznam listorohých brouků (Coleoptera: Scarabaeoidea) České republiky a Slovenska. [Checklist of Scarabaeoidea (Coleoptera) of the Czech Republic and Slovakia.]. Klapalekiana 44, 3–15.

Kaplan, R.M., 2004. Drug resistance in nematodes of veterinary importance: a status report. Trends Parasitol. 20, 477–481. https://doi.org/10.1016/j.pt.2004.08.001.

Král, D., Bezděk, A., 2017. Scarabaeoidea (vrubounovití). Červený seznam ohrožených druhů České republiky. Bezobratlí. [Red List of Threatened Species of the Czech Republic. Invertebrates.]. Agentura ochrany přírody a krajiny ČR, Prague, pp. 409–413.

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 Oecol. 19, 425–438. https://doi.org/10.1016/S1146-609X(98) 80048-9.

Landin, B., 1961. Ecological studies on dung beetles (Col. Scarabaeidae). Opusc. Entomol. Suppl. 19, 1–227.

Lobo, J.M., 1993. Estimation of dung beetle biomass (Coleoptera, Scarabaeoidea). Eur. J. Entomol. 90, 235–238.

Lumaret, J., Kadiri, N., 1995. The influence of the first wave of colonizing insects on cattle dung dispersal. Pedobiologia 39, 506–517.

Lumaret, J.P., Errouissi, F., 2002. Use of anthelmintics in herbivores and evaluation of risks for the non target fauna of pastures. Vet. Res. 33, 547–562. https://doi.org/ 10.1051/vetres:2002038.

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. Curr. Pharm. Biotechnol. 13, 1004–1060. https://doi.org/10.2174/ 138920112800399257.

Maldonado, M.B., Aranibar, J.N., Serranoa, A.M., Chacoff, N.P., Vázquez, D.P., 2019. Dung beetles and nutrient cycling in a dryland environment. Catena 179, 66–73. https://doi.org/10.1016/j.catena.2019.03.035.

Manning, P., Cutler, G.C., 2018. Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness. Agric. Ecosyst. Environ. 264, 9–14. https://doi.org/10.1016/j.agee.2018.05.002.

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 Euoniticellus intermedius (Coleoptera:

Scarabaeidae). Can. Entomol. 149, 461–472. https://doi.org/10.4039/tce.2017.11.

Metera, E., Sakowski, T., Sloniewski, K., Romanowicz, B., 2010. Grazing as a tool to maintain biodiversity of grassland - a review. Anim. Sci. Pap. Rep. 28, 315–334.

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/s00442-016-3756-5.

Milotić, T., Baltzinger, C., Eichberg, C., Eycott, A.E., Heurich, M., Müller, J., Noriega, J. A., Menendez, R., Stadler, J., Ádám, R., Bargmann, T., Bilger, I., Buse, J., Calatayud, J., Ciubuc, C., Boros, G., Jay-Robert, P., Kruus, M., Merivee, E., Miessen, G., Must, A., Ardali, E., Preda, E., Rahimi, I., Rohwedder, D., Rose, R., Slade, E.M., Somay, L., Tahmasebi, P., Ziani, S., Hoffmann, M., 2019. Functionally richer communities improve ecosystem functioning: dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. J. Biogeogr. 46, 70–82. https://doi.org/10.1111/jbi.13452.

Nervo, B., Tocco, C., Caprio, E., Palestrini, C., Rolando, A., 2014. The effects of body mass on dung removal efficiency in dung beetles. PLoS One 9 (9), 107699. https:// doi.org/10.1371/journal.pone.0107699.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria- Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L. P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G. M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520 (7545), 45–50. https://doi.org/10.1038/nature14324.

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. Biol. Conserv. 141, 1461–1474. https://doi.org/10.1016/j. biocon.2008.04.011.

O'Hea, N.M., Kirwan, L., Giller, P.S., Finn, J.A., 2010. Lethal and sub-lethal effects of ivermectin on north temperate dung beetles, *Aphodius ater* and *Aphodius rufipes* (Coleoptera: Scarabaeidae). Insect Conserv. Diver 3, 24–33. https://doi.org/ 10.1111/j.1752-4598.2009.00068.x.

Pecenka, J.R., Lundgren, J.G., 2019. Effects of herd management and the use of ivermectin on dung arthropod communities in grasslands. Basic. Appl. Ecol. 40, 19–29. https://doi.org/10.1016/j.baae.2019.07.006.

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.org/10.1371/journal.pone.0071454.

Pérez-Cogollo, L.C., Rodríguez-Vivas, R.I., Reyes-Novelo, E., Delfín-González, H., Muñoz- Rodríguez, D., 2017. Survival and reproduction of *Onthophagus landolti* (Coleoptera: Scarabaeidae) exposed to ivermectin residues in cattle dung. Bull. Entomol. Res. 107, 118–125. https://doi.org/10.1017/S0007485316000705.

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, 1440–1448. https://doi.org/10.1016/j. scitotenv.2017.10.171.

Puniamoorthy, N., Schäfer, M.A., Römbke, J., Meier, R., Blanckenhorn, W.U., 2014. Ivermectin sensitivity is an ancient trait affecting all ecdysozoa but shows phylogenetic clustering among sepsid flies. Evol. Appl. 7, 548–554. https://doi.org/ 10.1111/eva.12152.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project. org/.

Rodríguez-Vivas, R.I., Basto-Estrella, G.S., Reyes-Novelo, E., Arceo-Moran, A.A., 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 Entomol. 59, 368–374. https://doi.org/10.1111/aen.12450.

Rössner, E., 2012. Die Hirschkäfer und Blatthornkäfer Ostdeutschlands (Coleoptera: Scarabaeoidea). Verein der Freunde & Förderer des Naturkundemuseums Erfurt e. V.

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27. https://doi.org/10.1016/j. biocon.2019.01.020.

Sands, B., Wall, R., 2017. Dung beetles reduce livestock gastrointestinal parasite availability on pasture. J. Appl. Ecol. 54, 1180–1189. https://doi.org/10.1111/ 1365-2664.12821.

Sands, B., Wall, R., 2018. Sustained parasiticide use in cattle farming affects dung beetle functional assemblages. Agric. Ecosyst. Environ. 265, 226–235. https://doi.org/ 10.1016/j.agee.2018.06.012.

Skaloš, J., 2006. Patterns and changes of intensively utilised agricultural landscape in the Czech Republic between 1937 and 2002: Aerial photography analysis. Ekol. Bratisl. 25, 232–248.

Sladecek, F.X.J., Hrcek, J., Klimes, P., Konvicka, M., 2013. Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat. Acta Oecol. 46, 17–24. https://doi.org/10.1016/j.actao.2012.10.012.

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. https://doi.org/10.1017/ S0007485300051804.

Stebnicka, Z., 1973. Beitrag zur Systematik und Verbreitung einiger Arten aus der Familie Scarabaeidae (Coleoptera) Polens. Acta Zool. Cracov. 18, 1–22.

Strong, L., Wall, R., 1994. Effects of ivermectin and moxidectin on the insects of cattle dung. Bull. Entomol. Res. 84, 403–409. https://doi.org/10.1017/ S0007485300032533.

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. J. Appl. Entomol. 127, 481–488. https://doi.org/10.1046/j.0931-2048.2003.00780. x.

Sutherland, I.H., 1990. Veterinary use of ivermectin. Act. Leiden. 59, 211–216. Sutton, G., Bennett, J., Bateman, M., 2014. Effects of ivermectin residues on dung invertebrate communities in a UK farmland habitat. Insect Conserv. Divers. 7, 64–72. https://doi.org/10.1111/icad.12030.

Tixier, T., Lumaret, J.P., Sullivan, G.T., 2015. Contribution of the timing of the successive waves of insect colonisation to dung removal in a grazed agroecosystem. Eur. J. Soil. Biol. 69, 88–93. https://doi.org/10.1016/j.ejsobi.2015.06.001.

Tonelli, M., Verdú, J.R., Zunino, M.E., 2017. 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.org/10.7717/peerj.2780.

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.org/ 10.1007/s10841-020-00240-4.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol. Lett. 8, 857–874. https://doi.org/10.1111/j.1461- 0248.2005.00782.x.

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., Lobo, J.M., Sánchez-Piñero, F., Gallego, B., Numa, C., Lumaret, J.P., Cortez, V., Ortiz, A.J., Tonelli, M., García-Teba, J.P., Rey, A., Rodríguez, A., Durán, J., 2018. Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study. Sci. Total. Environ. 618, 219–228. https://doi.org/10.1016/j.scitotenv.2017.10.331.

Weaving, H., Sands, B., Wall, R., 2020. Reproductive sublethal effects of macrocyclic lactones and synthetic pyrethroids on the dung beetle

Onthophagus similis. Bull. Entomol. Res. 110, 195–200. https://doi.org/10.1017/S0007485319000567.

Webb, L., Beaumont, D.J., Nager, R.G., McCracken, D.I., 2010. Field-scale dispersal of *Aphodius* dung beetles (Coleoptera: Scarabaeidae) in response to avermectin treatments on pastured cattle. Bull. Entomol. Res. 100, 175–183. https://doi.org/ 10.1017/S0007485309006981.

Woodcock, B.A., Edwards, A.R., Lawson, C.S., Westbury, D.B., Brook, A.J., Harris, S.J., Brown, V.K., Mortimer, S.R., 2008. Contrasting success in the restoration of plant and phytophagous beetle assemblages of species-rich mesotrophic grasslands. Oecologia 154, 773–783. https://doi.org/10.1007/s00442-007-0872-2.

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 – Tankodrom	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

Table A2. List of recorded species, their guild assignment, and abundances in study treatments. D = dweller, R = relocator, 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

family species	guild	treated 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
Chilothorax distincus (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 obliteratus (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 (Kugelan, 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

family species	guild	treated 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
Phalacronothus 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

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

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, Rauhenebrach, 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 ofApplied 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

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 57 021 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.

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 (Vandekerkhove *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 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 (Prietzel & 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 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-coprophagous (Freude, 2009). The maintenance of dung-inhabiting beetle functional diversity has hence recently 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 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.

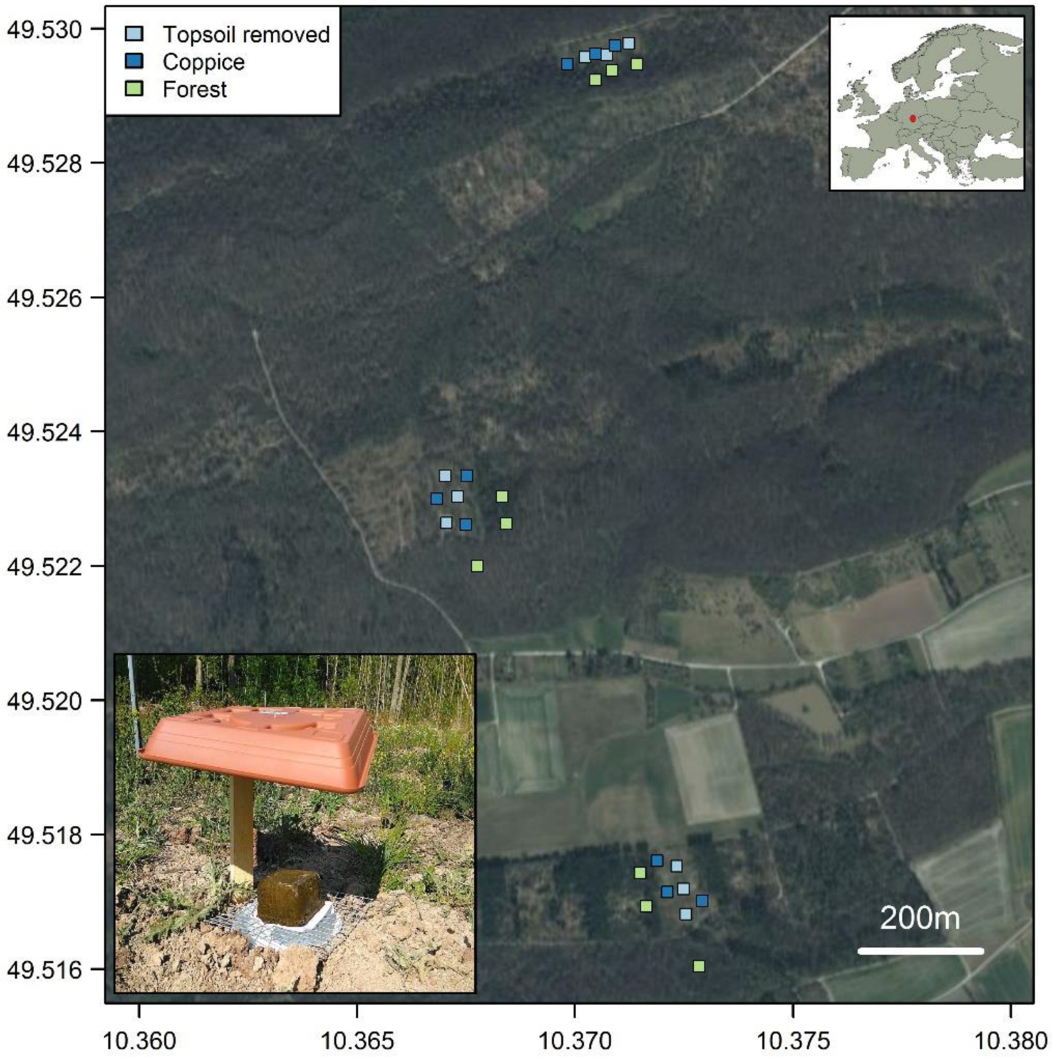

Figure 1

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.

