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Species richness and extinction debt in dung beetles of grazed  
grasslands: consequences of changes in land use and  
agricultural practices

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# Abstract

Over the last century, land use in Central Europe underwent major changes, following intensification and structural alterations in agriculture. Within this study the influence of changing livestock farming practices and land use on dung beetles was modelled. 34 pastures within the Pannonian Region (Austria and Czech Republic) were sampled for dung beetles, information on management practices gathered and land use changes analysed by digitizing maps and aerial photograph since 1900. This revealed a threefold increase in settlement areas, a 50% increase in forest cover, and a 50% reduction in pasture areas. Hereby, historic land cover data explained current species richness the best, indicating long-lasting impacts of land use change spanning at least 150 years. Extinction debt driven by land use changes may therefore have more extensive relaxation times than assumed, even for mobile, short-lived groups as dung beetles. The models also showed varying responses of different ecological groups to land use changes, with open land- and endocoprid species being more negatively impacted than forest- and paracoprid species. Among livestock farming practices, the use of veterinary medicines emerged as the most significant predictor, having strong negative effects on overall species diversity, whereby paracoprid species appear to be more resistant against these medical substances than endocoprid species. These findings offer crucial insights for dung beetle conservation efforts. Extinction debt and long-lasting effects of land use change underline the importance of protecting and promoting extensive grazing systems in the study area. Additionally, the widespread use of veterinary medicines should be diminished.

## Keywords

Conservation, grazing, insect decline, land use change, pastures, reforestation, veterinary medicine

# Zusammenfassung

Die Kulturlandschaft Mitteleuropas durchlief im letzten Jahrhundert durch Intensivierungen und Strukturänderungen im Agrarsektor einen starken Wandel. Im Zuge dieser Studie wurde der Einfluss von Landnutzungsänderungen auf die Dungkäferfauna modelliert. Dabei wurden 34 Weiden in der pannonischen Region (Österreich und Tschechien) beprobt und Informationen zu Bewirtschaftungspraktiken gesammelt. Landnutzungsänderungen wurden durch die Digitalisierung von Karten und Luftbildern seit 1900 analysiert. Dies ergab eine dreifache Zunahme der Siedlungsgebiete, eine 50%ige Zunahme der Waldfläche und eine 50%ige Reduzierung der Weideflächen. Hierbei erklärten historische Landbedeckungsdaten die aktuelle Artenvielfalt am besten, was auf tiefgreifende und langanhaltende Auswirkungen von Landnutzungsänderungen hindeutet, die sich über mindestens 150 Jahre erstrecken. Die durch Veränderungen in der Landnutzung verursachte Aussterbeschuld hat demnach möglicherweise längere Erholungszeiten als allgemein angenommen, selbst bei mobilen und kurzlebigen Gruppen wie Dungkäfern. Verschiedene ökologische Gilden waren in unterschiedlichem Maße von den Landnutzungsänderungen betroffen, wobei Offenland- und endokopride Arten stärker negativ beeinflusst wurden als Wald- und parakopride Arten. Unter den Viehhaltungsmethoden erwies sich der Einsatz von Tierarzneimitteln als der Faktor mit den stärksten negativen Auswirkungen auf die Gesamtartenvielfalt. Parakopride Arten scheinen gegenüber diesen medizinischen Substanzen widerstandsfähiger zu sein als endokopride Arten. Die Ergebnisse bieten wichtige Erkenntnisse für mögliche Arterhaltungsmaßnahmen von Dungkäfern. Die langanhaltenden Auswirkungen von Landnutzungsänderungen unterstreichen die Bedeutung des Schutzes und der Förderung extensiver Weidesysteme in der Untersuchungsregion. Darüber hinaus sollte der prophylaktische Einsatz von Tierarzneimitteln reduziert werden.

# Introduction

Over the last century, agricultural systems and land use practices have undergone severe structural changes in Central Europe. Particularly extensive grazing systems and traditional agro-pastoral activities have been affected by these transformation processes (Poschlod, 2017; Sartorello et al., 2020). The decline of extensive pasture farming was especially pronounced in lowlands such as the Pannonian region, where they were an essential component of agricultural land use until the early 20<sup>th</sup> century (Brettl & Prieler, 2017; Sandgruber, 1978). A key driver behind land use changes was the motorization of the agricultural sector as the introduction of machinery largely replaced horses and oxen and reduced the need of pastures. Furthermore, railway lines allowed not only the faster transport of animal products but also the transport of animals itself, which made pastoralism and transhumance superfluous. In this way, wandering shepherds were under the first of the traditional practices to go extinct, followed by specific types of grazing animals like pig or geese and the use of forests and meadows as pastures (Poschlod, 2017; Varga et al., 2016). Besides technological progress, mineral fertilizers and pesticides enabled the intensification of agricultural practices and substantial increases in crop production took place throughout Europe (Kapfer, 2010). This increased production of animal feed facilitated year-round indoor-housing of livestock (Strittmatter, 2005) leading to an intensification within the livestock sector characterized by rising livestock numbers with simultaneous decreasing pasture sizes and higher yields per animal. Consequently, pastures in the lowlands were either converted to arable land or afforested. All these processes brought about livestock farming's independence from land resources such as pastures, indicating a transition from rural, site-specific agricultural practices towards industrial agriculture. The shift of small scaled farms to large companies, alongside with new land consolidation laws, lead to a more monotonous landscape and to a stricter separation of different land use types (Arnold, 1979; Poschlod, 2017; Ratz, 2017). The declining use of forests and harvested fields as pastures, for instance, resulted in the loss of habitat-rich transitional zones (Malicky, 2001; Weller, 1997). Furthermore, many species-rich open-land habitats previously formed and maintained by traditional management are vanishing, as for example nutrient-poor grasslands, heathlands, and fallow lands (Kapfer, 2010). Many species that are adapted to these habitats and dependent on their existence are suffering severe declines in Europe. One of the groups most negatively affected by habitat loss and previously described changes in agricultural management types are dung beetles (Sánchez-Bayo et al., 2019; Sartorello et al., 2020).

As all dung beetles (coprophagous Scarabaeoidea) depend on dung as a resource for feeding, habitat and reproduction, they are directly affected by declining numbers of grazing animals and pastures (Jay-Robert et al., 2008). Besides the deprivation of their food source, dung beetles have also been shown to react especially sensitive to anthropogenic landscape modifications (Filgueiras et al., 2015; Halffter & Arellano, 2002; Salomão et al., 2019) and loss of habitat heterogeneity (Negro et al., 2011; Numa et al., 2009; Verdú et al., 2007), due to the high specialisation of many species (Macagno & Palestini, 2009; Spector, 2006). This led to declines in dung beetle richness and diversity (Fattorini, 2011; Filgueiras et al., 2015; Hutton & Giller, 2003; Jay-Robert et al., 2008) with specialised species declining particularly sharply (Buse et al., 2015; Carpaneto et al., 2005; Schernhammer & Denner, 2022a).

Another important factor accelerating the decline of dung beetle diversity is the increased prophylactic use of veterinary medicines against parasites on grazing animals, a practice that is nowadays often standard, especially in dairy and meat production. A high proportion of these medical substances is hardly metabolized and thus excreted in faeces (Floate et al., 2005; Kryger et al., 2005). These residues can remain in the dung and the environment for several months (Litskas et al., 2013; Virilouvet et al., 2006) and have been proven to have strong negative effects on dung beetle diversity and richness (Ambrožová et al., 2021; Kless & Scholtz, 2001; Tovar et al., 2023; Verdú et al., 2018). Physiological effects on dung beetles include reduction in body size, prolonged development time, lower reproduction rates, and decreases of olfactory and locomotor capacity (Koopmann & Kühne, 2017; Verdú et al., 2015). This does not only result in higher mortality rates and species decline, but also in altered behaviour, which can impact the whole grazing ecosystem, as dung beetles provide essential ecosystem services (Milotic et al., 2017; Sands & Wall, 2018; Tonelli et al., 2020; Verdú et al., 2018).

Dung beetles substantially contribute to the removal of dung from pastures, providing more potential forage area for grazing animals (Fincher et al., 1981; Hughes et al., 1978; Weeda, 1967). Through burying activities they also support soil aeration and water availability (Brown et al., 2010; Manning et al., 2016) and increase the input of nutrients into the soil, enhancing nutrient cycling and plant growth (Bang et al., 2005; Wu et al., 2011). Furthermore burying dung promotes secondary seed dispersal (Milotic et al., 2017; Nicholasa et al., 2008) and suppresses pests by minimizing potential reinfection area (Gregory et al., 2015; Ridsdill-Smith & Edwards, 2011). Thus, the ongoing decline of dung beetles has far-reaching consequences for the functioning of ecosystems.

