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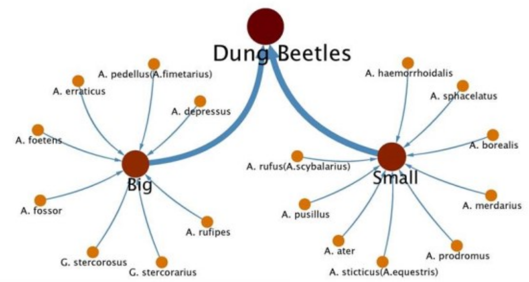
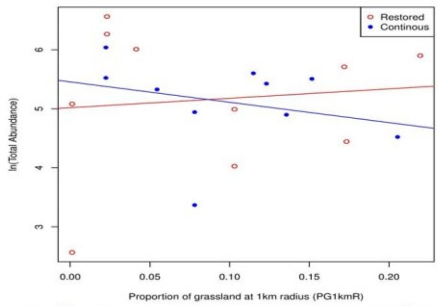
Department of Ecology

Effect Of Restoration And Surrounding Grassland Proportion On The Dung Beetle Metapopulation Abundance In The Fragmented Semi-Natural Grasslands

– Dung Beetles In Restored Semi-Natural Grasslands

Vivek Babu





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Effect Of Restoration And Surrounding Grassland Proportion On The Dung Beetle Metapopulation Abundance In The Fragmented Semi-Natural Grasslands - Dung Beetles In Restored Semi-Natural Grasslands

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Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Natural Resources and Agricultural Sciences
Department of Ecology

Dedicated with

Love & Respects To...

Late. Lalithamma. A & Late. Seshaiah. A.K.

(my beloved maternal grandparents)

Ramaiah. A, Lakshmaiah. A, Rajamma. A, Ramamma.A

(my beloved uncles and aunts)

Ambujamma. D & Babureddy. D

(my beloved aunty and uncle)

Balaramaiah. V

(my beloved paternal grandfather)

Naduvakkarai Village Community

(Native paternal village, that inspired my concerns about agricultural crisis)

Madhuri. S & Chandramohan. S

(my beloved sister and brother in law)

Mohan. A. K

(my beloved cousin)

Malini. V & Dinesh. V

(my beloved sister and brother in law)

Abstract

The importance of landscape composition surrounding the local habitats is increasingly recognized, especially with goal of enhancing the understanding about its role in various conservation frameworks. The dung beetles which depend on human mediated ephemeral resources (Dung from domestic animal) gives a valuable opportunity for understanding landscape moderated effects of both the landscape structure as well as sensitive grazing management on the local populations of semi-natural grasslands in Sweden.

The objectives of this study was to investigate the influence of surrounding landscape grassland proportion gradient and grassland management history on dung beetle species richness and composition. Dung pats (n=200) where collected from the 10 pairs (restored and continuously managed) of pastures. The local abundance and species richness was statistically tested using GLM and regression analysis for the effect of habitat type (restored or continuously grazed grassland) &/or grassland proportion (at 1km & 5km scale) and time since restoration respectively.

The field sampling yielded 4784 beetles of 17 species (*Aphodius and Geotrupes*) belonging to 14 functional guilds of which two generalist species *A. rufipes* and *A. rufus* itself contributed 2664 individuals. The total abundance was higher in restored pastures and total species richness was higher in continuously managed pastures. GLM analysis showed that independent of surrounding landscape grassland proportion the habitat type had an effect on abundance of *A. fossor* (Pasture specialist) and domestic feeder guild positively on continuously managed pastures. The 1km scale surrounding grassland proportion had positive influence on total abundance and abundance of various functional guilds confounded by metapopulation dynamics of generalist species in respective guilds. Whereas 5km scale grassland proportion had both independent and interactive (with habitat management) positive influence on species specific models.

This study concludes surrounding grassland proportion influences the local dung beetle abundance and the restored pastures has a delay in recovery of the population abundance of pasture specialists and intermediate species guild similar to continuously managed pastures. Further research is needed to increase the understanding about the persistence of species and species guilds which experience narrow niches in their life history.

Keywords: Dung Beetle, Grassland Proportion, Restoration, Aphodius, Geotrupes, Abundance, Semi-Natural Grassland, Scarabaeidae, Metapopulation, Habitat Fragmentation, Landscape Ecology

Popular science summary

Dung beetle diversity & abundance persistence depend on surrounding grassland proportion

Conservation programs are important to preserve the co-evolved species pool in the cultural landscapes which where globally shaped up ever since the Neolithic and Bronze Age pastoralism & agriculture. Exceptionally species rich systems are the cultural landscapes such as grasslands, meadows and semi-open woodlands, whose characteristic ecological feature is facilitation of the open to semi-open contiguous habitats for the diverse flora and fauna persistence. Optimal management continuity is necessary for maintenance of these biota, however the post war period abandonment had led to drastic shifts in the ecological characters of these landscapes.