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 (Sladecek *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 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 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 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 or 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).

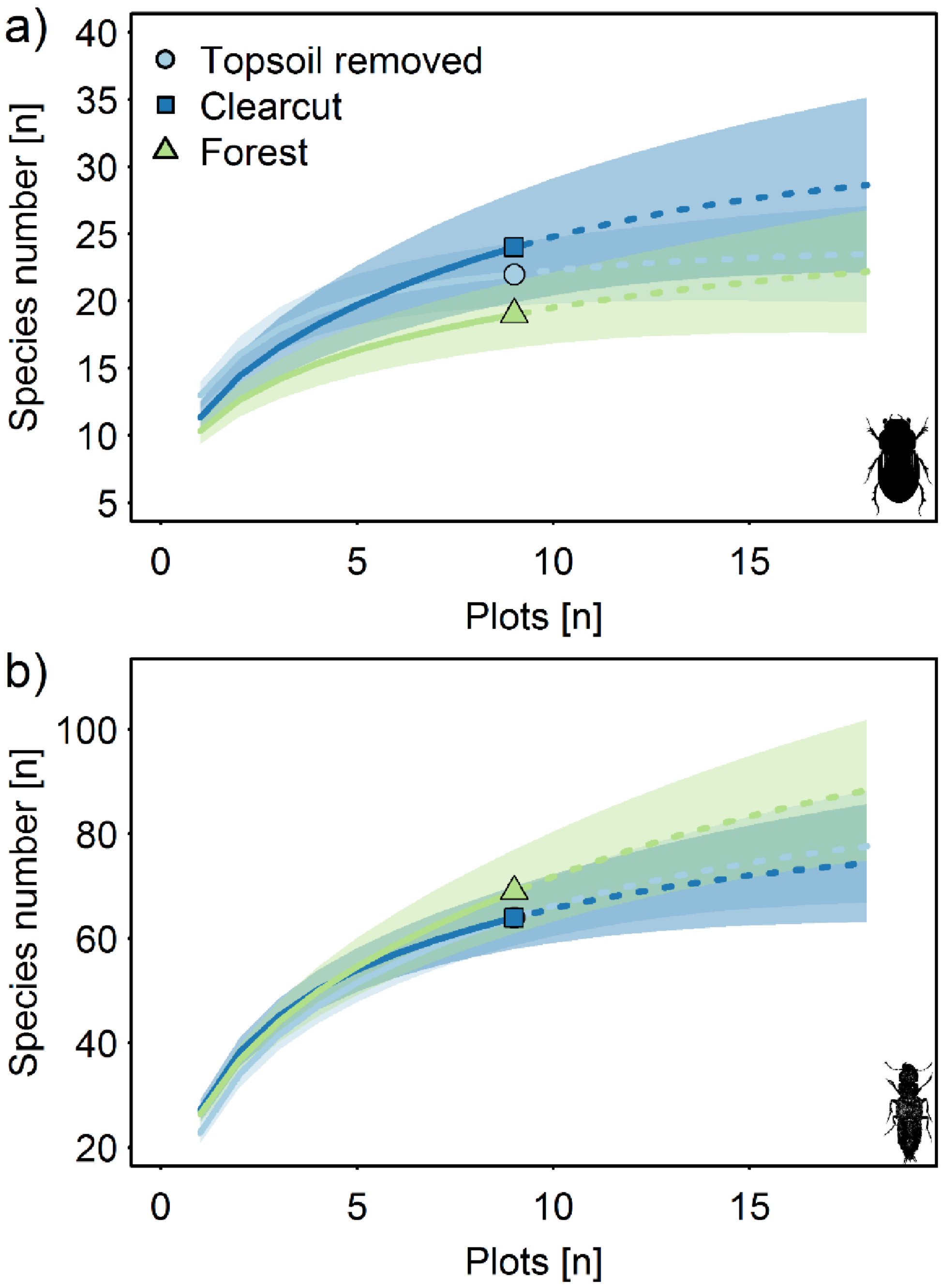

Figure 2

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).

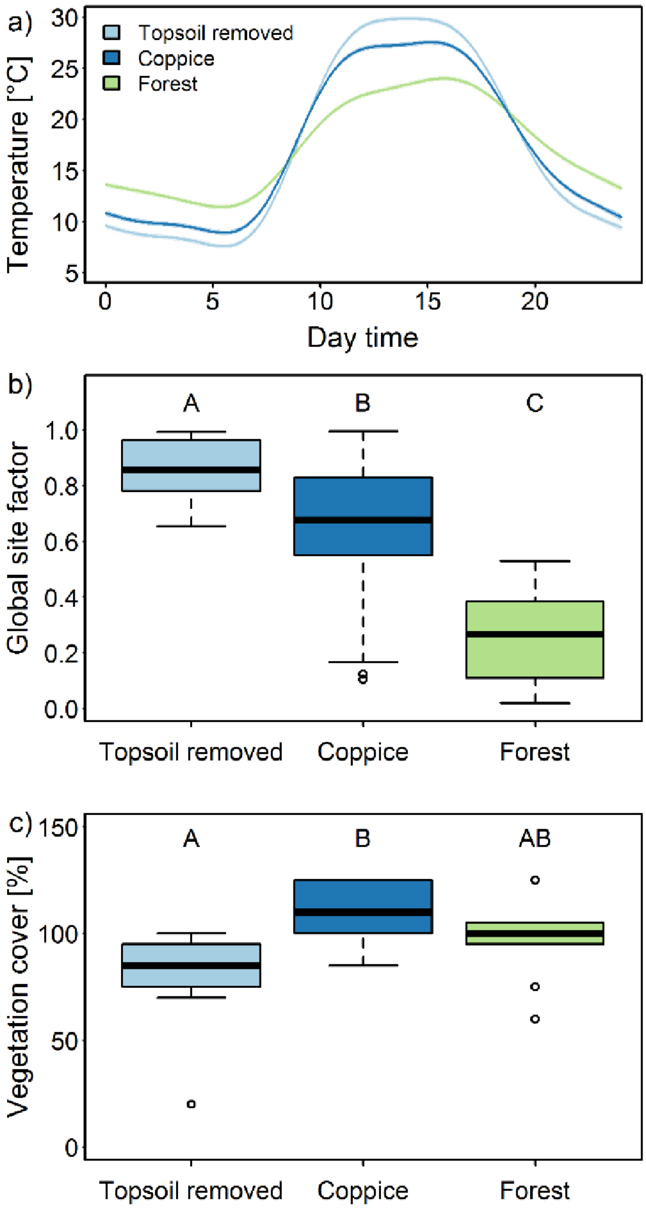

Figure 3

(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).

Five dung beetle species, namely, *Euorodalus paracoenosus* (Balthasar & Hrubant, 1960), *Melinopterus prodromus* (Brahm, 1790), *Onthophagus fracticornis* (Preyssler, 1790), *Onthophagus ovatus* (Linnaeus, 1767), *S. schaefferi* and four rove beetle species, *Anotylus tetracarinatus* (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).

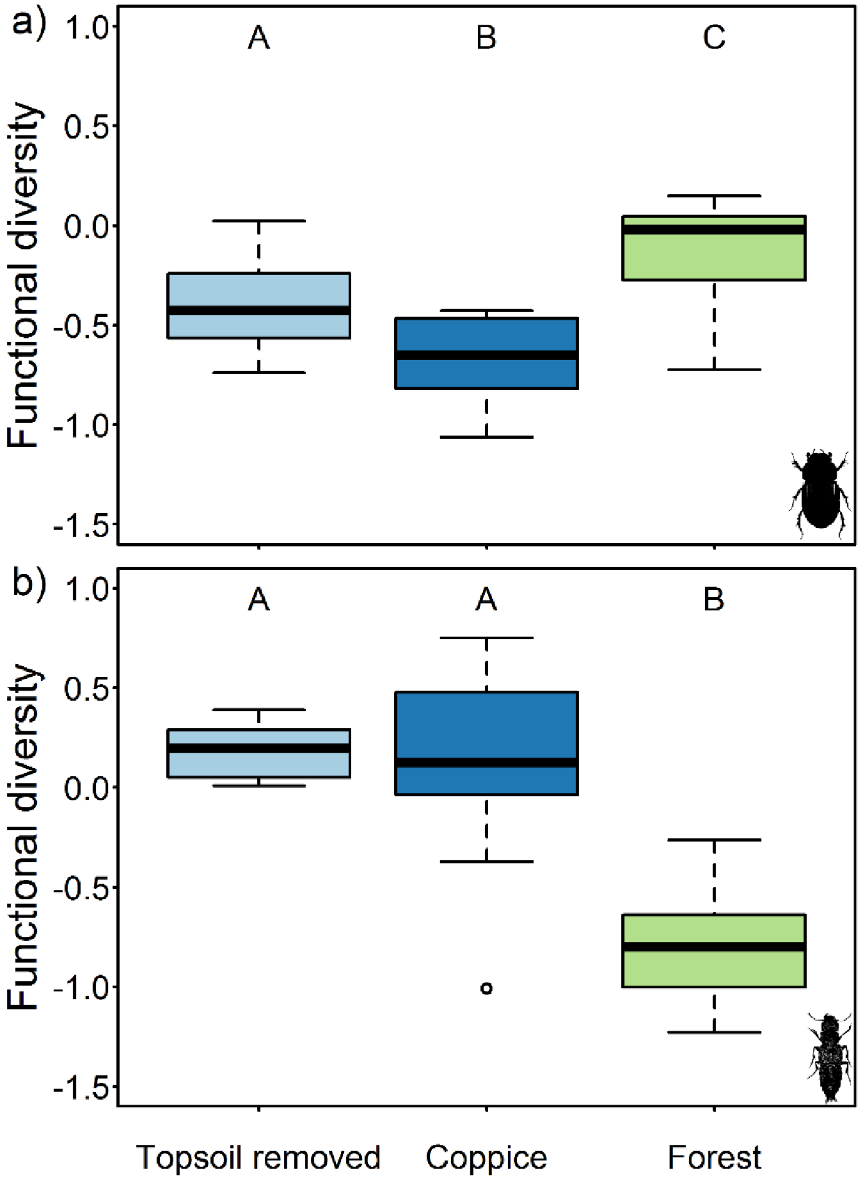

Figure 4

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.

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).