Species and populations might, however, respond to disturbances of their habitat with a considerable time lag, resulting in “extinction debt phenomena”. Hereby, the extinction of species occurs only a certain time after the actual alterations, which causes a state where the species composition of a habitat does not reflect its environmental conditions (Tilman et al., 1995). This phenomenon is especially likely to happen when changes of the habitat occur fast, as it is often the case with anthropogenic disturbances, and when the concerned taxa are long-lived or less mobile (Krauss et al., 2010). It has therefore mostly been observed for plants (Bommarco et al., 2014; Lindborg, 2007; Piqueray et al., 2011), but also for invertebrates (Polus et al., 2007; Sang et al., 2010) and red list species (Dullinger et al., 2013). Possible time lags of dung beetle species responses to land use changes have not been studied yet.

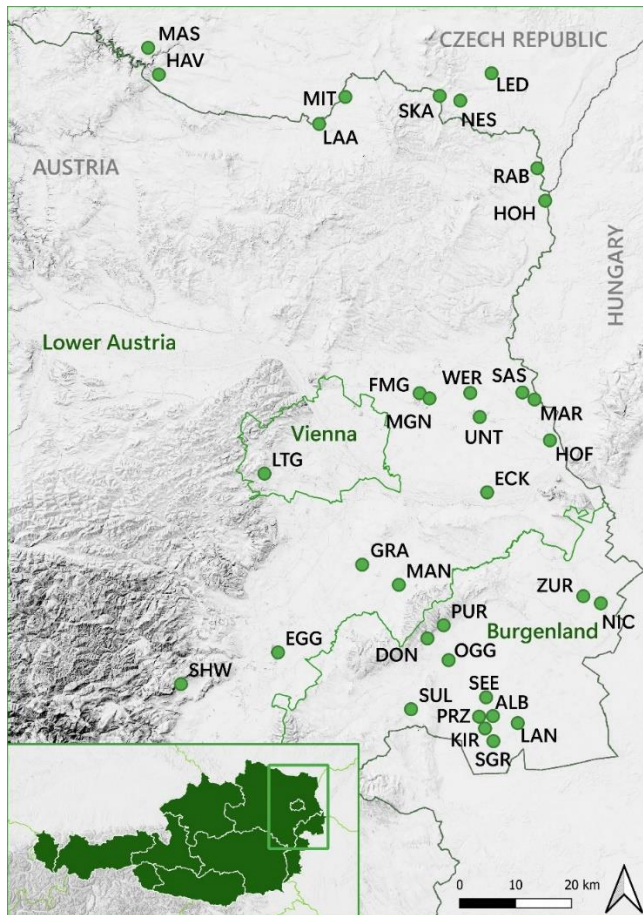
Thus, my master thesis investigates how changing land use affect dung beetle diversity in pastures in eastern Austria and the adjacent Czech Republic and if there is evidence for extinction debt. Specifically, I study the following research questions: (1) Which management practices influence current dung beetle diversity? (2) Are signals of historic land use still detectable in current dung beetle diversity? (3) Which drivers are responsible for time lags and do different ecological groups of dung beetle differ in terms of relaxation time and drivers of time lags?

## Methods

### Study area and sampled pastures

The study area comprises the Pannonian region of Eastern Austria (29 sites) and the adjacent Czech Republic (5 sites; Figure 1). Sampled pastures vary in size from 1.2 ha to 860 ha, and sites are grazed by cattle (28 sites) or horses (6 sites) (Table S1). The climate in the study region is continental temperate with cool winters and warm summers, annual average temperature of 8-10°C, and an annual precipitation from 500-700 mm (ZAMG, 2023).





*Figure 1: Overview on the study area with location of the sampled pastures (for more information on the sites, see Table S1). Country borders = grey; Federal state borders = green*

The selection of pastures was based on farmers agreeing to participate in the study, grazing species (cattle and horses) and best possible even spatial distribution.

Sampling of 13 study sites took place in 2022, data from the remaining pastures was collected by Schernhammer T., Denner F. and M., and Ambrožová L. in 2019-2021 (Ambrožová et al., 2021; Schernhammer, 2020, 2021; Schernhammer & Denner, 2022b, 2022a). All samples were taken between morning and noon (9:00 am – 1:00 pm) on fine days in spring to early summer (April to June).

Field sampling was carried out using a standard method on each pasture following (Krell, 2007): Five fresh dung pads and approximately five centimetres of the soil beneath the pad were collected in plastic bags. Afterwards the dung pads were transferred in a plastic tub which was then filled with water to collect the beetles floating on its surface. To collect all individuals in a sample, the remaining liquid was poured through a sieve twice. The specimens were then preserved in 70% alcohol.

In addition to the sampling, pasture owners were interviewed about the period of continuous grazing on the respective pastures – hereinafter referred to as “grazing history” and provided as number of years before 2020 -, the use of veterinary medicine, in particular anthelmintics (any use of anthelmintics, whether it is regular or only in case of worm infestation was treated as a “yes”) and the number of livestock on the pasture (Table S1).

## Species identification and ecological traits

Species were identified using relevant literature (i.e., Dellacasa et al. (2000), Fery & Rößner (2015), Frolov (2002), Krell & Fery (1992), Rößner (2006, 2012, 2018) and Rößner et al. (2010)). Taxonomy and nomenclature follow Löbl & Löbl (2016). Determined specimens were preserved either pinned or in 70% alcohol (all specimens are located in the collection of the author).

Further data on species ecology were retrieved from the literature (Table 1). For nesting behaviour, species were grouped into paracoprid (tunnelers) and endocoprid (dwellers) species following Rößner (2012) and Hanski & Cambefort (1991). In endocoprid species, egg deposition and larval development take place directly inside the dung pad, whereas paracoprid species bury tunnels beneath the dung pad and deposit eggs for larval development in chambers furnished with dung from above. Species showing any other nesting behaviors like telecoprid or phyto-saprophagous species were excluded from model calculation with nesting behavior as a grouping factor, as this related to only four species. The separation into habitat preferences included species affiliated to open habitats only (hereinafter referred to as “open landscape species”) and species using open *and* semi-open and/or forest habitats (hereinafter referred to as “semi-open landscape species”), as classified by Koch (1989) and Rößner (2012). Furthermore, species occurrence range was classified as stable, declining, or increasing in the study area based on occurrence data from Schernhammer et al (2023) and calculated as the proportion of currently (2020) versus historically (before 1950) occupied grid cells. Values bigger than one indicate species with an increasing range (for simplicity hereinafter referred to as “increasing species”) and smaller values species with a decreasing range (hereinafter referred to as “decreasing species”). For all model calculations with declining and increasing species, the sister species *Euorodalus coenosus* / *E. paracoenosus* and *Onthophagus illyricus* / *O. taurus* were left out, since these species were historically often subject to identification errors and as valid identification features were only published after 2000 (Pizzo et al., 2006; Rößner, 2004). Lastly, the species’ degree of specialisation was estimated by how many

different types of animal dung are used as a food source following Horion (1958), Koch (1989), Meurgey & Sadorge (2001, 2002, 2004) and Rößner (2012). Low numbers hereby indicate a high specialization.

*Table 1: Overview on the ecological traits used, including categories and main data sources*

trait	categories	main data source
nesting behaviour	paracoprid endocoprid	Hanski & Cambefort (1991) Rößner (2012)
habitat preferences	open landscape semi-open landscape species	Koch (1989) Rössner (2012)
occurrence trend	continuous values between 0 and 1 (<1 = decreasing range, >1 = increasing range)	Schernhammer et al (2023)
specialisation	continuous values between 0 and 1	Horion (1958) Koch (1989) Rößner (2012)

## Current and historic land-cover data

To assess the role of habitat availability in the wider landscape, I extracted and digitized land cover from historical maps and aerial photographs in a circular area of one kilometer around the sampling sites (conducted in QGIS Geographic Information System, version 3.28.2-Firenze). I used historical maps and aerial photographs from three different time points representing distinct periods of major changes in agricultural practices: i) c. 1880-1900, ii) c. 1950-1960, ii) c. 1990-1995 and current aerial photograph for reference (information on maps and data sources is given in Table S3)

The following nine land-cover categories were digitized: grasslands, pastures, forests, fields (incl. vineyards), water bodies, shrubland (e.g. hedges, patches of trees), settlements, infrastructure (e.g. roads, railways) and other (e.g., landfills, quarries). Figure 2 shows examples of digitized pastures. For analysis, only the main categories pasture, field, settlement and forest were used as predictors (representing the total area of each category within the one-kilometer radius around each pasture). The other categories were not included as they are considered not to provide main habitats for dung beetles.