European Agri-environmental schemes are focusing on the conservation of these endangered organisms through restoration measures. Beyond the local habitat scale measures for conservation, ecologists since recent decade emphasizing the need for landscape scale conservation measures through the investigation about landscape moderated patterns and processes in retaining biodiversity of these heterogeneous habitats. Among the diverse taxa, dung beetles of semi-natural grasslands suffer very rapidly due to the loss of management continuity and habitat loss & fragmentation, since they depend on the relatively rapidly degradable dung resource which is supplied by the grazing management practices of cultural landscapes by humans. Especially pasture specialist dung beetles with patchy distribution which co-evolved along with the semi-natural grasslands may suffer largely due to habitat fragmentation. For retaining the species richness and abundance of the dung beetles in the semi-natural grasslands it is very important to also conserve the heterogeneous habitats (meadows, forests, grassland proportion) which acts as the source for the dung beetles into pastures and vitally diverse domestic animal dung resources such as cow, horse, sheep etc.

Dung beetles since they depend on short living dung resources they migrate from one local habitat to the other habitat for foraging, therefore the population in one single pasture is not isolated completely from the surrounding (matrix) diverse/heterogeneous habitats and mainly surrounding semi-natural pastures. In this study to understand how the restoration success of dung beetles is determined or moderated by the proportion of grasslands in surrounding landscapes, I sampled 200 dung pats from 10 pairs of semi-natural pastures around Uppsala, during species rich seasons namely early summer (4 pairs) and late summer (6 pairs). Each pair consisted of a restored and a continuously managed pasture.

In total there was 4784 beetles belonging to 17 species (*Aphodius and Geotrupes*) and 14 functional groups. Of this total number of beetles two generalist habitat species *A. rufipes* and *A. rufus* itself contributed 2664 individuals. The statistical analysis showed population of *A. fossor* (a pasture specialist species) and domestic feeder functional group was higher in population only at continuously managed pastures,

i.e. probably restoration process needs some more years to reach the population turnover similar to continuous landscape. Many generalist dung beetle population confounds to form metapopulation dynamics that are positively influenced by the grassland proportion at 1km radius and some only in the presence of habitat management. Whereas grassland proportion at 5km radius had influence on various individual species abundance both in the presence and absence of management type.

This study concludes that, surrounding grassland proportion influences the local dung beetle abundance and the restored grassland has a delay in recovery of the population abundance of pasture specialists and intermediate species guild similar to continuously managed pastures. Further research is needed to increase the understanding about the persistence of species and species guilds which experience narrow niches in their life history.

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1 Introduction

Globally, since the innovation of farming, the agricultural land use had co-evolved diverse strategies of managing farming associated semi-natural habitats, with adaptation to the local environmental conditions and thereby facilitating the diversification of local species pool. The natural (pristine) habitat dependent native wildlife species pool had adapted to the analogous habitat i.e. semi-natural habitat (Poláková *et al.*, 2011). Among the various rich ecosystems on this earth, the semi-natural habitats associated with these centuries old agricultural landscapes are highly threatened and facing huge biodiversity loss, due to habitat fragmentation, abandonment of the landscapes as well as loss of diverse habitat management practices by local communities (Batáry *et al.*, 2011), which may have cascading effect on its own ecosystem services as well as on neighboring natural habitats (Tscharntke *et al.*, 2012).

In Europe, Agri-Environmental schemes are introduced by the European Union, to promote the conservation of biodiversity and ecosystem services. Similarly, various countries are also involved in schemes to compensate farmers, for their semi-natural habitat management measures (Poláková *et al.*, 2011). Among the various semi-natural habitats, different types of grasslands are very important, both for its conservation value as well as for its ecosystem functional value for adjacent arable fields. Temperate European grasslands have richly diverse flora and fauna at the scale of local habitat itself, for example high richness of vascular plants is found even at a few square centimetres to one square metre (Pärtel *et al.*, 2005). Decline of semi-natural grassland area is due to development of more efficient grassland farming in cultivable lands, urbanization and re-forestation (Cousins, 2009; Eriksson & Cousins, 2014), which resulted in highly fragmented semi-natural grasslands. Thus in this study semi-natural grassland is chosen for testing the efficiency of landscape scale management.