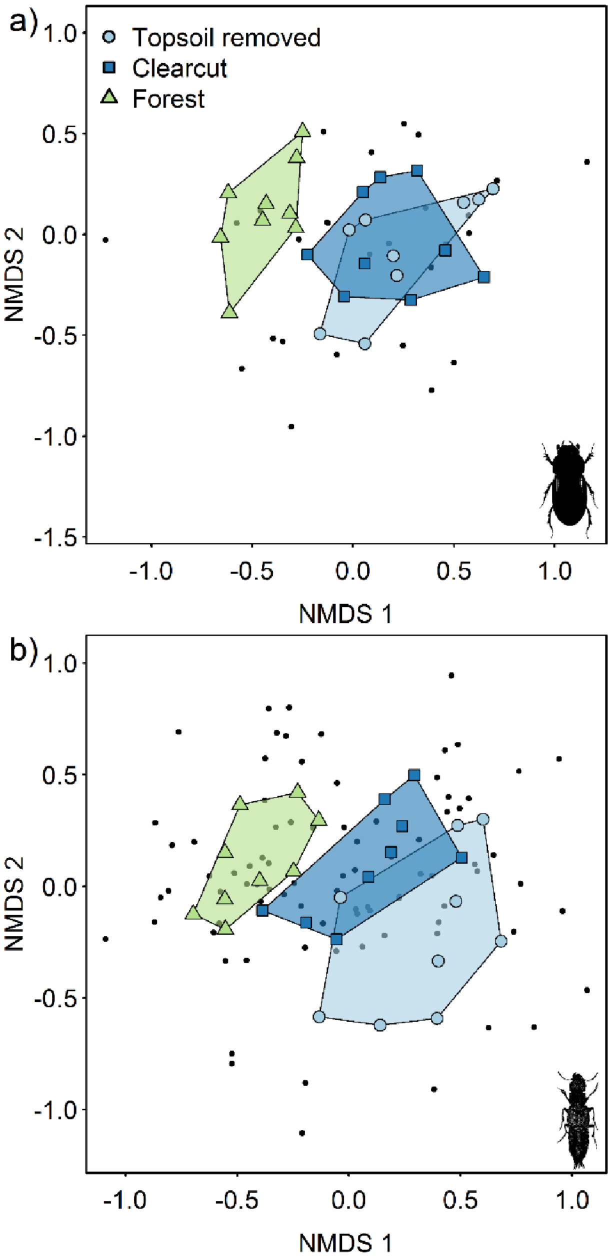

Figure 5

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.

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 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; Růžičková & 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 m^2 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 heterogenous 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 heterogenous 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-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 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.

References

Anderson, M.J., Ellingsen, K.E. & McArdle, B.H. (2006) Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9, 683–693.

Assing, V. & Schülke, M. (2012) Die Käfer Mitteleuropas. Band 4. Staphylinidae I. Zweite neu. Spektrum Akademischer Verlag, Germany. Barragán, F., Moreno, C.E., Escobar, F., Halffter, G. & Navarrete, D. (2011) Negative impacts of human land use on dung beetle functional diversity. PLoS One, 6, e17976.

Bartha, S., Canullo, R., Chelli, S. & Campetella, G. (2020) Unimodal relationships of understory alpha and beta diversity along chronosequence in coppiced and unmanaged beech forests. Diversity, 12, 101.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67, 1–48.

Battisti, C. & Fanelli, G. (2011) Does human-induced heterogeneity differently affect diversity in vascular plants and breeding birds? Evidences from three Mediterranean forest patches. Rendiconti Lincei, 22, 25–30.

Benes, J., Cizek, O., Dovala, J. & Konvicka, M. (2006) Intensive game keeping, coppicing and butterflies: the story of Milovicky wood, Czech Republic. Forest Ecology and Management, 237, 353–365.

Biel, P., Krawczynski, R., Lysakowski, B. &Wagner, H.-G. (2014) Emus hirtus in Niedersachsen (Germany) and Europe: contribution to the knowledge of the ecology and distribution of a locally endangered rove-beetle (Coleoptera: Staphylinidae). Entomologische Nachrichten und Berichte, 74, 75–80.

Bjørnstad, O.N. & Falck, W. (2001) Nonparametric spatial covariance functions: estimation and testing. Environmental and Ecological Statistics, 8, 53–70.

Bobbink, R., Hicks, K., Galloway, J. et al. (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications, 20, 30–59.

Bohac, J. (1999) Staphylinid beetles as bioindicators. Agriculture, Ecosystems and Environment, 74, 357–372.

Bolker, B.M., Brooks, M.E., Clark, C.J. et al. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution, 24, 127–135.

Borchard, F., Buchholz, S., Helbing, F. & Fartmann, T. (2014) Carabid beetles and spiders as bioindicators for the evaluation of montane heathland restoration on former spruce forests. Biological Conservation, 178, 185–192.

Bowler, D.E., Heldbjerg, H., Fox, A.D., de Jong, M. & Böhning-Gaese, K. (2019) Long-term declines of European insectivorous bird populations and potential causes. Conservation Biology, 33, 1120–1130.

Bradshaw, R.H.W., Hannon, G.E. & Lister, A.M. (2003) A long-term perspective on ungulate-vegetation interactions. Forest Ecology and Management, 181, 267–280.

Buckley, P. (2020) Coppice restoration and conservation: a European perspective. Journal of Forest Research, 25, 125–133.

Buse, J. & Entling, M.H. (2020) Stronger dung removal in forests compared with grassland is driven by trait composition and biomass of dung beetles. Ecological Entomology, 45, 223–231.

Buse, J., Šlachta, M., Sladecek, F.X.J., Pung, M., Wagner, T. & Entling, M.H. (2015) Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles. Biological Conservation, 187, 112–119.

Buse, J., Šlachta, M., Sladecek, F.X.J. & Carpaneto, G.M. (2018) Summary of the morphological and ecological traits of central European dung beetles. Entomological Science, 21, 315–323.

Cabrera Walsh, G. & Chani Posse, M. (2003) Abundance and seasonal distribution of predatory coprophilous argentine rove beetles (Coleoptera: Staphylinidae), and their effects on dung breeding flies. Coleopterists Bulletin, 57, 43–50.

de Castro-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.

Cesonienė, L., Daubaras, R., Tamutis, V. et al. (2019) Effect of clear-cutting on the understory vegetation, soil and diversity of litter beetles in scots pine-dominated forest. Journal of Sustainable Forestry, 38, 791–808.

Chao, A., Chiu, C.-H. & Jost, L. (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. Annual Review of Ecology, Evolution, and Systematics, 45, 297–324.

Dolek, M., Kőrösi, Á. & Freese-Hager, A. (2018) Successful maintenance of Lepidoptera by government-funded management of coppiced forests. Journal for Nature Conservation, 43, 75–84.

Douda, J., Boublík, K., Doudová, J. & Kyncl, M. (2017) Traditional forest management practices stop forest succession and bring back rare plant species. Journal of Applied Ecology, 54, 761–771.

Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C. & Lambin, X. (2001) Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. Parasitology, 122, 563–569.

Emsens, W.J., Aggenbach, C.J.S., Smolders, A.J.P. & van Diggelen, R. (2015) Topsoil removal in degraded rich fens: can we force an ecosystem reset? Ecological Engineering, 77, 225–232.

Ewald, J. & Pyttel, P. (2016) Leitbilder, Möglichkeiten und Grenzen der De-Eutrophierung von Wäldern in Mitteleuropa. Natur und Land- schaft, 91, 210–217.

Fartmann, T., Müller, C. & Poniatowski, D. (2013) Effects of coppicing on butterfly communities of woodlands. Biological Conservation, 159, 396–404.

Freude, H. (2009) Die Käfer Mitteleuropas. Band 5. Staphylinidae II.2. korr. Spektrum der Wissenschaft Verlag, Krefeld.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. Ecology, 81, 2606–2621.

Gower, J.C. (1971) A general coefficient of similarity and some of its properties. Biometrics, 27, 857.

Haddad, N.M., Haarstad, J. &Tilman, D. (2000) The effects of long-term nitrogen loading on grassland insect communities. Oecologia, 124, 73–84.

Hanski, I. & Hammond, P.M. (1986) Assemblages of carrion and dung Staphylinidae in tropical rain forests in Sarawak, Borneo. Annales Entomologici Fennici, 52, 1–19.

Hautier, Y., Niklaus, P.A. & Hector, A. (2009) Competition for light causes plant biodiversity loss after eutrophication. Science, 324, 636–638.

Helbing, F., Blaeser, T.P., Löffler, F. & Fartmann, T. (2014) Response of Orthoptera communities to succession in alluvial pine woodlands. Journal ofInsect Conservation, 18, 215–224.

Heneberg, P., Bogusch, P. & Řezáč, M. (2016) Off-road motorcycle circuits support long-term persistence of bees and wasps (hymenoptera: Aculeata) of open landscape at newly formed refugia within otherwise afforested temperate landscape. Ecological Engineering, 93, 187–198.

Hölzel, N. &Otte, A. (2003) Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. Applied Vegetation Science, 6, 131–140.

Horak, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P. & Pech, P. (2014) Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. Forest Ecology and Management, 315, 80–85.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. Biometrical Journal, 50, 346–363.

Hsieh, T.C., Ma, K.H. & Chao, A. (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution, 7, 1451–1456.

Hubbard, R.M., Vose, J.M., Clinton, B.D., Elliott, K.J. & Knoepp, J.D. (2004) Stand restoration burning in oak-pine forests in the southern Appalachians: effects on aboveground biomass and carbon and nitrogen cycling. Forest Ecology and Management, 190, 311–321.

Jentsch, A., Friedrich, S., Steinlein, T., Beyschlag, W. & Nezadal, W. (2009) Assessing conservation action for substitution of missing dynamics on former military training areas in Central Europe. Restoration Ecology, 17, 107–116.

Jones, L., Stevens,C., Rowe,E.C. et al. (2017) Can on-site management mitigate nitrogen deposition impacts in non-wooded habitats? Biological Conservation, 212, 464–475.

Kiehl, K., Kirmer, A., Donath, T.W., Rasran, L. & Hölzel, N. (2010) Species introduction in restoration projects—evaluation of different techniques for the establishment of semi-natural grasslands in central and northwestern Europe. Basic and Applied Ecology, 11, 285–299.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020) Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science, 368, 417–420.

Kopecký, M., Hédl, R. & Szabó, P. (2013) Non-random extinctions dominate plant community changes in abandoned coppices. Journal of Applied Ecology, 50, 79–87.

Krause, R.H., Buse, J., Matern, A., Schröder, B., Härdtle, W. & Assmann, T. (2011) Eresus kollari (Araneae: Eresidae) calls for heathland management. Journal of Arachnology, 39, 384–392.

Lanta, V., Mudrák, O., Liancourt, P. et al. (2020) Restoring diversity of thermophilous oak forests: connectivity and proximity to existing habitats matter. Biodiversity and Conservation, 29, 3411–3427.

Legendre, P. & Anderson, M.J. (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecological Monographs, 69, 1–24.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W. et al. (2014) New policies for old trees: averting a global crisis in a keystone ecological structure. Conservation Letters, 7, 61–69.

Lipkow, E. (2011) Observations to the life history of dung-inhabiting Staphylinidae (Coleoptera). Faunistisch-ökologische Mitteilungen, 9, 225–246.

Löbl, I. & Löbl, D. (2015) Catalogue of palaearctic coleoptera. Hydrophiloidea-Staphylinoidea. Revised and Updated Edition,Vol. 2. Brill, Boston, Massachusetts.

Löbl, I. & Löbl, D. (2016) Catalogue of palaearctic coleoptera. Scarabaeoidea, Scirtoidea, Dascilloidea, Buprestoidea, Byrrhoidea, Vol. 3. Brill, Boston, Massachusetts.

Lobo, J.M., Martin-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'Écologie et de Biologie du Sol, 25, 77–100.

Lundborg, A. (1997) Reducing the nitrogen harvesting load: whole-tree harvesting: a literature review. Ambio, 26, 387–393.

Maldonado, M.B., Aranibar, J.N., Serrano, A.M., Chacoff, N.P. & Vázquez, D.P. (2019) Dung beetles and nutrient cycling in a dryland environment. Catena, 179, 66–73.

Maus, C., Mittmann, B. & Peschke, K. (1998) Host records of Parasitoid Aleochara Gravenhorst species (Coleoptera, Staphylinidae) attacking Puparia of Cyclorrhapheous Diptera. Deutsche Entomologische Zeitschrift (neue Folge), 45, 231–254.

Meineke, T., Feldmann, B., Jung, M. & Marten, A. (2017) Käfer (Coleoptera) am Kot des Rothirsches im Hochharz - eine Stichprobenaufsammlung [beetles (Coleoptera) on droppings of Red Deer in the Harz Mountains—a random sample]. Entomologische Nachrichten und Berichte, 61, 137–147.

Mentil, L., Battisti, C.& Maria Carpaneto, G. (2018) The older the richer: significant increase in breeding bird diversity along an age gradient of different coppiced woods. Web Ecology, 18, 143–151.

Miklín, J., Sebek, P., Hauck, D., Konvicka, O. & Cizek, L. (2018) Past levels of canopy closure affect the occurrence of veteran trees and flagship saproxylic beetles. Diversity and Distributions, 24, 208–218.