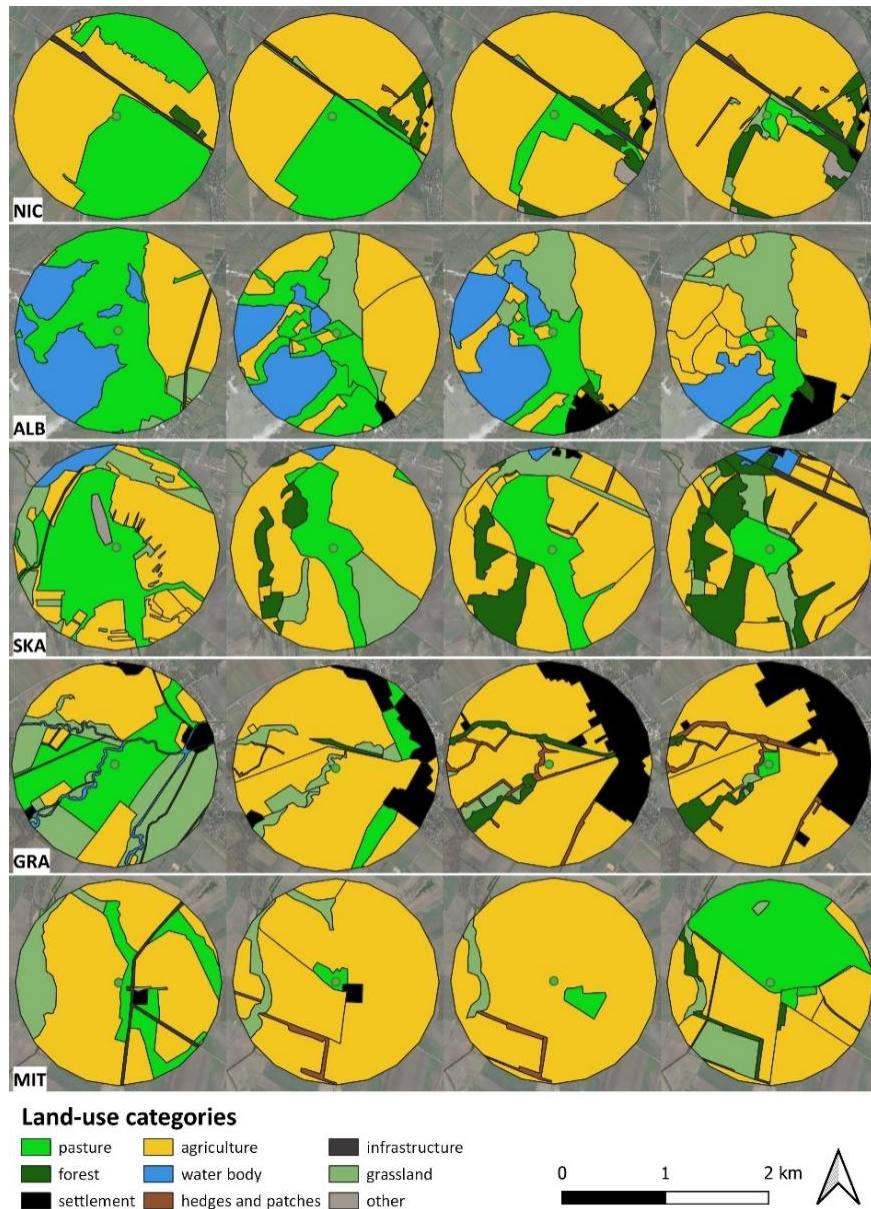


Figure 2: Examples of land cover changes over time for five study sites. Nickelsdorf (NIC), Albersee (ALB), Skalky (SKA) show typical severe declines in pasture areas due to abandonment of traditional agropastoral activities and transformation into forests and fields. On some sites pasture areas increased again within the last decade due to the establishment of organic livestock farms but barely ever reached former extensions (Gramatneusiedl (GRA)), with some exceptions like Mitterhof (MIT). Land cover from left to right: c. 1880, 1950, 1990, 2020.

## Analyses

To test my hypotheses I built Generalized Linear Mixed Models (GLMMs) with a Poisson error distribution using the lme4 package (Bates et al., 2015) in the programming language R (R Core Team, 2022).

To avoid collinearity across predictor variables in the models I checked predictor correlations using the *ggpairs* and the *ggcorr* function in the R package GGally (Schloerke et al., 2020). Since “number of livestock” and “pasture area” highly correlated, “number of livestock” was excluded as a predictor. All other predictor variable correlation was below 0.7 indicating a sufficiently low correlation to be used in the same model (Dormann et al., 2013).

As dung beetle samples were taken over three different months (April, May and June, see Table S1) they included both typical spring- and summer-species with different phenologies and therefore population peaks at different seasons. A NMDS-plot calculated with presence-absence data of the pastures illustrates these differences in the species communities due to different sampling months (Figure S1). In order to account for these differences in phenology and nevertheless enable a comparison of the samples, the sampling month was included in the GLMMs as a random effect. Since some sample points cluster together geographically (see Figure 1) an ACF plot was calculated for a generalized linear model with the same variables to preclude a possible bias from spatial autocorrelation (Venables & Ripley, 2002). The result did not show any spatial autocorrelation bias (Figure S2).

For each GLMM-model I calculated the corrected Akaike information criterion (AICc), which contains a second-order bias correction for small sample sizes. The land use models were then compared by means of Akaike weights (Burnham et al., 2004) and McFadden’s  $R^2$  values (McFadden, 1977).

To examine the influence of anthelmintics and grazing history compared to land use, I firstly built GLMMs using anthelmintics, grazing history and landcover data from 2022 (*see chapter “landcover data”*) as predictor variables. This was calculated with all species as the response variable first (using species richness of the pastures) and then using counts of species of each ecological group on the pastures as the response variable: open landscape and semi-open landscape species, declining and increasing species and para- and endocoprid species.

For analyses of historical imprints on current dung beetles species richness, the variables “grazing history” and “use of anthelmintics” were left out, as the former was unknown for some sites and the latter are only commonly used since the 1990s (Crump & Omura, 2011). Therefore, I restricted this analysis to land cover data (i.e. area of pastures, fields, settlements and forests in a circle of 1 km around the sites) as predictor variables; separate models were calibrated using historical and recent land cover data. As response variable dung species richness of all species, and subsets of different ecological species groups were used. To identify



which model best explains current species richness, I performed a model selection procedure based on the Akaike criterion (Dullinger et al., 2013).

## Results

### Dung beetle species composition and richness

The samples included a total of 9738 beetles belonging to 56 species (Table S2). Species number on sites varied between 24 and two (Figure 3), with the most species-rich sites being Lainzer Tiergarten (LTG, Vienna, 24 species) and Zurndorf (ZUR, Burgenland; 23 species). Numbers of individuals varied also widely between sites with highest numbers found in Zurndorf (ZUR, Burgenland, 1491 individuals), and lowest numbers in Albersee (ALB, Burgenland, 3 individuals). Neither species nor individual numbers showed any dependence on pasture size (Pearson correlation coefficient of -0.15 (species richness,  $p = 0.4122$ ) and -0.08 (individual richness,  $p = 0.6548$ )).

The species with the overall highest individual numbers were *Onthophagus ruficapillus* (2130), *Colobopterus erraticus* (1504) and *Onthophagus illyricus* (881), and the most common species among all pastures *Otophorus haemorrhoidalis*, *Euoniticellus fulvus* (both found on 26 pastures) and *Onthophagus ruficapillus* (found on 23 pastures).

Data on species ecology is given in Table S2. Following Koch (1989) and Rößner (2012), 16 of those species use exclusively open habitats and are therefore open landscape species, whereas 40 species also occur in forests and are semi-open landscape species; the remaining two species are strict forest species. The majority of species are paracoprid (tunnelers) and 30 species endocoprid (dwellers). Four species are using other nesting behaviors, namely *Sisyphus schaefferi* (telecoprid) and *Oxyomus sylvestris*, *Pleurophorus caesus* and *Pleurophorus pannonicus* (phyto-saprophagous). Even though the latter three species are sometimes not revered to as coprophagous, they were nevertheless included in the models since the adults are frequently found in dung and fulfill similar ecosystem functions as coprophagous species. As far as specialization is concerned, most species are polyphagous, feeding on at least three different kinds of dung. The comparison with the preferred habitat type shows that the collected open landscape species are more specialized than semi-open landscape species, as illustrated in Figure S3. The species occurrence trends assignment based on Schernhammer et

al. (2023) revealed that 16 species are increasing, four species are stable, and 37 species are declining in the study region.