Historically the ecological management focus was on the patch scale. There is however a need to broaden the focus to the landscape scale using Island biogeography (MacArthur & Wilson, 1963, 1967) and metapopulation theory (Levins, 1969; Hanski & Gilpin, 1991; Hanski & Ovaskainen, 2003), to find integrated solutions to the conservation goals like protecting local habitat sensitive species, increasing local biodiversity across different taxa and functional groups, promoting landscape-wide biodiversity and attached ecosystem services (Tscharntke *et al.*, 2012). Understanding the role of landscape complexity and characteristics over the biodiversity patterns and ecological process of the severely disturbed high natural value landscapes/habitats is important step in evolving the landscape moderated agri-environmental schemes. Only such evolved landscape-moderated agri-environmental schemes would result in effective strategies for conservation of biodiversity and ecosystem services management (Tscharntke *et al.*, 2012). Landscape complexity has larger effect on the beta biodiversity than on alpha biodiversity, which could be key beneficial factor in the terrestrial habitats where distinct alpha biodiversity would contribute to the landscape scale functional diversity and species-pool insurance (Batáry *et al.*, 2011; Tscharntke *et al.*, 2012). But such luxury of species pool insurance is not there for the biodiversity that is predominantly depends on the human management of the landscape.

One of the best examples for the organisms that depends on the human management of landscapes is dung beetles. Unlike other organisms, insects that depend on ephemeral resources like, domestic animal dung in the pastures would undergo local-extinction if those resources were absent due to the abandonment of cattle grazing in semi-natural grasslands. Such endangerment/extinctions had already happened vastly for many rare species (Gärdenfors, 2010) dependent on co-evolved cultural landscape management practices, hence to conserve at-least the remnant dung-beetle species and its populations, it is necessary to have landscape-moderated strategy of landscape scale management strategies by humans in agro-environments.

So this study tries to understand the effect of agro-environmental management measures like restoration of semi-natural grasslands on local dung beetle population, using the landscape moderated management concepts. I study the effect of habitat management (restoration & continuous management) and the proportion of grasslands (in the surrounding landscape), over the local semi-natural grassland habitat's dung beetle species richness and abundance. Also I study how the variable "time since restoration" affects the dung beetle population. In addition, I try to understand how the various functional guilds (such as habitat guilds, diet guilds, microclimate guilds, season guilds and size guilds) are affected by the grassland management type, proportion of grassland and time since restoration.

I predict that the dung beetle abundance and richness to increase with the increase in proportion of grassland in surrounding landscape because of decreased landscape isolation. And similarly the restoration measures would increase the immigration and colonization of dung beetles into the restored pastures. The increasing time since restoration would increase the abundance of dung beetle species and its richness. In the case of functional guilds, I predict pasture specialist species of local population would increase as the result of proportion of grassland increases in the surrounding landscape.

1.1 Status of semi-natural grasslands in Sweden

In Sweden the system of outfield grazing and management was prevalent until the mid -20th century or early 20th century until the introduction of high intensive technology (Introduction of tractors for tilling and the resultant decrease of horses), artificial fertilizer based production of ley & grain fields and forestry development in the Sweden, which resulted in 90 % decline in semi-natural grasslands due to abandonment, which they eventually transformed into forest (Eriksson *et al.*, 2002; Kiviniemi & Eriksson, 2002). Various studies on land use histories and species richness have revealed that management continuity and land use history played a vital role in maintaining the biodiversity (Eriksson *et al.*, 2002; Öckinger *et al.*, 2006) .

The various taxa respond individualistically to the different changes to the semi-natural grasslands and so far many studies carried out in Sweden have been focusing on the plants, (Söderström *et al.*, 2001; Kiviniemi & Eriksson, 2002; Lindborg & Eriksson, 2004) birds (Part & Soderstrom, 1999) and insects like ants (Dahms *et al.*, 2010) & butterflies (Öckinger & Smith, 2006). In this study I focus on another new group of insects which depend distinctly on ephemeral dung resource (Finn, 2001) and hence in recent decades it is also highly being recognized as the model organism group in applied ecological research, i.e. Dung beetles (Söderström *et al.*, 2001; Vessby, 2001; Nichols & Gardner, 2011).