Milotić, T., Baltzinger, C., Eichberg, C. et al. (2019) Functionally richer communities improve ecosystem functioning: dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. Journal of Biogeography, 46, 70–82.

Minchin, P.R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio, 69, 89–107.

Müllerová, J., Szabó, P. & Hédl, R. (2014) The rise and fall of traditional forest management in southern Moravia: a history of the past 700 years. Forest Ecology and Management, 331, 104–115.

Neff, F., Resch, M.C., Marty, A. et al. (2020) Long-term restoration success of insect herbivore communities in seminatural grasslands: a functional approach. Ecological Applications, 30, 1–12.

Newbold, T., Hudson, L.N., Hill, S.L.L. et al. (2015) Global effects of land use on local terrestrial biodiversity. Nature, 520, 45–50.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S. & Favila, M.E. (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation, 141, 1461–1474.

Niemeyer, M., Niemeyer, T., Fottner, S., Härdtle, W. & Mohamed, A. (2007) Impact of sod-cutting and choppering on nutrient budgets of dry heathlands. Biological Conservation, 134, 344–353.

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.

Oksanen, J., Blanchet, F.G., Kindt, R., et al. (2020) Vegan: community ecology package [WWW document]. URL https://cran.r-project.org/web/packages/vegan/vegan.pdf [accessed on 15 December 2020].

Oksanen, J., Blanchet, F.G., Friendly, M., et al. (2018) Vegan: community ecology package.

Pausas, J.G. & Verdú, M. (2010) The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. Bioscience, 60, 614–625.

Prietzel, J. & Kaiser, K.O. (2005) De-eutrophication of a nitrogen-saturated scots pine forest by prescribed litter-raking. Journal of Plant Nutrition and Soil Science, 168, 461–471.

Rich, P.M., Clark, D.B., Clark, D.A. & Oberbauer, S.F. (1993) Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. Agricultural and Forest Meteorology, 65, 107–127.

Růžičková, J. & Hykel, M. (2019) Habitat mosaic of gravel pit as a potential refuge for carabids: a case study from Central Europe. Community Ecology, 20, 215–222.

Sayer, E.J. (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biological Reviews of the Cambridge Philosophical Society, 81, 1–31.

Schultheiß, W. (1963) Urkundenbuch der Reichsstadt Windsheim von 741-1400. Veröffentlichungen der Gesellschaft für Fränkische Geschichte 3/4, Würzburg.

Sebek, P., Altman, J., Platek, M. & Cizek, L. (2013) Is active management the key to the conservation of Saproxylic biodiversity? Pollarding promotes the formation of tree hollows. PLoS One, 8, e60456.

Sebek, P., Bace, R., Bartos, M. et al. (2015) Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests. Forest Ecology and Management, 358, 80–89.

Seibold, S., Gossner, M.M., Simons, N.K. et al. (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature, 574, 671–674.

Šipoš, J., Hédl, R., Hula, V. et al. (2017) Patterns of functional diversity of two trophic groups after canopy thinning in an abandoned coppice. Folia Geobotanica, 52, 45–58.

Sladecek, F.X.J., Hrcek, J., Klimes, P. & Konvicka, M. (2013) Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat. Acta Oecologica, 46, 17–24.

Soto, D.P. & Puettmann, K.J. (2018) Topsoil removal through scarification improves natural regeneration in high-graded Nothofagus old-growth forests. Journal of Applied Ecology, 55, 967–976.

Spector, S. (2006) Scarabaeine dung beetles (coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. The Coleopterists Bulletin, 60, 71–83.

Spitzer, L., Konvicka, M., Benes, J., Tropek, R., Tuf, I.H. & Tufova, J. (2008) Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities. Biological Conservation, 141, 827–837.

Streitberger, M., Hermann, G., Kraus,W. & Fartmann, T. (2012) Modern forest management and the decline of the woodland Brown (Lopinga achine) in Central Europe. Forest Ecology and Management, 269, 239–248.

Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? Annual Review of Entomology, 47, 561–594.

Tarvainen, O., Strömmer, R. & Markkola, A. (2011) Urban forest regeneration: responses of scots pine seedlings to partial humus removal in mid-boreal N-enriched forests. Landscape and Urban Planning, 102, 209–214.

Thorn, S., Bässler, C., Svoboda, M. & Müller, J. (2017) Effects of natural disturbances and salvage logging on biodiversity—lessons from the bohemian Forest. Forest Ecology and Management, 388, 113–119.

Thorn, S., Seibold, S., Leverkus, A.B. et al. (2020) The living dead: acknowledging life after tree death to stop forest degradation. Fron- tiers in Ecology and the Environment, 18, 505–512.

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. Journal of Insect Conservation, 24, 643–654.

Tropek, R., Cizek, O., Kadlec, T. & Klecka, J. (2017) Habitat use of Hipparchia semele (Lepidoptera) in its artificial stronghold: necessity of the resource-based habitat view in restoration of disturbed sites. Polish Journal of Ecology, 65, 385–399.

Vandekerkhove, K., Thomaes, A., Crèvecoeur, L., De Keersmaeker, L., Leyman, A. & Köhler, F. (2016) Saproxylic beetles in non-intervention and coppice-with-standards restoration management in Meerdaal forest (Belgium): an exploratory analysis. iForest—Biogeosciences and Forestry, 9, 536–545.

Vera, F.W.M. (2000) Grazing Ecology & Forest History. Oxon and New York: CABI Publishing.

Vild, O., Roleček, J., Hédl, R., Kopecký, M. & Utinek, D. (2013) Experimental restoration of coppice-with-standards: response of understorey vegetation from the conservation perspective. Forest Ecology and Management, 310, 234–241.

Volf, M., Holec, M., Holcová, D. et al. (2018) Microhabitat mosaics are key to the survival of an endangered ground beetle (Carabus nitens) in its post-industrial refugia. Journal of Insect Conservation, 22, 321–328.

Warren, S.D. & Büttner, R. (2008) Active military training areas as refugia for disturbance-dependent endangered insects. Journal of Insect Conservation, 12, 671–676.

Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics, 24, 2098–2100.

Weiss, M., Kozel, P., Zapletal, M. et al. (2021) The effect of coppicing on insect biodiversity. Small-scale mosaics of successional stages drive community turnover. Forest Ecology and Management, 483, 118774.

Wohlgemuth, T., Bürgi, M., Scheidegger, C. & Schütz, M. (2002) Dominance reduction of species through disturbance — a proposed management principle for central European forests. Forest Ecology and Management, 166, 1–15.

Yang, L.H. & Gratton, C. (2014) Insects as drivers of ecosystem processes. Current Opinion in Insect Science, 2, 26–32.

Appendix S1. Supporting information

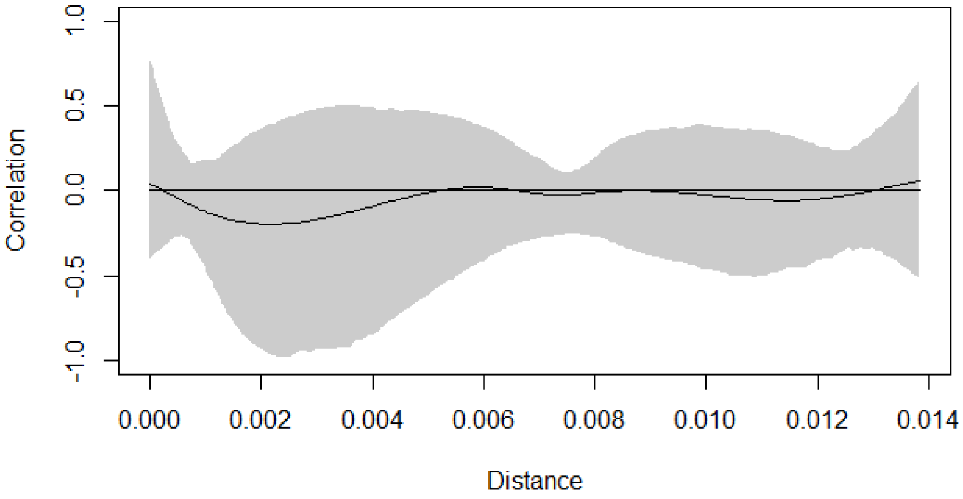

Figure S1: Spline correlogram of the number of collected dung beetle species. The figure indicates the lack of spatial dependencies in the model residuals (black line in the centre of grey confidence shading).

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 = relocator, 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
Agrilinus 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

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
Chilothorax 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

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

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 tetracarinatus	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

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

species	size	feeding mode	feeding
Ocalea badia	3.85	G	CR
Ocypus 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
Platydracus chalcocephalus	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 curtipennis	12.5	R	CR
Quedius invreae	9.5	R	CR
Quedius lateralis	12.5	R	CR
Quedius picipes	9.5	R	CR

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

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
	Chilothorax 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
	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

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 tetracarinatus (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

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
	Gabrius piliger Mulsant & Rey, 1876	1	0	0
	Gabrius splendidulus (Gravenhorst, 1802)	0	0	1
	Gyrohypnus 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

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
	Ocypus nitens (Schrank, 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 chalcocephalus (Fabricius, 1801)	13	75	441
	Platystethus arenarius (Geoffroy, 1785)	4	3	7

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 curtipennis 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

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

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

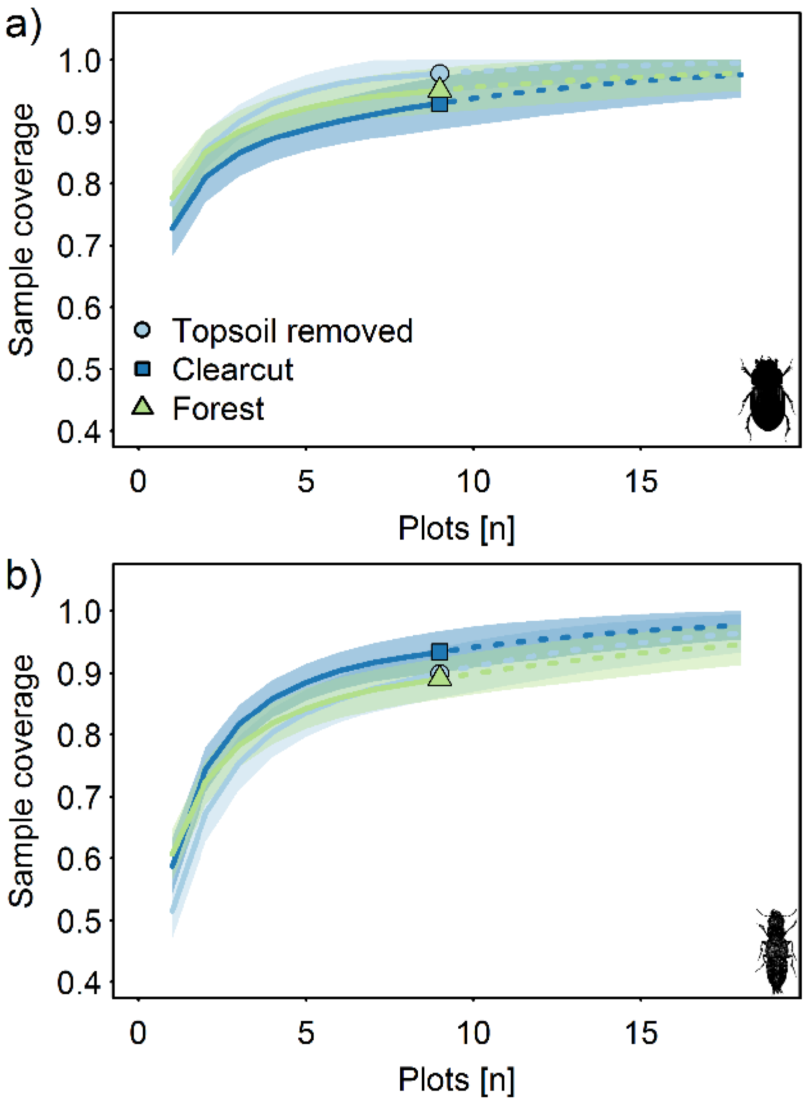

Figure S2. Observed sample coverage (solid lines) and extrapolated sample coverage (dotted lines, up to twice the sample size taken) of a) dung beetles and b) rove beetles sampled in baited pitfall traps on topsoil-removed plots, coppices, and forest plots. Transparent shading indicates 95% confidence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