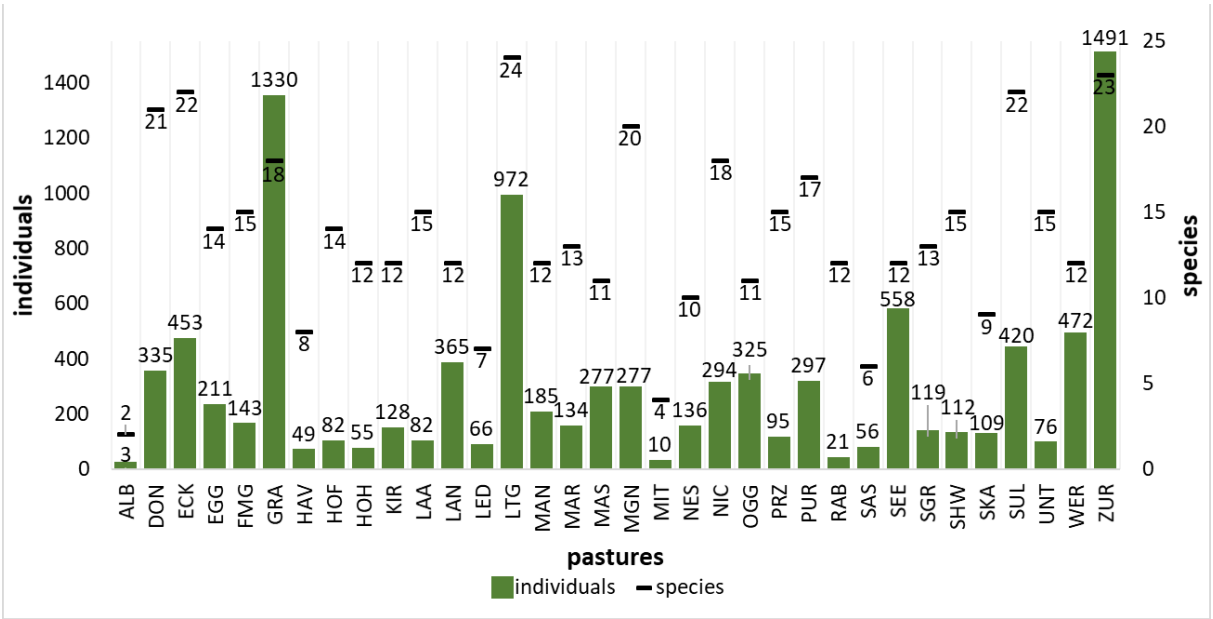


Figure 3: Number of collected dung beetle individuals and species at the 34 study sites.

### Land use change

While land use change differed among study sites, some general trends in land cover changes over time are obvious: Settlement areas increased in all sample sites, as did forest areas. Pasture area decreased sharply (Figure 4), with only eight sites showing an increase (Figure S4 illustrates changes in pastures sizes in detail). Change in agricultural fields varied, with an increase at 22 sites and a decrease at 12 sites. Detailed land use change for all sampled sites is illustrated in Figure S3.

The total land cover area at the four different points in time over all sampled sites reflects these trends (Table S3): The increase in settlement and forest areas and the decrease in pasture areas are clearly visible. The total size of settlement areas almost tripled, forest areas increased strongly and pasture area reduced to half. While changes in all other land cover types happened

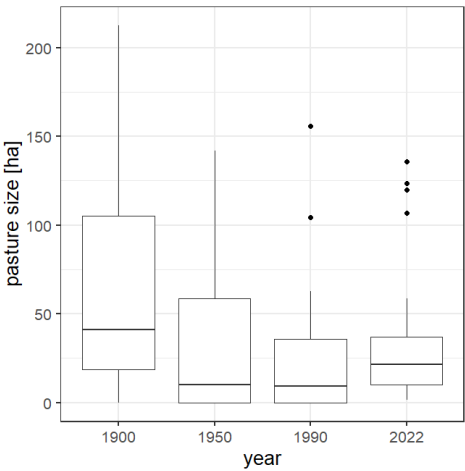
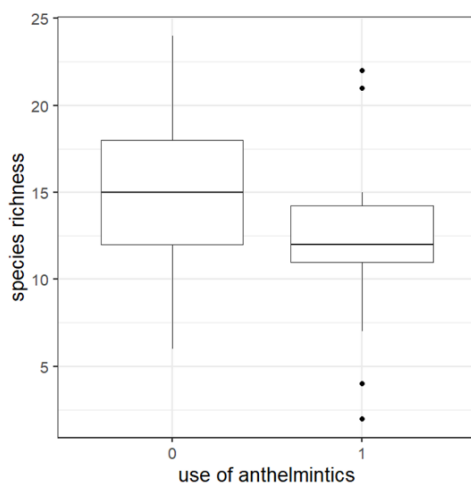


Figure 4: Changes of pasture size over all sampled sites

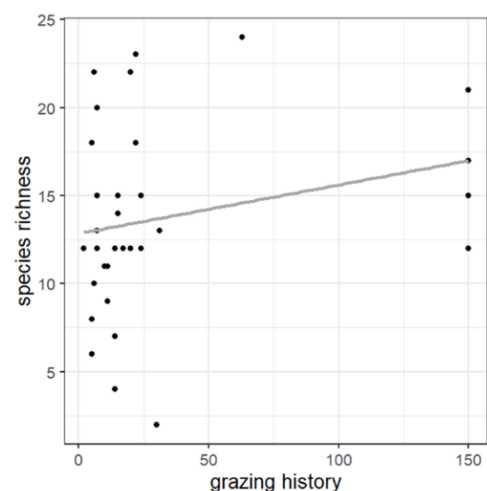
continuously over the years, pasture area had already dropped to its half in 1950 and had decreased even more in 1990, before increasing again to its current size.

### Species richness explained by current land cover and land use data

To analyse which currently acting factors explain dung beetle species richness in the plots, I used GLMMS including current land cover variables and current land use practices (i.e. application of anthelmintics) as explanatory variables. I found that the application of anthelmintics had a significant negative effect on species richness (Figure 5, Table 3). When compared to a GLMM not including anthelmintics as an explanatory variable, Anova showed significant differences between both models, with the model including anthelmintics describing species richness better. Grazing history did not have a significant positive impact on species richness in the model, although it is over all positively related with species richness (Figure 6). Two of the sampled pastures exist since over 150 years but were not grazed for two years in between - when not considering this as an interruption in the model, the influence of grazing continuity was significantly positive.



*Figure 5: Species richness on sampled pastures with (1) and without use of anthelmintics (0)*



*Figure 6: Influence of grazing history on species richness. Grazing history is measured in years*

The results of the models calibrated for the ecological groups separately are similar concerning grazing history with no significant impact on any of the groups. The use of anthelmintics, however, affects the ecological groups to a varying extent. While their application does only have a slightly negative, not significant influence on paracoprid species, it has a strong significant negative impact on endocoprid species. Anthelmintics also seem to affect semi-open



landscape species more than open land species, this however comes from the fact that the majority of semi-open landscape species is endocoprid and therefore more strongly affected by the medicine, regardless of their habitat preference. The influence of anthelmintics on species decline is also illustrated by the results of the model calculated with decreasing species only, where anthelmintics are the factor with the strongest negative impact. Compared by Anova, the model including anthelmintics is significantly superior to the model excluding this factor, with a clear difference in AIC-values. For increasing species, neither significant impact of anthelmintics nor a difference in models with or without this predictor was detected.

*Table 2: Impact of anthelmintics on the different ecological groups. Diagnostic model values: ., \* and \*\* = significance levels, est = estimates, AICc = corrected Akaike information criterion, 2022anth/ 2022 = models calibrated with anthelmintics and without*

ecological group	p-values	est	AICc		R <sup>2</sup>	
			2022anth	2022	2022anth	2022
all	0.01 **	-0.31	228.04	231.70	0.35	0.18
open landscape	0.06 .	-0.41	175.67	175.78	0.50	0.41
semi-open landscape	0.03 *	-0.30	194.25	188.63	0.30	0.19
paracoprid	0.41	-0.13	174.97	172.15	0.21	0.19
endocoprid	0.01 *	-0.42	190.30	193.11	0.29	0.08
decreasing	0.01 *	-0.38	187.11	189.89	0.27	0.16
increasing	0.10	-0.30	165.52	164.76	0.38	0.29

## Modelling land cover changes reveals evidence for time lags

To test if current dung beetle species numbers show legacies of historic land cover changes, I calibrated one model based on current variables, and three historic models based on land cover data from c. 1880, 1950, 1990 and 2020. The model comparison among the resulting models (based on Akaike weights) revealed that models based on historic land cover data better explain current species richness, and that the best model is the one that dates back the longest (Figure 7).

For species subsets, the general finding is mostly corroborated, with some exceptions. Richness of semi-open landscape species is also best explained by the 1880-model. Older models also reveal a significant positive influence of forest extent, which decreases continuously with the models using more current landcover data.

Interestingly, results for open landscape species were different, with the model based on current land cover being the best model and forest cover having a negative effect in the current model.

For paracoprid species, the model using current landcover data has the best fit, but the differences between the models are not as big as in other groups. In the 2022- and 1990-model settlement areas have a significant positive impact on this group.

As far as endocoprid species are concerned, the model fitting the data best is again the one using landcover data from 1900. None of the landcover categories has a significant impact on this group in any of the years. The latter is also the case for the model calculated with increasing species only. While for this group, the 1900-model is only slightly superior to the other models, it is by far better in describing the richness of declining species than models using more recent data. Settlement is positively influencing decreasing species in the 2022- and 1990-models.