If landscape-scale processes are important for the conservation of biodiversity, then Agri-environmental schemes should include the landscape moderated management (by conservation authorities) in addition to the various agricultural management of the local habitat. The landscape moderated management, will take into account the effect of isolation of the source and sink habitats, composition of landscape matrix on local species pool, to understand the various dynamics that determine the local and landscape scale population of dung beetles. Therefore, in this study I have assessed the effect of grassland management (restoration/continuous management) as well as the landscape composition (Proportion of Grassland in 1km and 5km radius) on the local population of the dung beetles. The second objective is to check the efficiency of Agri-environmental management of Semi-Natural grassland i.e. restoration over the period of years.

1.2 Dung beetles

Animal droppings are the nutritionally rich ephemeral resource patches and micro-habitats, which are exploited by some group of insects with varying breeding behavior. *Scarabaeidae* family includes the true dung beetles belonging to subfamily *Aphodiinae* and *Geotrupinae*. Also relatively smaller species like *Hydrophyllidae*, *Staphylinidae* and *Histeridae* are also seen in high numbers (Hanski, 1991b). In the north temperate regions, the small *Aphodius* species dominates the dung patches also co-exists with small number of larger *Geotrupes*. Researches so far revealed that, among northern temperate beetles the interspecific competition is lesser among the species of *Aphodius* and *Geotrupes* (Hanski, 1991a; Roslin & Viljanen, 2011). The species richness patterns of the northern temperate dung beetles could be more explained by the evolutionary and bio-geographical processes, for example; the dung beetle species in southern Finland are those which prefer warmer climate and northern Finland species prefer cooler climate, which can also be seen in the cooler southern mountains (Roslin & Viljanen, 2011). Thus the disturbances created by humans, influence drastic changes in the structure and composition of the assemblages due to the changes to the complexity of microclimates or vegetation. Hence dung beetle communities were widely used as the model organism to study landscape scale processes and patterns, also because of their amenability for both monitoring as well as the experimental studies (Gittings *et al.*, 1994; Gittings & Giller, 1997; Roslin & Koivunen, 2001; Finn & Gittings, 2003). Also for the assessment of landscape scale behavior of dung beetles many studies have been reported in the recent decade (Roslin, 1999, 2000, 2001a; b; Rosenlew & Roslin, 2008).

2 Materials and methods

2.1 Study area

All semi-natural grassland pastures included in this study are located in Uppsala County & Västmanland County and each restored pasture is paired with a continuously managed pasture and it was also sampled on the same day along with the restored pasture, this constitutes a single “site pair” (See Table 1).

In this study, totally I had sampled at 6 distinct locations (see Figure 1), from which there were 8 distinct “pasture pairs” (See Table 1). There was in total 8 distinct continuously managed pastures and 7 distinct restored pastures were sampled. These 7 distinct restored pastures, represents 1 to 16 years range for the variable “Time since restoration”. Among the total 10 site pairs studied, first six pairs belong to Early Summer (ES) and other six pairs belong to High Summer (HS) sub-seasons (See Table 1).

There were constraints to choose patches for this study, which had to be decided based on the conditions such as fresh (2 or 3 Days prior to sampling) cattle grazing for availability of fresh dung pat during every event of sampling “site pair” in the specific location. In addition, the sampling cannot take place while it’s raining. Due to these constraints, replication of same pastures for sampling in early and high summer was not possible. Instead, similar (w.r.t patch area) pastures located around the early summer pastures where selected owing to above said constraints of sampling.

Out of the total 4 distinct sites sampled during early summer 3 restored (M20R, M16R & M15R) and 2 continuously (M20C & M15C) managed patches were repeatedly sampled again in high summer sub-season (See Table 1). The continuously managed patches of sites, M16 and M10 where sampled in high summer sub-season by substituting with similar sized continuously managed patches. Also the restored patch of M10 site is substituted with alternate patch in high summer sub-season. The sites M14 and M27 where sampled only during high summer sub-season.

2.2 Sampling method

A total of 10 site pairs were sampled and among which first four belongs to early summer (Henceforth “ES”) sub-seasons and the next six site pair were of high summer (Henceforth “HS”) sub-season samples. The rationale of choosing the early summer and high summer sub-seasons are based on the previous study of Finn *et al.*, (1998, 1999) on *Aphodius* sub-seasonal assemblages, also Vessby *et al.*, (2002) recommended that the sampling of early summer sub-seasonal assemblage sampling would be having maximum species richness and carries the representative species of maximum sub-seasons. Each “site Pair” sampling (See Table 1) had the design of collecting samples from both continuously & restored semi-natural grassland pastures on the same day.