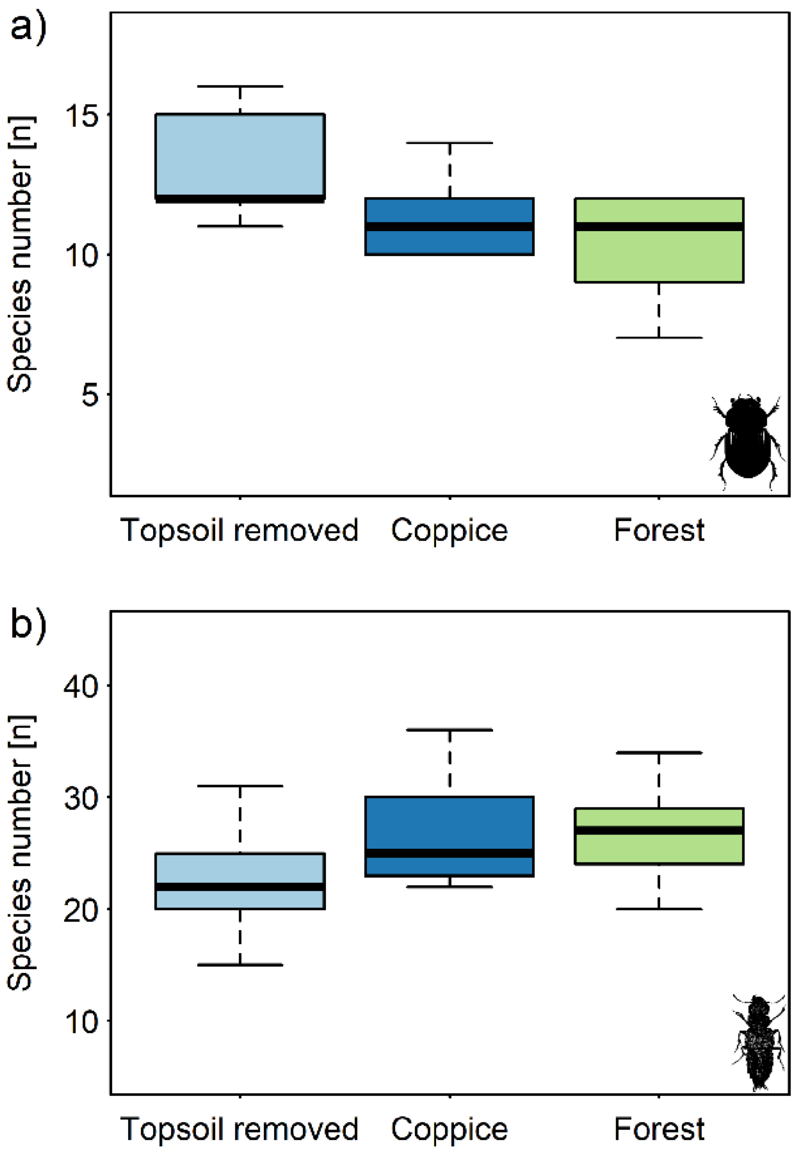

Figure S3: Mean number of species of dung beetle and rove beetles species among treatments.

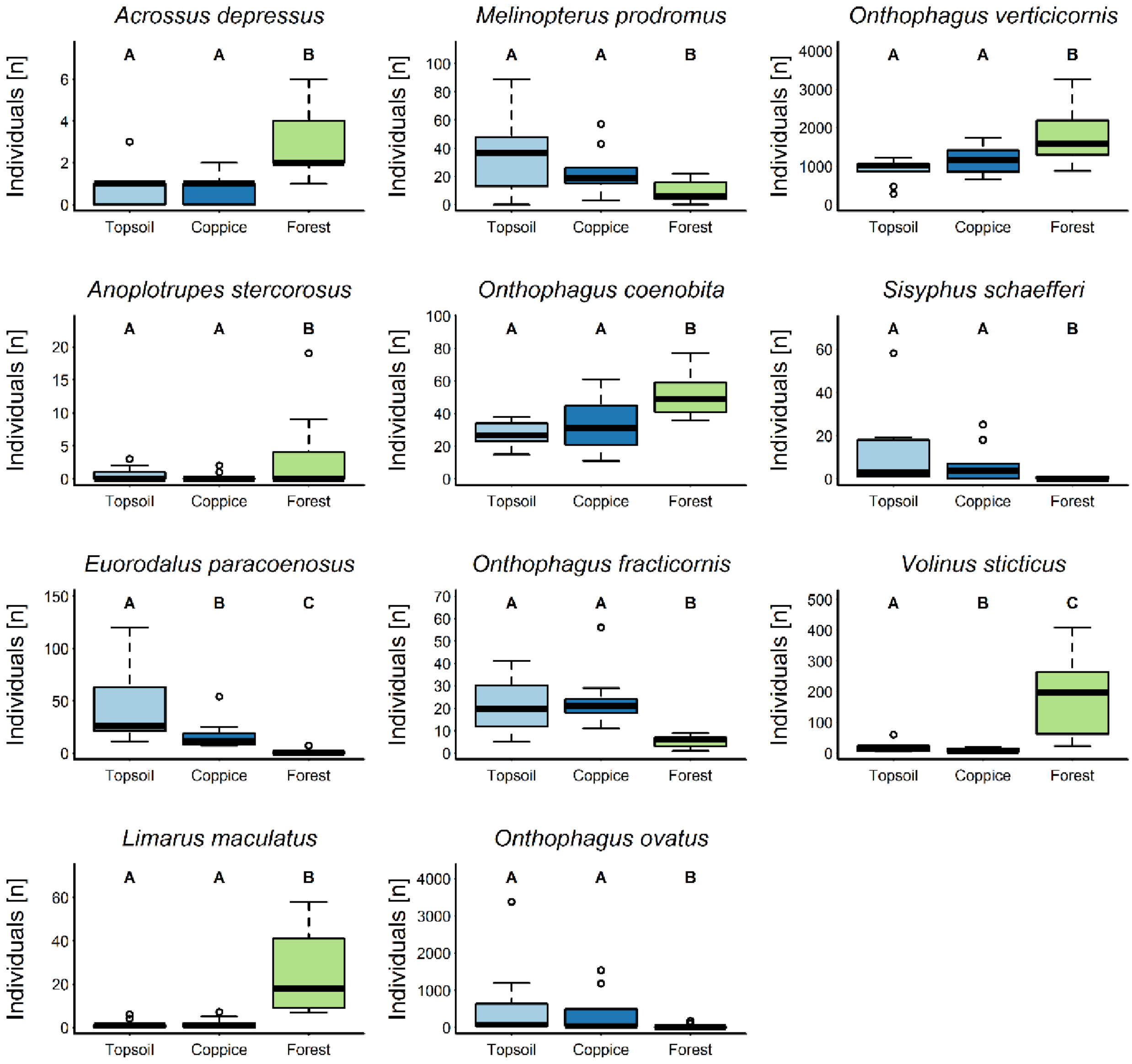

Figure S4: Response of abundances of single dung beetle species to topsoil removal, coppicing, and forest control. Uppercase letters indicate statistically significant differences.

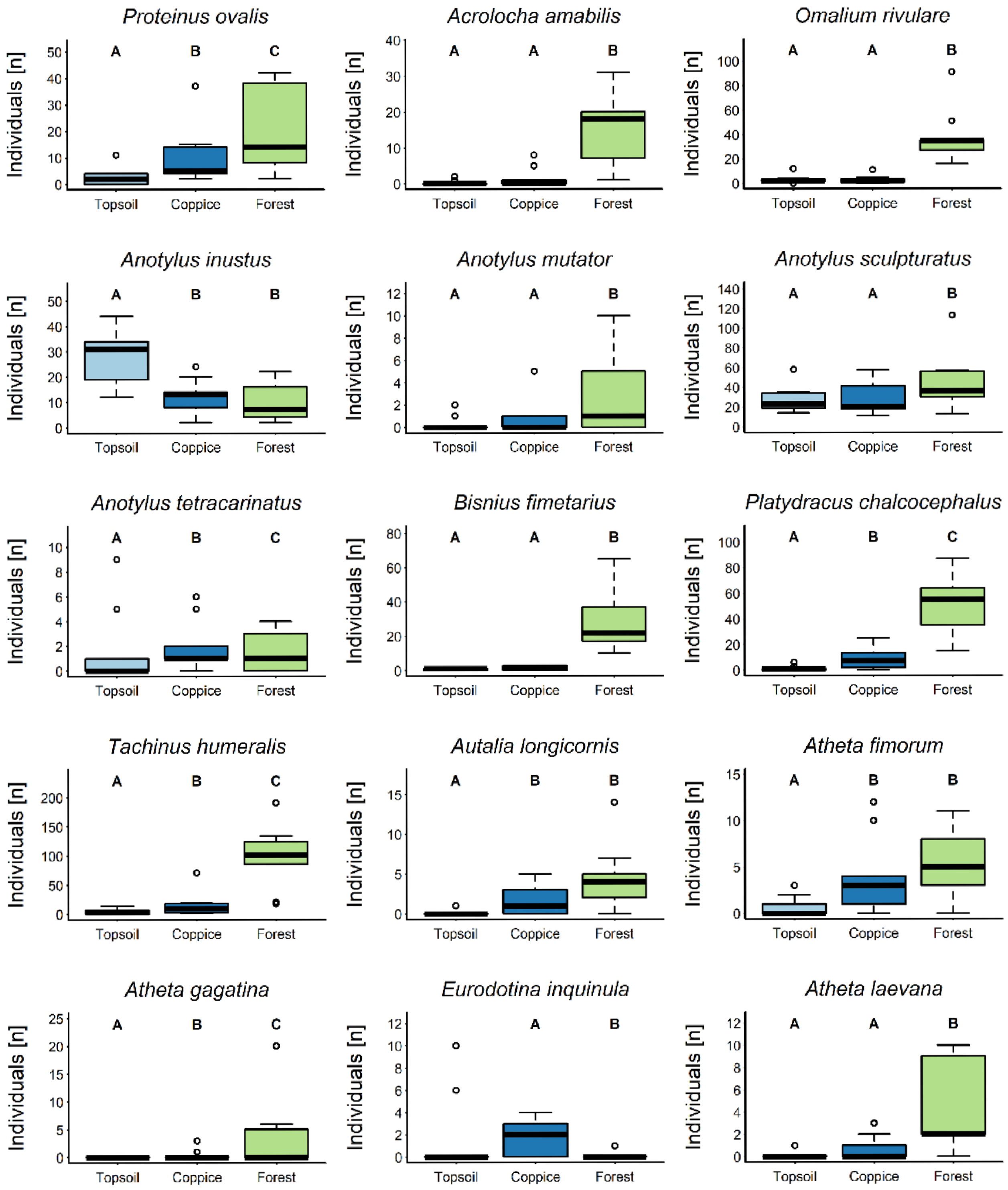

Figure S5 (part I): Response of abundances of single rove beetle species to topsoil removal, coppicing, and forest control. Uppercase letters indicate statistically significant differences.

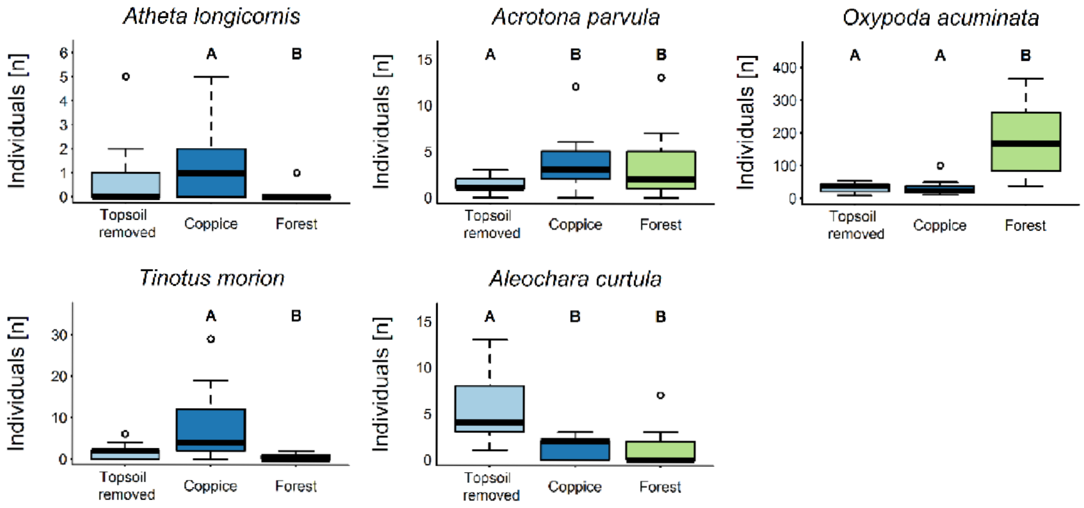

Figure S5 (part II): Response of abundances of single rove beetle species to topsoil removal, coppicing, and forest control. Uppercase letters indicate statistically significant differences.