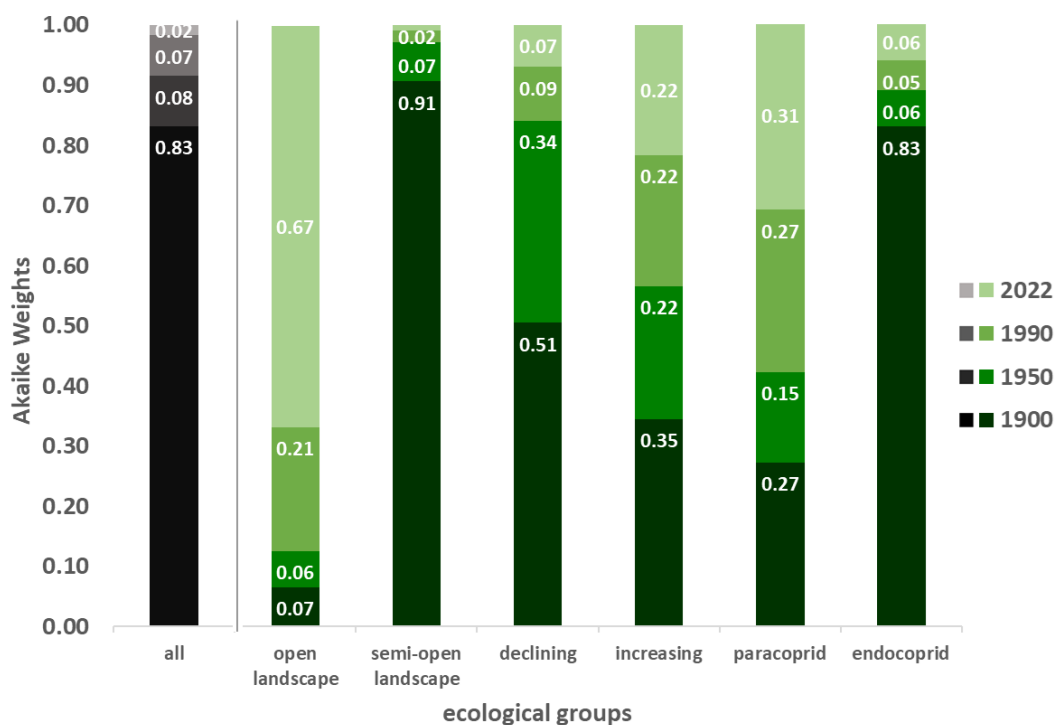


Figure 7: Relative support (Akaike Weights) for general linear models explaining the proportions of ecological species-groups by land-use data of four different points in time.

# Discussion

## Patterns of dung beetle species richness

The 56 species found within this study almost entirely represent the documented species inventory of the region, which is 62 species following the checklist of Schernhammer et al., 2023 (submitted). As samples were taken in spring/ early summer and most pastures represent open land habitats, typical autumn and forest species were not detected. The strongly varying individual numbers of sampled site are typical for dung beetle samples and should not always be seen as an indicator for a good habitat, but can also only be due to the presence of certain species with seasonal individual-rich populations. As the dung beetle fauna of the region was a regular subject of entomological investigations over the last century, the species inventory at the beginning of the 20<sup>th</sup> can be used as a reference before the beginning of profound land use changes. The comparison with the current species inventory shows a strong decline in species numbers (Schernhammer et al., 2023, submitted). Notable dung beetle species detected within the sampling for this study in 2022 include: *Trichonotulus scrofa* (Zurndorf (ZUR); first record in the province of Burgenland since 1920), *Biralus satellitius* (Donnerskirchen (DON); first record in the province of Burgenland since 1960s, only one known occurrence in the region in Lower Austria), *Onthophagus lemur* (Sulzhof (SUL); first record in the province of Burgenland since 1960s, only one known occurrence in the region in Lower Austria) and *Phalacronotus biguttatus* (Nickelsdorf (NIC); only occasional observations from 1990s and one from 2021).

## Time lags and extinction debt due to land cover changes

The analysis of historical land cover imprints on current dung beetle species richness revealed that historic land cover data explain species richness better than current data, and that the best models are the ones dating back the longest. Notably, the model based on land use conditions from 1880 best describes the total current species richness. This finding indicates that historic land cover in the surrounding of the study sites has profound and long-lasting impacts on current dung beetle species richness extending over at least 150 years. The consequences of grassland losses only become fully apparent after considerable time lags. Such extinction debt phenomena (Tilman et al., 1995) due to land use change have been observed for plants (Bommarco et al., 2014; Lindborg, 2007; Piqueray et al., 2011), red list species (Dullinger et al., 2013) and other invertebrates (Polus et al., 2007), but until now not specifically for dung

beetles. However, none of these studies has tested extinction debt over such an extensive time period (i.e. 150 years) as this study. Given the high mobility of dung beetles and their short generation time (mostly annual), the extended relaxation time of dung beetles to historic land cover changes is astonishing. Further, it is likely that many dung beetle species are currently living just above their local extinction threshold and are facing high local extinction risks. Species that have gone locally extinct in the last decades were predominantly specialists (Filgueiras et al., 2015; Schernhammer & Denner, 2022a), which aligns with the tenets of extinction debt theory stating that specialist species are the first to disappear in response to habitat alterations (Tilman et al., 1995).

The digitization of land cover in the study region revealed that total forest area has steadily grown from 1900 to 2022, while pasture area halved within this time span (Table S4). Comparable processes have happened in various Central European countries within the same ecoregions (Bičík et al., 2001; Cegielska et al., 2018; Kozak, 2003), as well as in the other parts of Europe (Dallimer et al., 2009; Otero et al., 2015). The primary factors driving the expansion of forests are rural depopulation and the abandonment of small-scale farms (Kozak, 2003; van Doorn & Bakker, 2007) along with the implementation of the Common agricultural policy following EU memberships (Griffiths et al., 2013; Senetra et al., 2013). Changes in pasture areas were visible much earlier than in forest cover: The total pasture area decline of 50% between 1900 and 1950 reflects first big conversions in the agricultural sector during this time, including the adoption of large-scale cultivation of forage crops which enabled year-round indoor livestock farming and reduced reliance on outdoor pastures (Poschlod, 2017; Sandgruber, 1978). The ongoing decrease in pasture land observed between 1950 and 1990 indicates loss of pastures due to the intensification of agricultural methods following mechanisation (Bauer, 2012). Similar changes occurred in other countries within the Pannonian region that have a long history of herding pastures (Varga et al., 2016). Interestingly, total pasture size in the study region increased again between 1990 and 2022 and is currently about half of the size of 1900. This development can be attributed, in part, to nature conservation initiatives that have established pastures and grazing as a means of conservation, as observed in two sampled sites. However, the main driving force behind the increase is the establishment of large-scale agricultural companies that have created new intensive pastures, as evident in four sampled sites. Despite the expansion of total pasture area and its potential to provide increased food sources for dung beetles, these newly established pastures were found to be among the least

species-rich sites. This is likely due to factors such as intensive grazing, veterinary treatments, and the relatively short period of existence of these pastures. They also differ strongly in appearance from pastures established as a conservation measure, characterized by lower structural and floral diversity and a lack of a wide range of microhabitats, features that are typically found in natural pastures (Bunzel-Drücke et al., 2019).

The models calibrated for each ecological group individually clearly reflected their different requirements and responses to changes of land cover and showed the importance of incorporating ecological features in this type of analysis.