The sampling was conducted only during sunny days and the 10 randomly distributed full sized pats were collected from each pastures i.e. 20 pats for each “site pair” and totally 200 pats where collected. Since the beetles attracted to pats only few days after dropping, the pat samples were carefully collected based on physical appearance (See Figure 2), i.e. fresh looking wet dung pats (Roslin & Koivunen, 2001). And in the pastures where dung pats are scarce, the pats available in the single closest location was collected and made up for 10 pats. The collected pats were carefully packed into 2-liter polythene bags along with the 2 to 4 cm soil below the pats to collect the soil dwelling beetles. Collected pats were transported to the laboratory in the same day and stored inside the 4 °C cold room until the pats where processed for beetle collection. The stored pats were processed for separating beetles within 2-3 days. The beetles were separated from dung pats by immersing the pats into the bucket of water. Also this method of dung beetle collection found to be 95 % efficient (Koskela & Hanski, 1977).

2.3 Identification of beetles

The collected beetles from each pat were cleaned & stored in 70% ethanol tubes. The preserved beetles were identified using the Swedish dung beetle identification key (Ljungberg & Hall, 2009). A recent paper by Miraldo *et al.*, (2014), unequivocally proved the distinctness between the two species *A. pedellus* & *A. fimetarius.* This has not been accounted in our identification process and hence it’s important note that, our *A. pedellus* abundance data might include individuals of the both species.

2.4 Dung beetle functional guilds

The co-occurring *Aphodius* and *Geotrupes* were classified into various functional guilds (Fauth *et al.*, 1996) based on the following characteristics: habitat selection (Roslin, 2001a; Roslin & Koivunen, 2001; Isaksson & Vessby, 2006), micro-climatic preferences (Landin, 1957; Landin, 1961), diet preferences (Isaksson & Vessby, 2006), seasons (Landin, 1957; Landin, 1961; Ljungberg, 2006) and Size guild is chosen as the functional guild (Hanski & Cambefort, 1991; Barragán *et al.*, 2011) (see Table 2).

Table 1. *Dung beetle sampling design and time since restoration of restored pastures.*

Site Pair	Sub-Seasons	Name of "Sampling Location" (6 distinct)	Name of "Pasture Pairs" (8 distinct)	Restored Pastures (7 distinct)	Continuously Managed Pastures (8 distinct)	Date	Co-ordinates of Restored Pastures		Time Since Restoration (Yrs.)
							X	Y	
1	ES-Early Summer	**M20 Ahlezons hage**	**M20 Ahlezons hage**	M20R	M20C	2012-06-15	6670468	1679654	3
2		M16 Södra Lunger	M16 Södra Lunger 1	M16R	M16C-1	2012-06-19	6577022	1493470	5
3		**M15 Tyringe**	**M15 Tyringe**	M15R	M15C	2012-06-19	6577251	1506161	9
4		M10 Sjöängen Ängsö	M10 Sjöängen Ängsö 1	M10R-1	M10C-1	2012-06-27	6601569	1560300	1
5	HS-High Summer	**M20 Ahlezons hage**	**M20 Ahlezons hage**	M20R	M20C	2012-07-06	6670468	1679654	3
6		M14 Reutersberg	M14 Reutersberg	M14R	M14C	2012-07-11	6587670	1509611	5
7		**M15 Tyringe**	**M15 Tyringe**	M15R	M15C	2012-07-18	6577251	1506161	9
8		M27 Forsbacka Rimbo	M27 Forsbacka Rimbo	M27R	M27C	2012-07-24	6632151	1635742	11
9		M10 Sjöängen Ängsö	M10 Sjöängen Ängsö 2	M10R-2	M10C-2	2012-07-25	6601569	1560300	16
10		M16 Södra Lunger	M16 Södra Lunger 2	M16R	M16C-2	2012-07-30	6577022	1493470	5