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

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 tetracarinatus	Coppice vs. Topsoil removed	0.258	0.003	90.100	<0.001
	Forest vs. Topsoil removed	0.116	0.003	40.600	<0.001

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

Family, species	Comparison	Estimate	Std. Error	z-value	p-value
Platydracus 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	-0.6177	**<0.001**

Table S9: Results of permutational multivariate analysis of variance based on Bray-Curtis distance matrices.

Species group	**Comparison**	**R^2**	**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**

Chapter III

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

Biological Conservation (2022) 273, 109682
DOI: 10.1016/j.biocon.2022.109682

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

Lucie AMBROŽOVÁ[1,2,*], Lukáš ČÍŽEK[1,2], František Xaver Jiří SLÁDEČEK[1,2], Simon THORN[2,3,4]

Affiliations:

[1] Faculty of Science, Department of Zoology, University of South Bohemia in České Budějovice, Branišovská 1760, CZ-37005 České Budějovice, Czech Republic

[2] Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 1160/31, CZ-37005 České Budějovice, Czech Republic

[3] Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology (Zoology III), Julius Maximilians University Würzburg, Glashüttenstraße 5, D-96181 Rauhenebrach, Germany

[4] Hessian Agency for Nature Conservation, Environment and Geology, State Institute for the Protection of Birds, Netanyastraße 5, D-35394 Gießen, Germany

[*] Corresponding author:

Faculty of Science, Department of Zoology, University of South Bohemia in České Budějovice, Branišovská 1760, CZ-37005 České Budějovice, Czech Republic. E-mail address: L.Ambrozova@seznam.cz (L. Ambrožová)

Abstract

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.

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 heterogenous 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.*, 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

(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 climatical 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.

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 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.

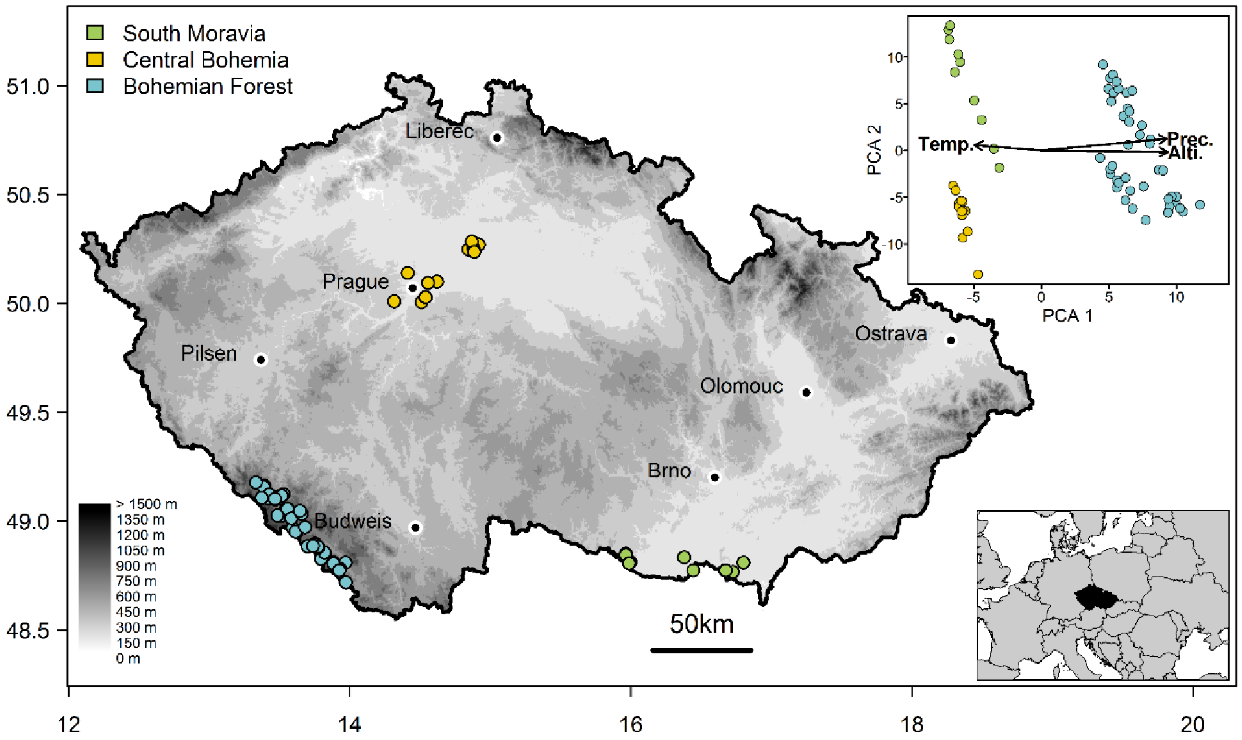

Fig. 1. Study sites across the Czech Republic and one site at the border in Austria. The upper right inset depicts a principal components analysis including mean annual temperature, altitude, and total annual precipitation; bottom right inset indicates the position of the Czech Republic in Central Europe.

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

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.

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 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).

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).

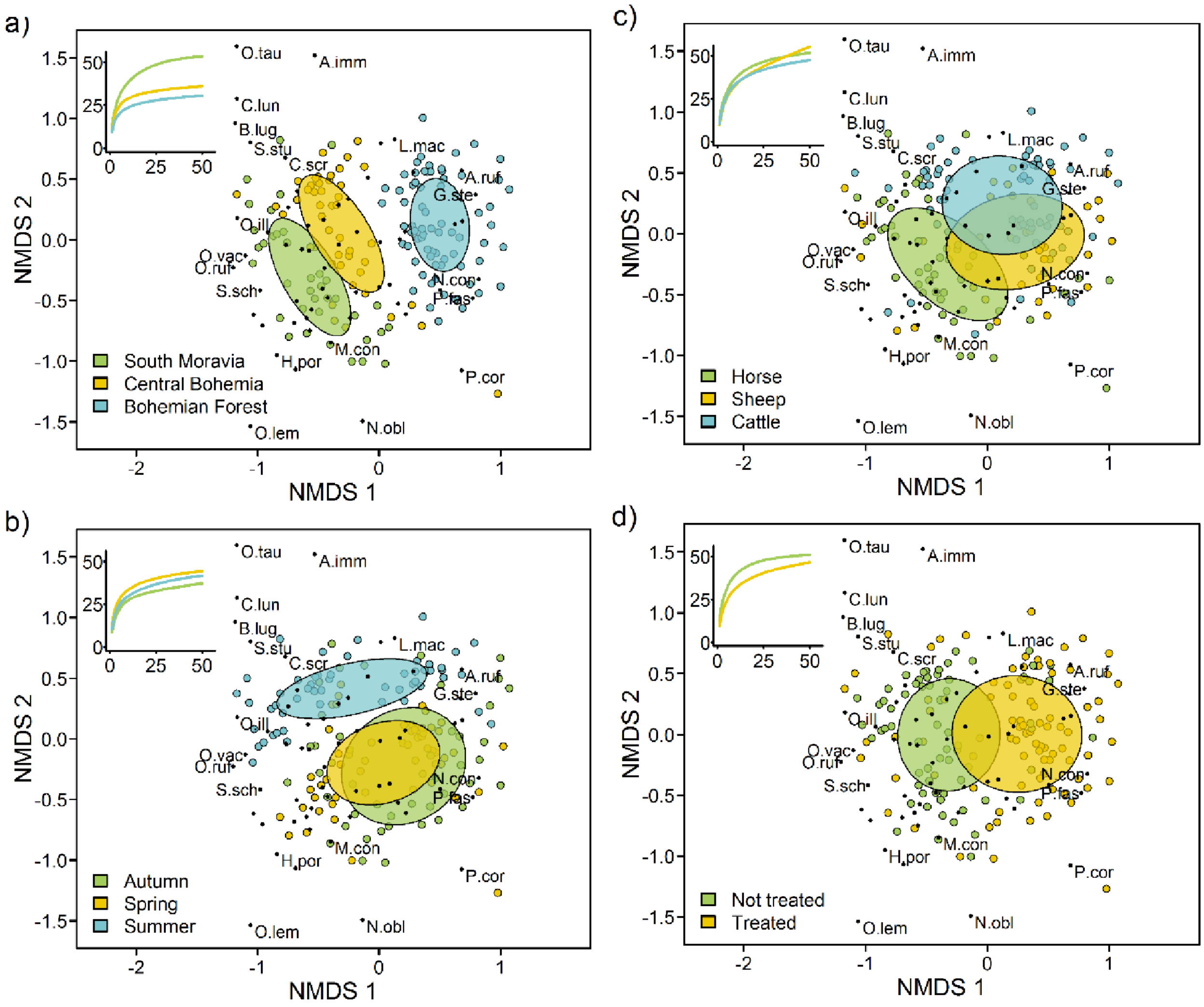

Fig. 2. Non-metric multidimensional scaling of dung beetle communities separated into a) study regions, b) seasons, c) herbivores, and d) sites treated and not treated by antiparasitics. Stress value = 0.2073449. Insets show species richness of 50 samples based on incidence-based rarefaction/extrapolation.

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).

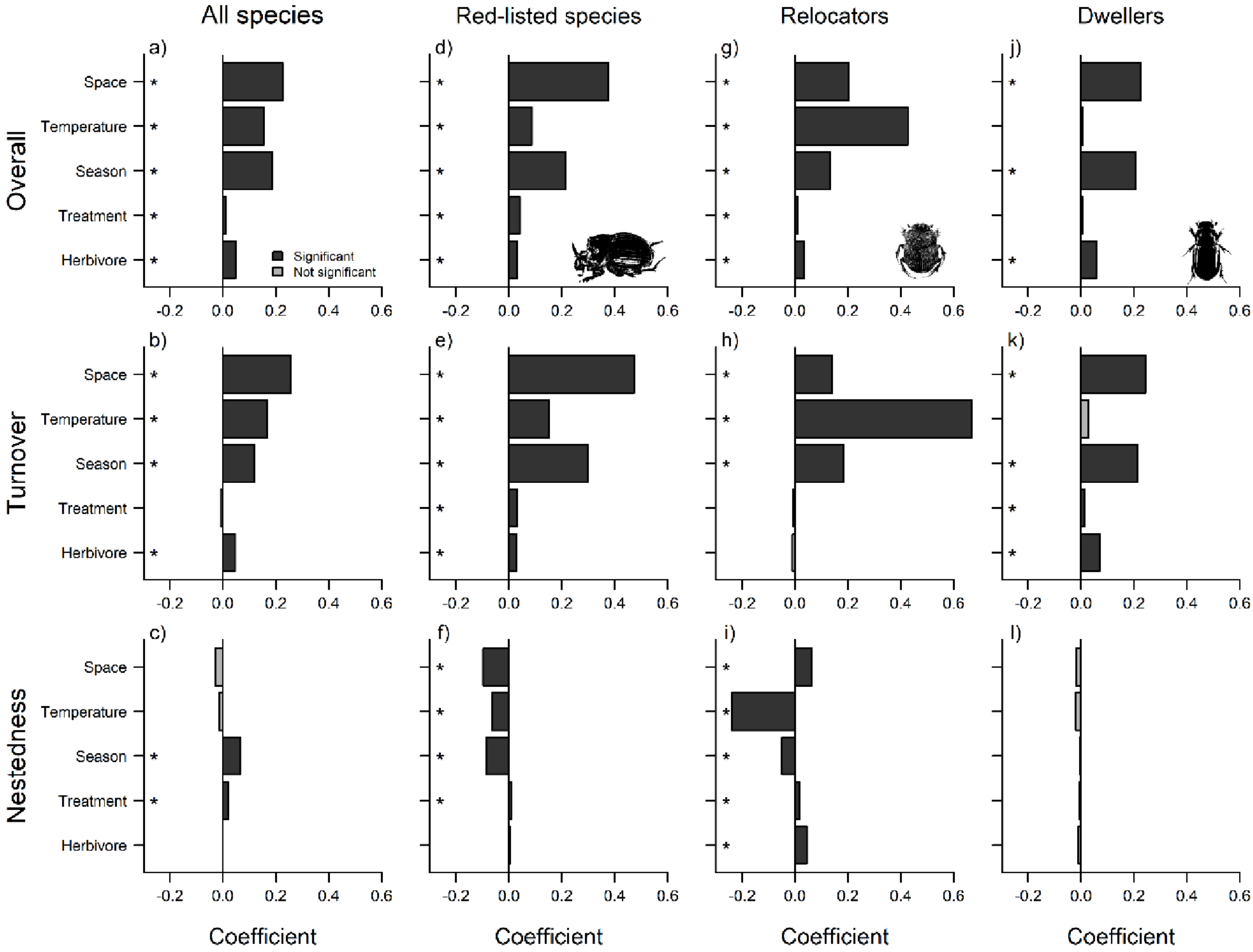

Fig. 3. Regression coefficients of multiple regression on distance matrices are given for the significant predictors. Results are given for overall β-diversity, turnover, and nestedness component separately. Statistical details may be found in the Appendix, Table A2.