The different influence of forest cover on open landscape and semi-open landscape species over all four points in time is consistent with total forest cover change in the region: The expected positive influence of forest cover on semi-open landscape species is only significant in earlier models (1900, 1950 and 1990) whereby significance and impact continuously decrease with newer models and is not given in the 2022-model. The continuous increase in total forest cover from 1900 to 2022 likely explains its significance in the earlier 20th century, when limited forest areas acted as refugia and the only suitable habitat within a landscape predominantly dominated by open grasslands. Conversely, for open landscape species, the impact of forest cover displayed an opposite trend: It is only significantly negative in the current landscape (2022-model) where forest areas strongly increased, while the negative effect diminished in older models that described a more open landscape. Interestingly, the oldest model emerged as the most suitable in describing semi-open landscape species diversity based on Akaike weights - which again indicates a time-lag phenomenon – whereas open landscape species diversity is best described by current land use data (Figure 7). This might indicate a change in the species inhabiting the open-land habitats of the study region. As mentioned earlier, specialised species are often more sensitive to change and loss of habitat (Filgueiras et al., 2015; Hilpold et al., 2018) and many of the species that have gone extinct in the study region were (dung-rolling) species specialized on open habitats, like for example *Gymnopleurus mopsus*, *Gymnopleurus geoffroyi*, *Euonthophagus amyntas* and *Aphodius hydrochaeris*, suffering from the loss of these areas and increasing forest cover. The analysis of the specialisation of the sampled species on different dung as a food source also shows a higher specialisation among open landscape species (Figure S2). The newly available ecological niches resulting from the extinction of specialists were likely taken up by more generalized species adapted to current land use, which is reflected by the 2022-model describing species diversity

the best. Similar shifts in dung-beetle communities due to land-cover changes have been documented previously, particularly in tropical landscapes (e.g. Halffter & Arellano, 2002). Macagno & Palestini (2009) observed a comparable species-turnover in the alps and proposed that especially open landscape species undergo these changes in species communities because of dung resources being shifted to forests since local wild ungulates prefer closed habitats over open ones, in contrast to the extinct large herbivores which preferred open landscapes. Endocoprid species were not significantly impacted by any land-cover type, yet the comparison of Akaike weights suggests a time-lag phenomenon for this ecological group as well: The 1900-model remarkably provided the most accurate description of the current species richness. These species appear to be more susceptible to the effects of land use change compared to paracoprid species, where Akaike weights across all models show only marginal differences. Interestingly, settlement areas have a significant positive impact on paracoprid species in the 2022- and 1900-model. A possible explanation for this finding could be that pastures are often geographically close to settlement areas to facilitate management (Poschlod, 2017), and settlements yield a high amount of dung from domestic animals like dogs but also working horses (Bauer, 2012), which can be quite attractive for dung beetles (Carpaneto et al., 2005). In general, very little is known about the response of dung beetles to urbanization processes but the results of this study corroborate the findings of Salomão et al. (2019), who described a high sensitivity of dung beetles to urbanization but also contrasting effects among different functional groups. A study conducted in Rome reported an extinction of 65% of the species through urbanization processes (Fattorini, 2011). This pattern is also evident in the results of the model calibrated with declining species only, wherein settlement emerges as the primary driver of the occurrence of declining species in the study area. Moreover, these species are better represented as the models extend further back in time, once again suggesting potential time-lag processes, while the models for increasing species perform almost equally well. The latter seem to include the profiteers of land use changes, likely being more undemanding generalist species.

### **The importance of anthelmintics and grazing continuity for dung beetle species richness**

I found that the use of anthelmintics had a profound negative impact on dung beetle species richness. Interestingly, it played a crucial role in explaining the richness of declining beetle

species, but had no discernible impact on increasing species. These results corroborate the findings of several studies demonstrating the negative impact of veterinary medicine on dung beetles (e.g. Ambrožová et al., 2021; Tonelli et al., 2017; Verdú et al., 2015). Treatment was shown to result in more homogenous species communities with rare specialists disappearing first and generalist species, mostly dwellers, remaining (Ambrožová et al., 2022; Tonelli et al., 2017), which reflects the species composition trends in the study area. Furthermore, I showed that the effects of anthelmintics on dung beetle species of different nesting behaviour varied: Endocoprid species exhibited negative impacts, whereas paracoprid species remained unaffected. Earlier studies on this topic lead to contrasting results: While my findings align with Kless & Scholtz (2001), others like Ambrožová et al. (2022), Sands & Wall (2018) and Tovar et al. (2023) reported that paracoprid species were more adversely impacted by veterinary treatments than endocoprid species. Research conducted on the specific effects of veterinary medicine revealed that larvae of dung beetles are more sensitive to medical substances than adults (Lumaret et al., 2012; Wardhaugh et al., 2001). This could be a possible explanation for endocoprid species being more affected since their larvae, developing directly inside the faeces, are exposed to larger quantities of dung and therefore to higher concentrations of the medical substances than larvae of tunnelers, which develop in the soil and are surrounded by a smaller amount of faeces. Additional investigations focusing on the specific impacts of anthelmintics on different functional groups would be essential to validate this hypothesis. Hereby it is also important to highlight that the influence of medical substances on arthropods depends on other environmental factors such as season and weather as well (Koopmann & Kühne, 2017).

The number of years of continuous grazing (“grazing history”) did not demonstrate a significant influence on species richness in the model. This may be attributed to the interpretation of even one year of grazing abandonment as an interruption (as especially big species of dung beetles were shown to be suffering from short grazing disruptions (Correa et al., 2021)). Furthermore, there was a substantial disparity in the grazing history among the sampled pastures, with the majority existing since less than 50 years and only four pastures being subject to continuous grazing for over 150 years. Despite not being a significant predictor in the model, grazing continuity over all positively correlated with species richness (Figure 6), an effect that has repeatedly been shown in previous studies (e.g. Buse et al., 2015; Tonelli et al., 2018). A good example of the impact of interruption of grazing regimes on species diversity in the study area

is the pasture in Mannersdorf (MAN): It is among the oldest pasture in the region but the grazing regime was interrupted for approximately 50 years, during which the area was used as an intensive hay meadow. Only 12 dung beetle species were found, compared to between 20 and 23 species on pastures of the same age without interruptions of the grazing regimes.

Overall, clear impacts of management and land use change were identified in certain groups of dung beetles, while reasons for effects on other groups still require further investigation. It is important to acknowledge that certain factors known to influence dung beetle diversity and richness, such as weather, microclimate, and soil types (Leandro et al., 2023; Lumaret & Jay-Robert, 2002) were not integrated into the constructed models. Additionally, only spring- and summer-species were sampled and it is conceivable that the influence of land use predictors might differ when considering autumn- and winter-species as well.

## Conclusions and implications for management

I studied the species richness of the dung beetle fauna in grazed grassland patches in the Pannonian region using a set of current land use and current and historic land cover to analyse the underlying factors explaining current dung beetle species richness, and tested for time lag effects extending over 150 years of land cover change. I found deep time consequences of historic land use on dung beetle species richness, which have strong implications. First, extinction debt driven by changes in land use may have more extensive relaxation times than widely assumed, even for mobile and short-lived groups as dung beetles. Second, this has severe implications for conservation assessments as the full extent of local species decline and losses due to changes in land use may only be fully realized over extensive time periods, indicating that extinction risks may be underestimated. This finding corroborates the conclusions of Dullinger et al. (2013) who found that national scale extinction risk assessments (i.e. national Red lists) seem to underestimate extinction risks as historical models explain Red list assessments better than current ones.

Following my results, conservation measures for dung beetles should prioritize the preservation of suitable habitats. A particular focus should hereby lie on the protection of long-existing pastures, as this study, along with several others (Buse et al., 2015; Jay-Robert et al., 2008; Sartorello et al., 2020), demonstrates the importance of grazing continuity in promoting species richness. In addition, the establishment of new extensively managed pastures, including wood-pastures, will not only counteract the ongoing process of habitat loss but will also provide



necessary stepping-stones for dispersion and repopulation (Ambrožová et al., 2022). Furthermore, reducing the extensive use of veterinary medicines is essential, as also proposed by several other studies (e.g. Koopmann & Kühne, 2017; Sands & Wall, 2018; Tonelli et al., 2017; Tovar et al., 2023). Informing farmers about the negative and long-lasting side-effects of these substances is crucial for achieving this reduction. Treatment should only be implemented on livestock individually when required or be timed with indoor housing. All these measurements will not only help to counteract the decline of dung beetles, but will also maintain the crucial ecological functions these beetles provide in grazing ecosystems and especially for the livestock farming sector.

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# Supplementary information

Table S1: Sampled pastures within the study area. \* = no detailed information on grazing breed