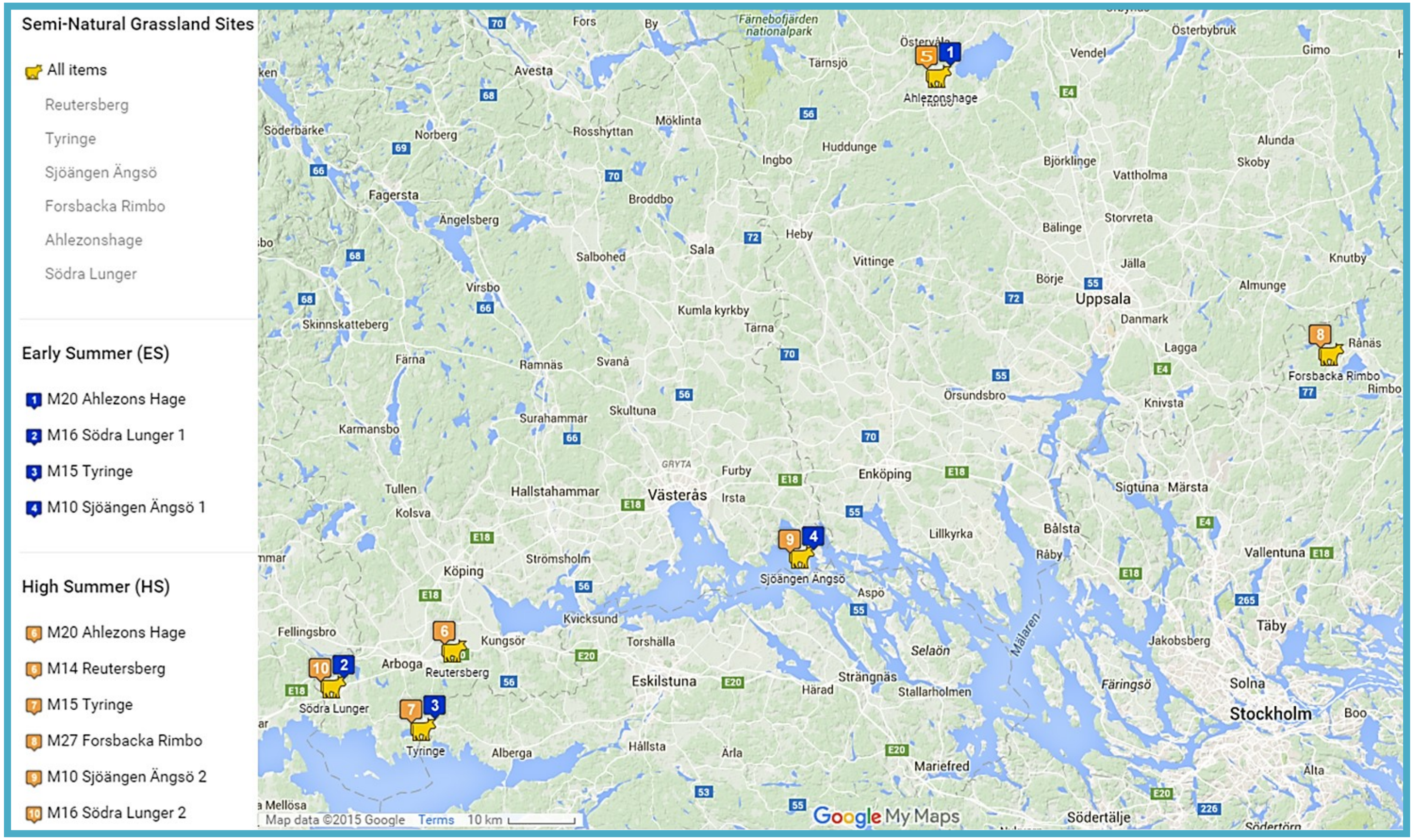

Figure 1. Map showing dung beetle sampling locations and respective sub-seasons (Each sampling pair (1-10) has 1 restored and 1 continuously managed as constituent pastures)

Figure 2. Physical appearance of dung pats

2.4.1 Habitat guilds

The functional guild based on habitat are divided as follows (Roslin, 2001a; Roslin & Koivunen, 2001) (see Table 1). (1) "Generalists", species which breed or feed regularly in all kinds of habitat. (2) "Pasture specialists", are exclusively found on open pastures; (3) "Pasture preferring intermediate species" are more common in open pasture habitats than in shady forests, but it is often found in both habitats. (4) "Forest specialists", species are which mostly reproduce in shady habitats but the adults are found often in open pastures.

2.4.2 Diet guild

The dung beetles found only in the dungs of domestic animals such as horses, cattle and sheep are classified as domestic feeder (DF) functional guild and species which are found in all types of dungs from domestic animals, game animals and other forest animal dungs are classified as generalist feeder (GF) functional guild (see Table 2) (Landin, 1957; Landin, 1961; Isaksson & Vessby, 2006; Ljungberg, 2006).