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).

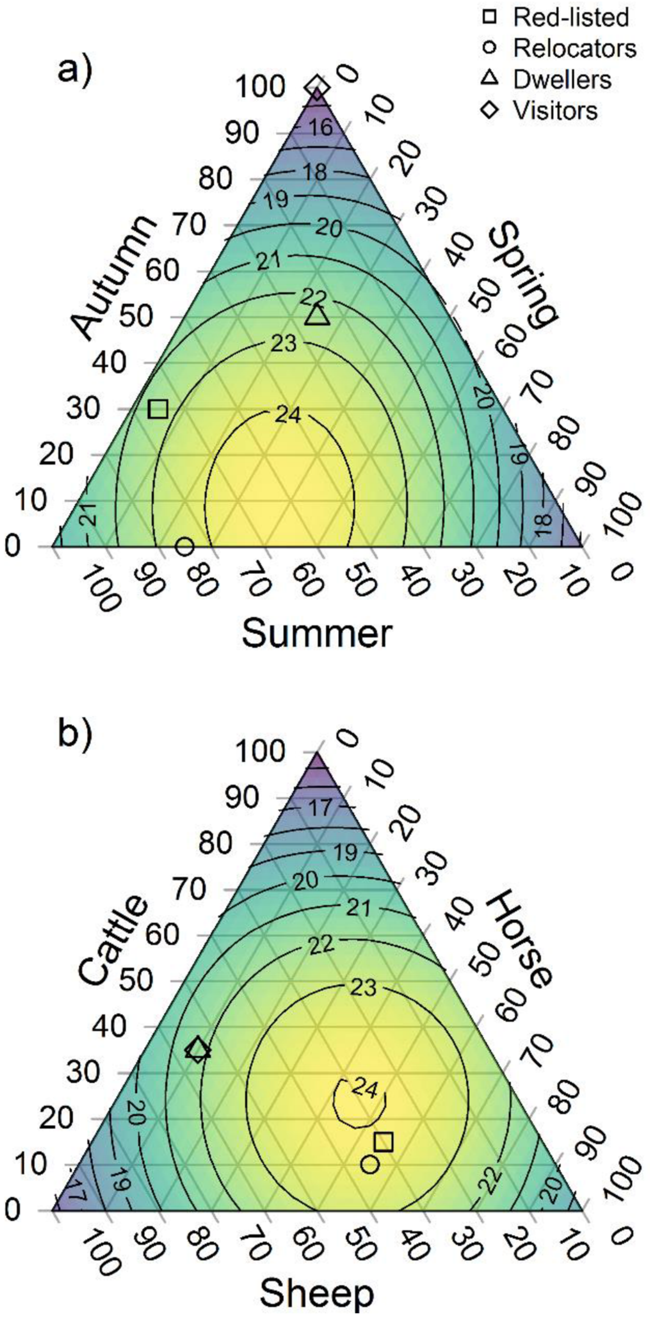

Fig. 4. Ternary plots depicting γ-diversity of dung beetles along compositional gradients of a) season and b) herbivore.

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 Soininen *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, 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. lemur*, *O. furcatus*, *Copris* *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.

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 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.

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.

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, and to Matthew Sweney for language correction. This work was partially funded by the Program AV21 (Czech Academy of Sciences), the Regional Cooperation of the Regions and Institutes of the Czech Academy of Sciences (R200961701), Institute of Entomology, Biology Centre, Czech Academy of Sciences (RVO//:60077344), MSM200961902 (Czech Academy of Sciences), and LIFE15 NAT/CZ/001028, and GACR (22-27166S).

References

Albrecht, M., Gotelli, N.J., 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126, 134–141. https://doi.org/10.1007/s004420000494.

Ambrožová, L., Sládeček, F.X.J., Zítek, T., Perlík, M., Kozel, P., Jirků, M., Čížek, L., 2021. Lasting decrease in functionality and richness: effects of ivermectin use on dung beetle communities. Agric. Ecosyst. Environ. 321, 107634 https://doi.org/10.1016/ j.agee.2021.107634.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol. Lett. 14, 19–28. https://doi.org/10.1111/ j.1461-0248.2010.01552.x.

Barbero, E., Palestrini, C., Rolando, A., 1999. Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeoidea). J. Insect Conserv. 3, 75–84. https://doi.org/10.1023/A:1009609826831.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. 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. J. Appl. Ecol. 49, 1365–1372. https://doi.org/10.1111/j.1365-2664.2012.02210.x.

Buse, J., Šlachta, M., Sladecek, F.X.J., Pung, M., Wagner, T., Entling, M.H., 2015. Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles. Biol. Conserv. 187, 112–119. https://doi. org/10.1016/j.biocon.2015.04.011.

Bush, A., Harwood, T., Hoskins, A.J., Mokany, K., Ferrier, S., 2016. Current uses of beta- diversity in biodiversity conservation: a response to Socolar et al. Trends Ecol. Evol. 31, 337–338. https://doi.org/10.1016/j.tree.2016.02.020.

Cabrero-Sanudo, F.J., Lobo, J.M., 2006. Determinant variables of Iberian Peninsula Aphodiinae diversity (Coleoptera, Scarabaeoidea, Aphodiidae). J. Biogeogr. 33, 1021–1043. https://doi.org/10.1111/j.1365-2699.2006.01485.x.

Chesson, P., Huntly, N., 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am. Nat. 150, 519–553. https://doi.org/ 10.1086/286080.

Correa, C.M.A., Peres, N.D., Holdbrook, R., 2020. Patterns of alimentary resource use by dung beetles in introduced Brazilian pastures: cattle versus sheep dung. Entomol. Sci. 23, 271–279. https://doi.org/10.1111/ens.12425.

Davies, K.F., Margules, C.R., Lawrence, J.F., 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology 85, 265–271. https://doi. org/10.1890/03-0110.

Davis, A.L.V., Scholtz, C.H., Philips, T.K., 2002. Historical biogeography of scarabaeine dung beetles. J. Biogeogr. 29, 1217–1256. https://doi.org/10.1046/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. https://doi.org/ 10.2307/2389480.

Errouissi, F., Jay-Robert, P., 2019. Consequences of habitat change in euromediterranean landscapes on the composition and diversity of dung beetle assemblages (Coleoptera, Scarabaeoidea). J. Insect Conserv. 23, 15–28. https://doi.org/10.1007/s10841-018- 0110-8.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68. https://doi.org/10.1007/ BF00038687.

Ferreira, S.C., da Silva, P.G., Paladini, A., Di Mare, R.A., 2019. Climatic variables drive temporal patterns of α and β diversities of dung beetles. Bull. Entomol. Res. 109, 390–397. https://doi.org/10.1017/S0007485318000676.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/ 10.1002/joc.5086.

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/S0929-1393(02)00011-2.

Frank, K., Brückner, A., Hilpert, A., Heethoff, M., Blüthgen, N., 2017a. Nutrient quality of vertebrate dung as a diet for dung beetles. Sci. Rep. 7, 12141. https://doi.org/ 10.1038/s41598-017-12265-y.

Frank, K., Hülsmann, M., Assmann, T., Schmitt, T., Blüthgen, N., 2017b. Land use affects dung beetle communities and their ecosystem service in forests and grasslands. Agric. Ecosyst. Environ. 243, 114–122. https://doi.org/10.1016/j. agee.2017.04.010.

Friedman, J.H., 1989. In: Regularized Discriminant Analysis, 84, pp. 165–175. Gaston, K.J., Blackburn, T.M., 2000. Pattern and Process in Macroecology. Blackwell Science, Oxford.

Gebert, F., Steffan-Dewenter, I., Moretto, P., Peters, M.K., 2020. Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. J. Biogeogr. 47, 371–381. https://doi.org/ 10.1111/jbi.13710.

Gittings, T., Giller, P.S., 1998. Resource quality and the colonisation and succession of coprophagous dung beetles. Ecography (Cop.) 21, 581–592. https://doi.org/ 10.1111/j.1600-0587.1998.tb00550.x.

Goslee, S.C., Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data. J. Stat. Softw. 22 https://doi.org/10.18637/jss.v022.i07.

Gower, J.C., 1971. A general coefficient of similarity and some of its properties. Biometrics 27, 857. https://doi.org/10.2307/2528823.

Halffter, G., Edmonds, W.D., 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae). An Ecological and Evolutive Approach. Institúto de Ecología, México.

Hanski, I., Cambefort, Y., 1991. Dung Beetle Ecology. Princeton University Press, New Jersey.

Harrison, S., Ross, S.J., Lawton, J.H., 1992. Beta diversity on geographic gradients in Britain. J. Anim. Ecol. 61, 151. https://doi.org/10.2307/5518.

Holter, P., 2016. Herbivore dung as food for dung beetles: elementary coprology for entomologists. Ecol. Entomol. 41, 367–377. https://doi.org/10.1111/een.12316.

Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A., Lobo, J.M., 2011. Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. Ecol. Lett. 14, 741–748. https://doi.org/10.1111/j.1461-0248.2011.01634.x.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A., Balmford, A., 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. Nature 394, 472–475. https://doi. org/10.1038/28843.

Jacobs, C.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. https://doi.org/10.4102/ojvr.v82i1.858.

Jacquemyn, H., Honnay, O., Pailler, T., 2007. Range size variation, nestedness and species turnover of orchid species along an altitudinal gradient on Réunion Island: implications for conservation. Biol. Conserv. 136, 388–397. https://doi.org/ 10.1016/j.biocon.2006.12.008.

Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., Lebrun, P., 2004. Hotspots, complementarity or representativeness? Designing optimal small-scale reserves for biodiversity conservation. Biol. Conserv. 120, 471–480. https://doi.org/10.1016/j. biocon.2004.03.020.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., Chase, J.M., 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368, 417–420. https://doi.org/10.1126/science.aax9931.

Köhler, M., Hiller, G., Tischew, S., 2016. Year-round horse grazing supports typical vascular plant species, orchids and rare bird communities in a dry calcareous grassland. Agric. Ecosyst. Environ. 234, 48–57. https://doi.org/10.1016/j. agee.2016.03.020.

Konvička, M., Ričl, D., Vodičková, V., Beneš, J., Jirků, M., 2021. Restoring a butterfly hot spot by large ungulates refaunation: the case of the milovice military training range, Czech Republic. BMC Ecol. Evol. 21, 73. https://doi.org/10.1186/s12862-021- 01804-x.

Král, D., Bezděk, A., 2017. Scarabaeoidea (vrubounovití). In: Hejda, R., Farkač, J., Chobot, K. (Eds.), Červený Seznam Ohrožených Druhů České Republiky. Bezobratlí. [Red List of Threatened Species of the Czech Republic. Invertebrates.]. Agentura ochrany přírody a krajiny ČR, Praha, pp. 409–413.

Legendre, P., Fortin, M.-J., 2010. Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. Mol. Ecol. Resour. 10, 831–844. https://doi.org/10.1111/j.1755- 0998.2010.02866.x.

Legendre, P., Lapointe, F.-J., Casgrain, P., 1994. Modeling brain evolution from behavior: a permutational regression approach. Evolution 48, 1487. https://doi.org/ 10.2307/2410243.

Legendre, P., Fortin, M., Borcard, D., 2015. Should the mantel test be used in spatial analysis? Methods Ecol. Evol. 6, 1239–1247. https://doi.org/10.1111/2041-210X.12425.