code	long	lat	breed	sampling date	anthel-mintics	grazing history [years]	number of livestock
ALB	16.77	47.77	Angus/Fleckvieh, Limousin	22.06.2021	YES	30	100
DON	16.64	47.9	Fleckvieh, Pinzgauer	14.06.2022	YES	150	8
ECK	16.79	48.13	Galloway	07.06.2022	NO	20	20
EGG	16.28	47.88	Waldviertler Blondvieh	01.05.2019	NO	15	23
FMG	16.62	48.29	Tiroler Grauvieh, Aubrac, Murbodner, Angus, Piemonteser	08.06.2020	NO	7	6
GRA	16.48	48.02	Galloway	15.06.2022	NO	5	14
HAV	15.99	48.81	Horse*	12.05.2018	NO	5	5
HOF	16.94	48.22	Horse	07.06.2022	YES	15	10
HOH	16.93	48.6	Galloway	15.06.2022	YES	17	7
KIR	16.78	47.76	Angus/Fleckvieh, Limousin	22.06.2021	YES	20	100
LAA	16.38	48.73	Dexter	11.06.2020	YES	15	13
LAN	16.86	47.76	Fleckvieh	22.06.2021	YES	150	40
LED	16.8	48.81	Horse*	14.04.2018	YES	14	15
LTG	16.25	48.17	Heckrind	16.06.2021	NO	63	22
MAN	16.57	47.99	Charolais, Angus	15.06.2022	YES	24	12
MAR	16.9	48.28	Konik	28.06.2019	NO	7	19
MAS	16.72	48.81	Horse*	12.05.2018	YES	11	11
MGN	16.65	48.29	Tiroler Grauvieh, Aubrac, Murbodner, Angus, Piemonteser	28.04.2020	NO	7	18
MIT	16.45	48.77	Cow*	14.04.2018	YES	14	230
NES	16.73	48.77	Horse*	14.04.2018	NO	6	3
NIC	17.06	47.95	Dahomey-Zwergrind	29.06.2022	NO	22	9
OGG	16.69	47.87	Angus	14.06.2022	YES	10	7
PRZ	16.76	47.77	Przewalski horses, Angus	22.06.2021	YES	24	12
PUR	16.68	47.92	Angus	14.06.2022	NO	150	11
RAB	16.91	48.66	Aubrac x Tiroler Grauvieh	15.06.2022	NO	2	13
SAS	16.87	48.3	Tiroler Grauvieh, Aubrac, Murbodner, Angus, Piemonteser	08.06.2020	NO	5	3
SEE	16.78	47.81	Angus	22.06.2021	YES	14	30
SGR	16.8	47.73	Graurinder, Wasserbüffel	22.06.2021	YES	31	300
SHW	16.06	47.85	Fleckvieh	28.06.2022	NO	150	52
SKA	16.68	48.77	Cow*	14.04.2018	NO	11	3
SUL	16.6	47.79	Angus	14.06.2022	YES	6	64
UNT	16.77	48.26	Tiroler Grauvieh, Aubrac, Murbodner, Angus, Piemonteser	28.04.2020	NO	7	10
WER	16.75	48.29	Tiroler Grauvieh, Aubrac, Murbodner, Angus, Piemonteser	08.06.2020	NO	7	16
ZUR	17.01	47.97	Dexter	29.06.2022	NO	22	8

Table S2 Species found in the study area with total number of counts, total number of occupied pastures by each species, nesting behaviour, habitat preference, dung specialisation and population trend (see text for detailed explanation). Nesting behaviour: e = endocoprid, p = paracoprid, t = telecoprid, \* = phyto-saprophagous species with development in detritus; habitat: o = open landscape, s-o = semi-open landscapes; dung specialization: number of different animal-dung used as a food source (low numbers indicate higher specialization). \*\*trend calculation considered invalid due to taxonomic changes.

species	total counts	inhabited pastures	nesting behaviour	habitat	dung specialisation	trend
<i>Acanthobodilus immundus</i>	131	13	e	o	4	1.07
<i>Acrossus depressus</i>	1	1	e	s-o	8	0.75
<i>Acrossus luridus</i>	17	5	e	s-o	7	0.61
<i>Acrossus rufipes</i>	1	1	e	s-o	9	0.25
<i>Agrilinus ater</i>	3	2	e	s-o	7	0.38
<i>Aphodius fimetarius</i>	124	18	e	s-o	8	0.48
<i>Biralus satellitius</i>	4	2	e	s-o	3	0.10
<i>Bodilopsis rufus</i>	108	14	e	s-o	8	2.20
<i>Bodilus lugens</i>	190	12	e	o	5	0.56
<i>Calamosternus granarius</i>	132	10	e	s-o	9	0.34
<i>Chilo thorax distinctus</i>	100	4	e	s-o	8	0.68
<i>Colobopterus erraticus</i>	1504	23	p	s-o	8	0.84
<i>Coprimorphus scrutator</i>	212	18	e	s-o	4	0.88
<i>Copris lunaris</i>	26	8	p	s-o	6	0.30
<i>Esymus pusillus</i>	368	20	e	s-o	7	1.50
<i>Euoniticellus fulvus</i>	814	26	p	o	4	1.00
<i>Euorodalus coenosus</i>	6	1	e	s-o	8	0.22**
<i>Euorodalus paracoenosus</i>	176	16	e	o	5	7.50**
<i>Eupleurus subterraneus</i>	11	6	e	s-o	7	0.29
<i>Geotrupes spiniger</i>	9	2	p	s-o	5	0.71
<i>Geotrupes stercorarius</i>	1	1	p	s-o	6	0.50
<i>Labarrus lividus</i>	18	4	e	s-o	4	1.50
<i>Limarus maculatus</i>	2	1	e	s-o	7	1.50
<i>Melinopterus consputus</i>	1	1	e	o	6	1.57
<i>Melinopterus prodromus</i>	80	3	e	s-o	9	0.58
<i>Melinopterus sphacelatus</i>	94	2	e	s-o	8	0.57
<i>Nialis varians</i>	5	2	e	o	3	0.44
<i>Onthophagus coenobita</i>	64	11	p	s-o	8	0.85
<i>Onthophagus fracticornis</i>	49	9	p	s-o	8	0.86
<i>Onthophagus furcatus</i>	69	5	p	o	6	0.39
<i>Onthophagus illyricus</i>	881	22	p	s-o	5	23.00**
<i>Onthophagus joannae</i>	118	9	p	s-o	9	2.00
<i>Onthophagus lemur</i>	37	2	p	o	7	0.25
<i>Onthophagus medius</i>	3	3	p	o	3	0.57
<i>Onthophagus nuchicornis</i>	66	8	p	s-o	8	0.60
<i>Onthophagus ovatus</i>	513	22	p	s-o	8	1.00
<i>Onthophagus ruficapillus</i>	2130	23	p	o	2	0.80
<i>Onthophagus taurus</i>	429	20	p	s-o	6	1.09
<i>Onthophagus vacca</i>	46	14	p	o	3	0.69
<i>Onthophagus verticicornis</i>	211	9	p	s-o	8	0.39
<i>Onthophagus vitulus</i>	3	2	p	o	7	0.11
<i>Otophorus haemorrhoidalis</i>	341	26	e	s-o	8	1.80
<i>Oxyomus sylvestris</i>	11	5	*	s-o	4	2.00
<i>Phalacrothothus biguttatus</i>	2	2	e	s-o	7	0.40
<i>Plagiogonus arenarius</i>	4	4	e	o	6	0.15

<i>Planolius borealis</i>	1	1	e	s-o	5	1.00
<i>Pleurophorus caesus</i>	2	2	e	o	3	0.11
<i>Pleurophorus pannonicus</i>	2	2	*	o	3	0.60
<i>Rhodaphodius foetens</i>	30	7	*	s-o	4	1.57
<i>Sigorus porcus</i>	1	1	e	s-o	6	1.20
<i>Sisyphus schaefferi</i>	22	3	t	s-o	7	0.95
<i>Subrinus sturmi</i>	433	9	e	o	3	3.50
<i>Teuchestes fossor</i>	91	13	e	s-o	6	0.25
<i>Trichonotulus scrofa</i>	15	5	e	s-o	7	0.44
<i>Trypocopris vernalis</i>	10	3	p	s-o	5	1.22
<i>Volinus sticticus</i>	16	8	e	s-o	7	0.90
<b>total: 56</b>	<b>9738</b>					

Table S3: Maps and aerial photographs used for land cover digitization

time period	digitized map	data source
1880-1900	administrative map of Lower Austria (1867-1882)	Office of the State Government of Lower Austria, 2022
	“Third Military Survey” (Franzisco-Josephinische Landesaufnahme; 1880s)	Hofstätter, 1989
1950-1960	aerial photographs	Austrian Federal Office of Metrology and Surveying
1990-1995	aerial photographs	Austrian Federal Office of Metrology and Surveying
2020-2022	satellite images	Google Maps, 2022

Table S4: Total land cover area [ha] of the main land cover types in all sampled sites at different time points.

year	Land cover types [ha]			
	fields	settlements	forests	pastures
2022	4875	614	2101	1218
1990	5649	501	1892	821
1950	5901	352	1471	1177
1900	4477	211	1424	2293