2.4.3 Microclimate guilds

The dung beetles where classified based on their functional micro-climatic preferences as eurytopic, oligotopic and stenotopic (Landin, 1957; Landin, 1961). The stenotopic species are the ones restricted to single kind of environment, oligotopic are the ones found preferably in certain kinds of habitat but not exclusive to them. Eurytopic are the ones found in all kinds of habitats (see Table 2). According to Landin's (1961) study it includes only *A. zenkeri* as the stenotopic species, which is restricted to forests due to its limited tolerance to high temperatures, therefore except stenotopic classification, the other two micro-climatic guilds are included in this study.

2.4.4 Season guilds

The seasonal sub-assemblages of Aphodius are whether effectively be maintained by the respective interspecific competitions, that must be resolved by studying these assemblages as sub-seasonal groups (Finn *et al.*, 1998). The season guilds are classified based on the occurrence of dung beetles in various periods of the season, such as spring (March-April), Early Summer (May-June), High summer (July-August), late summer (sept) and Fall (October-November) (Landin, 1957; Landin, 1961; Isaksson & Vessby, 2006; Ljungberg, 2006). The species occur in all seasons are divided as generalist season species, the species which occur in spring, early summer, late summer and fall as spring specialist and the species which found only in early summer to high summer are classified into Summer specialist (see Table 2) functional guild.

2.4.5 Size guilds

Given the size being very important functional characteristics for the dispersal ability (Roslin, 2000), understanding these guilds are very important for assessing the effectiveness of landscape moderated management measures. The dung beetles whose maximum size (length) is between 5-7 mm are classified as small beetles and between 8 – 13 mm are classified as big beetles (Hanski & Cambefort, 1991) (see Table 2).

Table 2. *Dung beetle species functional guilds*

Sl.No.	Species	Size (mm)	Max (mm)	Size Guild	Diet Guild[1]	Habitat Guild[2]	Micro-Climate	Season Guild[3]
1	*Aphodius borealis_ nordlig dyngbagge*	3 to 4,5	4,5	Small	GF	FS	Oligotopic	SS
2	*Aphodius merdarius _ streckdyngbagge*	4 to 4,5	4,5	Small	DF	PS	Oligotopic	SS
3	*Aphodius pusillus _ smådyngbagge*	3 to 4,5	4,5	Small	GF	PS	Eurytopic	SS
4	*Aphodius haemorrhoidalis _ rödspetsad dyngbage*	3.5 to 5	5,0	Small	DF	PPIS	Eurytopic	SmS
5	*Aphodius sticticus (A. equestris) _ hästdyngbagge*	4 to 5	5,0	Small	GF	PPIS	Oligotopic	SS
6	*Aphodius ater _ mattsvart dyngbagge*	4 to 6	6,0	Small	DF	PPIS	Eurytopic	SS
7	*Aphodius sphacelatus _ brämdyngbagge*	4 to 6	6,0	Small	GF	PPIS	Eurytopic	SS
8	*Aphodius prodromus _ vårdyngbagge*	4 to 7	7,0	Small	DF	PPIS	Eurytopic	SS
9	*Aphodius rufus (A. scybalarius) _ rostbrun dyngbagge*	5 to 7,5	7,5	Small	GF	G	Eurytopic	GSS
10	*Aphodius erraticus _ slät dyngbagge*	6 to 8	8,0	Big	DF	PS	Oligotopic	SmS
11	*Aphodius foetens _ rödbukig dyngbagge*	5 to 8	8,0	Big	DF	PPIS	Oligotopic	SmS
12	*Aphodius pedellus (A.fimetarius) _ rödvingad dyngbagge*	5 to 8	8,0	Big	DF	G	Eurytopic	GSS
13	*Aphodius depressus _ plattad dyngbagge*	6 to 9	9,0	Big	GF	G	Oligotopic	GSS
14	*Aphodius fossor _ stor dyngbagge*	8.5 to 13	13,0	Big	DF	PS	Oligotopic	GSS
15	*Aphodius rufipes _ aftondyngbagge*	9 to 13	13,0	Big	GF	G	Eurytopic	GSS
16	*Geotrupes stercorosus_ skogstordyvel*	12 to 19	19,0	Big	GF	FS	Eurytopic	GSS
17	*Geotrupes stercorarius_ fälttordyvel*	16 to 25	25,0	Big	DF	PPIS	Eurytopic	GSS

[1]Diet Guild: GF=Generalist Feeder, DF= Domestic Feeder (Landin, 1957; Landin, 1961; Isaksson & Vessby, 2006; Ljungberg, 2006)
[2]Habitat Guild: FS=Forest Specialists, PS=Pasture Specialists, PPIS=Pasture Preferring Intermediate Sps, G=Generalists (Roslin, 2001a; Roslin & Koivunen, 2001),
[3]Season Guild: SS= Spring Species, SmS=Summer Species, GSS=Generalist Season Species (Landin, 1957; Landin, 1961; Isaksson & Vessby, 2006; Ljungberg, 2006)