Lerman, Z., Csaki, C., Feder, G., 2004. The arena and the common heritage. In: Agriculture in Transition: Land Policies and Evolving Farm Structures in Post-Soviet Countries. Lexington Books, Oxford, pp. 13–54.

Lichstein, J.W., 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol. 188, 117–131. https://doi.org/10.1007/s11258-006-9126- 3.

Löbl, I., Löbl, D., 2016. Catalogue of Palaearctic Coleoptera. Volume 3, Scarabaeoidea, Scirtoidea, Dascilloidea, Buprestoidea, Byrrhoidea. Brill, Leiden, Boston.

Lobo, J.M., Lumaret, J.-P., Jay-Robert, P., 2002. Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. Glob. Ecol. Biogeogr. 11, 265–277. https://doi.org/10.1046/j.1466-822X.2002.00291.x.

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 and aquatic environments. Curr. Pharm. Biotechnol. 13, 1004–1060. https://doi.org/10.2174/ 138920112800399257.

Mamantov, M.A., Sheldon, K.S., 2021. Behavioural responses to warming differentially impact survival in introduced and native dung beetles. J. Anim. Ecol. 90, 273–281. https://doi.org/10.1111/1365-2656.13366.

Martín-Piera, F., Lobo, J.M., 1996. A comparative discussion of trophic preferences in dung beetle communities. Misc. Zool. 19, 13–31.

Michel, G., Malard, F., Deharveng, L., Di Lorenzo, T., Sket, B., De Broyer, C., 2009. Reserve selection for conserving groundwater biodiversity. Freshw. Biol. 54, 861–876. https://doi.org/10.1111/j.1365-2427.2009.02192.x.

Milotić, T., Baltzinger, C., Eichberg, C., Eycott, A.E., Heurich, M., Müller, J., Noriega, J. A., Menendez, R., Stadler, J., Ádám, R., Bargmann, T., Bilger, I., Buse, J., Calatayud, J., Ciubuc, C., Boros, G., Jay-Robert, P., Kruus, M., Merivee, E., Miessen, G., Must, A., Ardali, E., Preda, E., Rahimi, I., Rohwedder, D., Rose, R., Slade, E.M., Somay, L., Tahmasebi, P., Ziani, S., Hoffmann, M., 2019. Functionally richer communities improve ecosystem functioning: dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. J. Biogeogr. 46, 70–82. https://doi.org/10.1111/jbi.13452.

Mládek, J., Pavlů, V., Hejcman, M., Gaisler, J. (Eds.), 2006. Pastva jako prostředek údržby trvalých travních porostů V chráněných územích. VÚRV, Praha.

Moilanen, A., Wilson, K., Possingham, H. (Eds.), 2009. Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press, New York.

Mori, A.S., Isbell, F., Seidl, R., 2018. β-Diversity, community assembly, and ecosystem functioning. Trends Ecol. Evol. 33, 549–564. https://doi.org/10.1016/j. tree.2018.04.012.

Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. J. Biogeogr. 26, 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria- Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L. P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G. M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, 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.

Palestrini, C., Rolando, A., Barbero, E., 1995. Analysis of temporal segregation in a dung- inhabiting beetle community at a low-altitude area of the Italian Alps. Bolletino di Zool. 62, 257–265. https://doi.org/10.1080/11250009509356074.

Puniamoorthy, N., Schäfer, M.A., Römbke, J., Meier, R., Blanckenhorn, W.U., 2014. Ivermectin sensitivity is an ancient trait affecting all ecdysozoa but shows phylogenetic clustering among sepsid flies. Evol. Appl. 7, 548–554. https://doi.org/ 10.1111/eva.12152.

Qian, H., Ricklefs, R.E., White, P.S., 2004. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. Ecol. Lett. 8, 15–22. https://doi. org/10.1111/j.1461-0248.2004.00682.x.

R Core Team, 2021. R: A Language and Environment for Statistical Computing.

Righi, C.A., Sandoval Rodríguez, C., Ferreira, E.N.L., Godoy, W.A.C., Cognato, A.I., 2018. Microclimatic conditions for dung beetle (Coleoptera: Scarabaeidae) occurrence: land use system as a determining factor. Environ. Entomol. 47, 1420–1430. https:// doi.org/10.1093/ee/nvy163.

Roslin, T., 2001. Large-scale spatial ecology of dung beetles. Ecography (Cop.) 24, 511–524. https://doi.org/10.1034/j.1600-0587.2001.d01-207.x.

Samways, M.J., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch, A., Kaila, L., Kwak, M.L., Maes, D., Mammola, S., Noriega, J.A., Orfinger, A.B., Pedraza, F., Pryke, J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F., Vorster, C., Cardoso, P., 2020. Solutions for humanity on how to conserve insects. Biol. Conserv. 242, 108427 https://doi.org/10.1016/j. biocon.2020.108427.

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27. https://doi.org/10.1016/j. biocon.2019.01.020.

Schall, P., Heinrichs, S., Ammer, C., Ayasse, M., Boch, S., Buscot, F., Fischer, M., Goldmann, K., Overmann, J., Schulze, E., Sikorski, J., Weisser, W.W., Wubet, T., Gossner, M.M., 2020. Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems? J. Appl. Ecol. 57, 1363–1375. https://doi.org/10.1111/1365-2664.13635.

Schmera, D., Podani, J., Legendre, P., 2020. What do beta diversity components reveal from presence-absence community data? Let us connect every indicator to an indicandum! Ecol. Indic. 117, 106540 https://doi.org/10.1016/j. ecolind.2020.106540.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674. https://doi.org/10.1038/s41586-019-1684-3.

Sladecek, F.X.J., Hrcek, J., Klimes, P., Konvicka, M., 2013. Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat. Acta Oecol. 46, 17–24. https://doi.org/10.1016/j.actao.2012.10.012.

Smith, M.R., 2017. Ternary: An R Package for Creating Ternary Plots. Ternary: An R Package for Creating Ternary Plots. https://doi.org/10.5281/zenodo.1068996.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016a. How should beta-diversity inform biodiversity conservation? Conservation targets at multiple spatial scales. Trends Ecol. Evol. 31, 67–80.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. Sparse data necessitate explicit treatment of beta-diversity: a reply to Bush et al. Trends Ecol. Evol. 31, 338–339. https://doi.org/10.1016/j.tree.2016.02.019.

Soininen, J., Heino, J., Wang, J., 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. Glob. Ecol. Biogeogr. 27, 96–109. https://doi.org/10.1111/geb.12660.

Sowig, P., 1996. Brood care in the dung beetle *Onthophagus vacca* (Coleoptera: Scarabaeidae): the effect of soil moisture on time budget, nest structure, and reproductive success. Ecography (Cop.) 19, 254–258. https://doi.org/10.1111/ j.1600-0587.1996.tb01252.x.

Spector, S., 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. Coleopt. Bull. 60, 71–83. https://doi.org/10.1649/0010-065X(2006)60[71:SDBCSS]2.0.CO;2.

Tonelli, M., Verdú, J.R., Zunino, M.E., 2017. 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. https://doi.org/10.7717/peerj.2780.

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/j.ecolind.2018.09.010.

Upham, N.S., Esselstyn, J.A., Jetz, W., 2019. Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS Biol. 17, e3000494 https://doi.org/10.1371/journal.pbio.3000494.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics With S, Statistics and Computing. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387- 21706-2.

Verdú, J.R., Lobo, J.M., Sánchez-Piñero, F., Gallego, B., Numa, C., Lumaret, J.P., Cortez, V., Ortiz, A.J., Tonelli, M., García-Teba, J.P., Rey, A., Rodríguez, A., Durán, J., 2018. Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study. Sci. Total Environ. 618, 219–228. https://doi.org/10.1016/j.scitotenv.2017.10.331.

Verdú, J.R., Sánchez-Piñero, F., Lobo, J.M., Cortez, V., 2020. Evaluating long-term ivermectin use and the role of dung beetles in reducing short-term CH 4 and CO 2 emissions from livestock faeces: a mesocosm design under Mediterranean conditions. Ecol. Entomol. 45, 109–120. https://doi.org/10.1111/een.12777.

WallisDeVries, M.F., Noordijk, J., Colijn, E.O., Smit, J.T., Veling, K., 2016. Contrasting responses of insect communities to grazing intensity in lowland heathlands. Agric. Ecosyst. Environ. 234, 72–80. https://doi.org/10.1016/j.agee.2016.04.012.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338. https://doi.org/10.2307/1943563.

Wiersma, Y.F., Urban, D.L., 2005. Beta diversity and nature reserve system design in the Yukon, Canada. Conserv. Biol. 19, 1262–1272. https://doi.org/10.1111/j.1523- 1739.2005.00099.x.

Wood, S.N., 2006. Low-rank scale-invariant tensor product smooths for generalized additive mixed models. Biometrics 62, 1025–1036. https://doi.org/10.1111/j.1541- 0420.2006.00574.x.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B (Stat. Methodol.) 73, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Wright, David, H., Reeves, J.H., 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia 92, 416–428.

Appendix A. Supplementary data

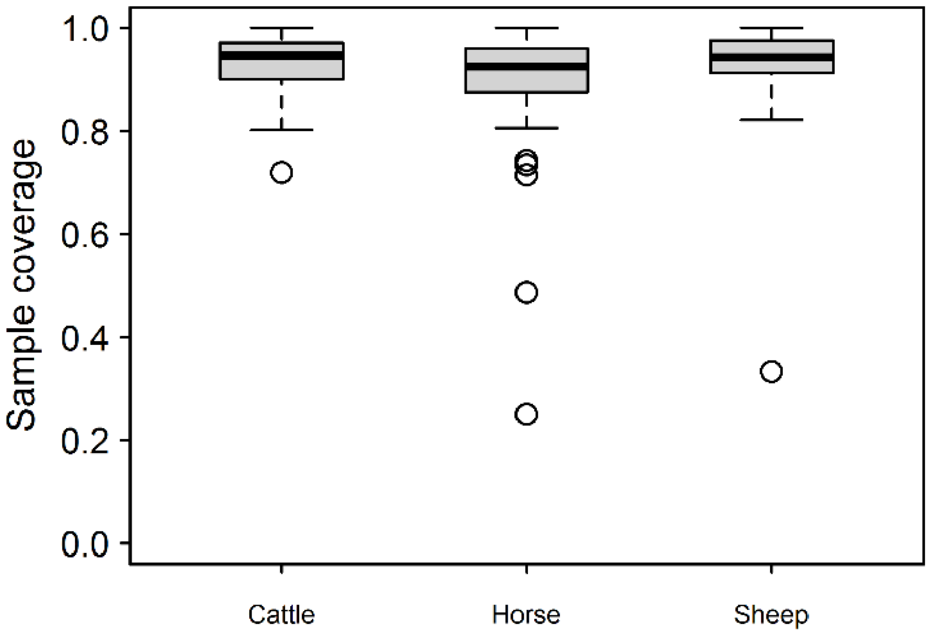

Figure A1: Observed sample coverage for all underlying observations, *i.e.*, dung beetle species aggregated on sites, seasons, herbivore, and treatment type.

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
Chilothorax 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 (Frivaldszky, 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 obliteratus (Panzer, 1823)	89	yes

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 (Kugelan, 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

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				

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				

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				

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				

Summary

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.

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 × 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 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.

Author’s Curriculum Vitae

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

Internship

November 2021 – Field Station Fabrikschleichach, Biozentrum, Julius-Maxmilians Universität Würzburg, Germany
Supervisor: Dr. Simon Thorn

September – December 2020 – Field Station Fabrikschleichach, Biozentrum, Julius-Maxmilians 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)

Publications with impact factor (IF)

Ambrožová, L., Sládeček, F. X. J., Zítek, T., Perlík, M., Kozel, P., Jirků, M. & Čížek, L. (2021). 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). 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.

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, Scarabeaidae) 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). 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. & Hogreve, J. V. C. (Eds.): 50th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland. Book of Abstracts. 30th August to 1st September 2021. Braunschweig, Germany.

e-mail: L.Ambrozova@seznam.cz

Dung beetles of Central Europe: Diversity and conservation.
Ph.D. Thesis Series, 2023, No. 1

Printed in the Czech Republic by Typodesign
Edition of 10 copies

University of South Bohemia in České Budějovice
Faculty of Science
Branišovská 1760
CZ-37005 České Budějovice, Czech Republic

Phone: +420 387 776 201
www.prf.jcu.cz, e-mail: sekret-fpr@prf.jcu.cz