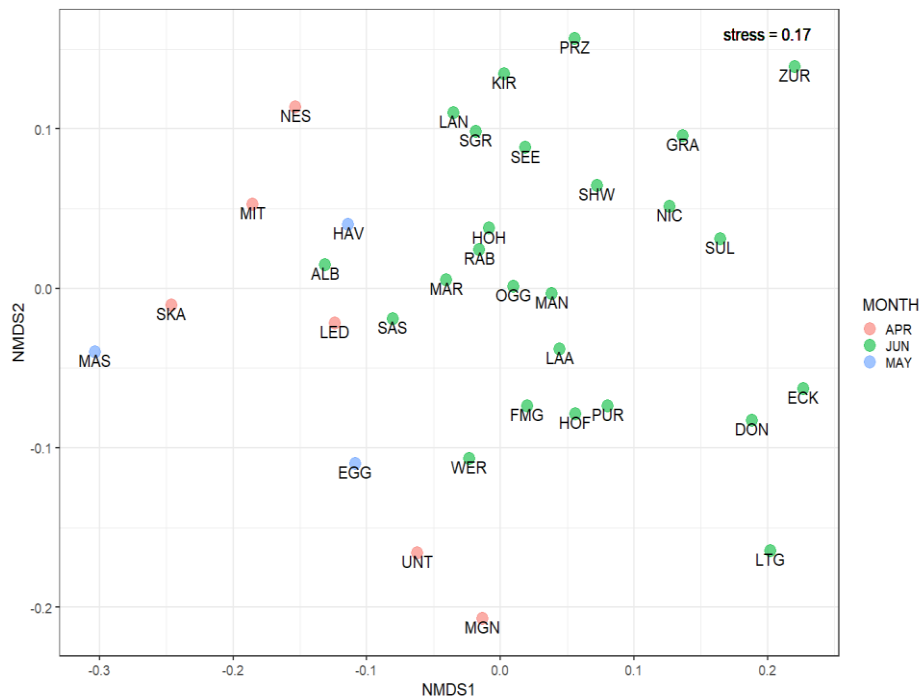


Figure S1: NMDS-plot calculated with presence-absence data of all sampled pastures, illustrating different occurrence-peaks of spring- (April) and summer-species

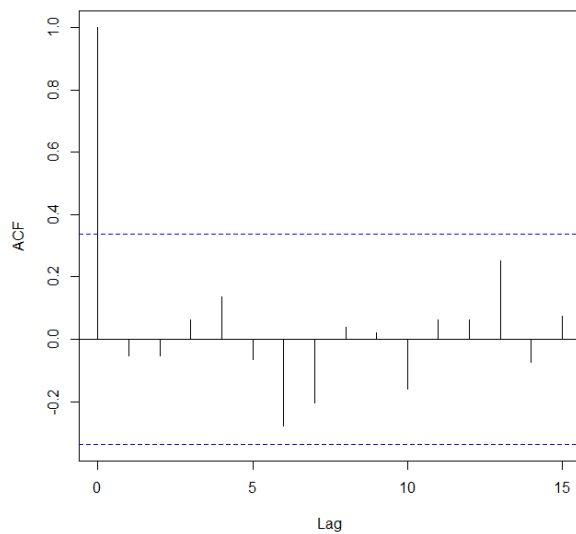


Figure S2: ACF plot calculated to preclude a possible bias from spatial autocorrelation. No spatial autocorrelation bias detected.

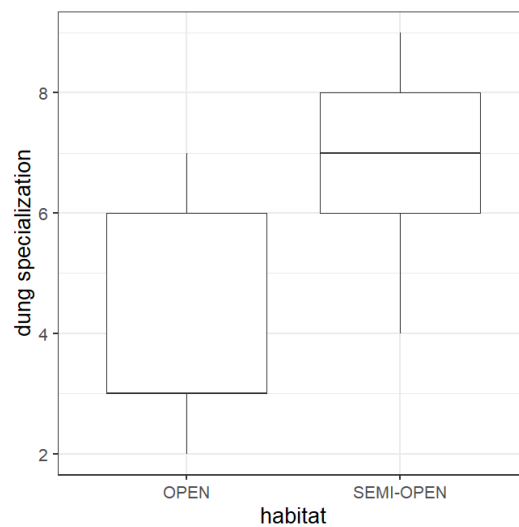


Figure S3: Comparison of dung specialization (number of different used animal faeces) of the collected species, separated by preferred habitat

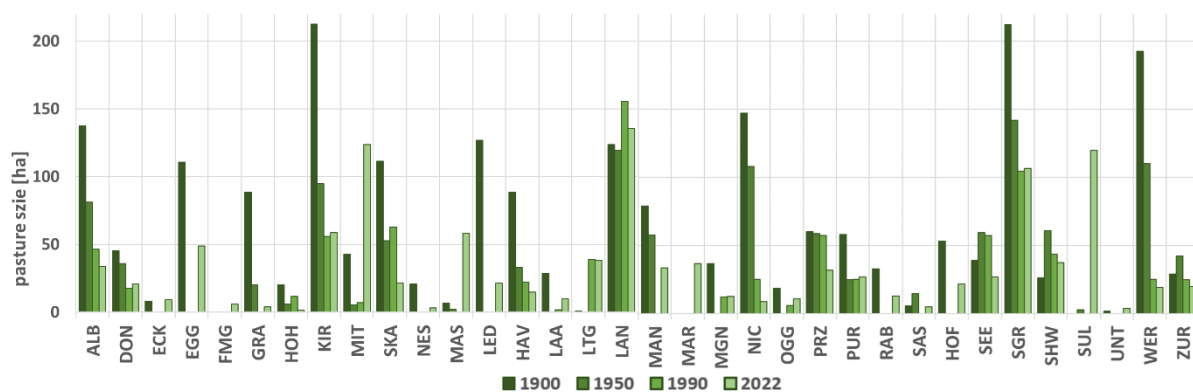


Figure S4: Pasture sizes at sampled points calculated from digitization of maps, aerial photograph and orthophotos of the four points in time

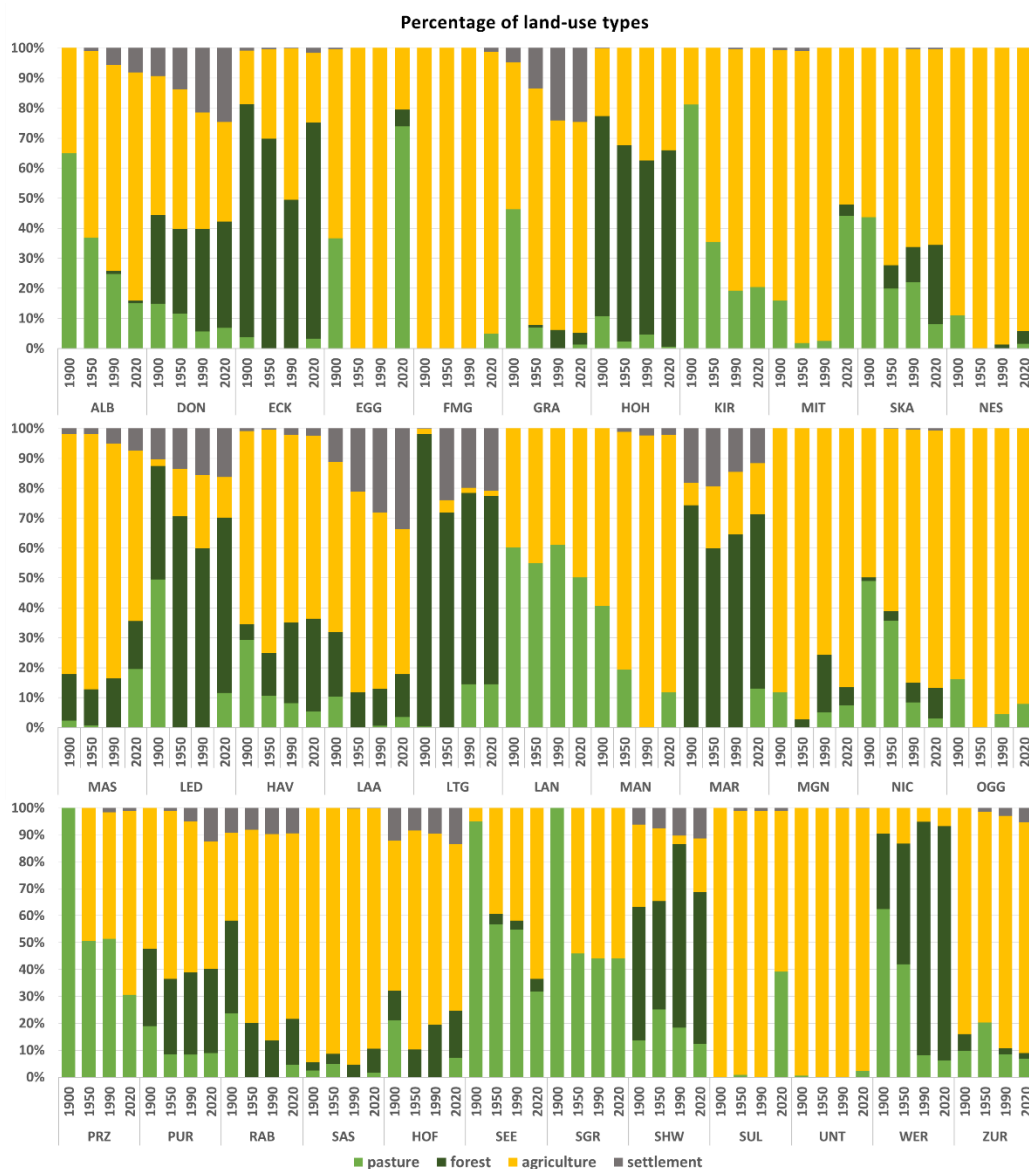


Figure S5: Land use change at sampled points calculated from digitization of maps, aerial photograph and orthophotos of the four points in time