2.5 Proportion of grassland in the landscape

Semi-natural grasslands studied here are surrounded by landscape matrix, which is constituted of arable lands, forest, grasslands and human infrastructures. Grassland in the landscape matrix could be source for the populations into the local (restored pasture or continuously managed pastures) habitat, due to the availability of dung resources in those habitats. To understand the potential influence of the grassland proportion on the restoration measures carried through human moderated habitat management schemes (restoration or continuous management); in this study I included the grassland proportion as the single landscape matrix variable (See Table 3). For this study the landscape matrix radius was selected based on the dispersal ability of the dung beetles discussed in the previous studies as 1 Km (PG1kmR= Proportion of grassland in 1 Km radius) and 5 Km (PG5kmR= Proportion of grassland in 5 Km radius) (Roslin, 2001a; Roslin & Viljanen, 2011). The grassland proportion measures were obtained from previously existing database of semi-natural grassland restoration assessment project.

2.6 Time since restoration

Landscapes of the semi-natural grasslands need human moderation in maintaining the habitats, where the species that are specialised in these habitats could be able to get requisite biotic and abiotic local conditions. The landscapes, which don't get enough landscape management interventions, had undergone the process of abandonment, i.e. grasses and herbs are replaced by the succession of shrubs and trees, which alters the necessary abiotic and biotic local conditions. Agro-environmental schemes implemented in recent decade had enabled some of the farmers to restore the abandoned semi-natural grasslands. It's very important to understand how the dung beetles as an individual species or as a guild, respond to the time (in Years) since restoration. Therefore, in this study "Time since restoration" is taken as important variable and it ranges from 1 to 16 years for the sampled restored pastures.

2.7 Statistical methods

The species richness, total abundance, species specific abundance and functional guild abundance obtained from Early Summer and High Summer sampling of 4 "Site Pairs" and 6 "Site Pairs" respectively were analyzed in relation to the management type, proportion of surrounding grassland and time since restoration. In this study general linear model (GLM) and regression analysis were used to analyse the abundance and species richness data. The Early and High summer response variables such as species richness, total abundance, species-wise abundance and functional guild abundance, as well as the predictor variable “time since restoration” was natural-log (ln) transformed before including in the above said analysis (see Table 3).

Table 3. *Variables list and description*

Variable Name	Variable Type	df	Description
ES Site Pair	Random Variable	3	Site Pair 1 to 4 for GLM
HS Site Pair	Random Variable	5	Site Pair 5 to 10 for GLM
ln(ES Total Abundance)	Response Variable	3	For GLM & Regression Analysis
ln(HS Total Abundance)	Response Variable	5	For GLM & Regression Analysis
ln(ES Species Richness)	Response Variable	3	For GLM & Regression Analysis
ln(HS Species Richness)	Response Variable	5	For GLM & Regression Analysis
ln(ES Species-wise Abundance)	Response Variable	3	For GLM & Regression Analysis
ln(HS Species-wise Abundance)	Response Variable	5	For GLM & Regression Analysis
ln(ES Functional Guild Abundance)	Response Variable	3	For GLM & Regression Analysis
ln(HS Functional Guild Abundance)	Response Variable	5	For GLM & Regression Analysis
ln(ES Time Since Restoration)	Predictor Variable	NA	Regression Analysis
ln(HS Time Since Restoration)	Predictor Variable	NA	Regression Analysis
Habitat Type	Fixed Factor/Predictor	1	For GLM (Restored & Continuous)
ES PG1kmR	Covariate	1	For GLM
HS PG1kmR	Covariate	1	“Landscape Proportion”
ES PG5kmR	Covariate	1	(Proportion of Grasslands at 1 km Radius [PG1kmR] & 5 Km Radius
HS PG5kmR	Covariate	1	[PG5kmR])

NA=Not Applicable

General linear model (GLM) were analysed using the Minitab 16 software, the species richness and abundance data was taken as the response variable. The model included the Site Pair as random variable, habitat management type as the fixed factor and proportion of grassland as the covariate (See Table 3). The interaction between the proportion of grassland and habitat management type was analyzed by crossing the two factors, i.e. fixed factor and covariate in the models (see Table 4). Only the variables which are having p-value < 0.05, was included in the results and the variables which has p-value between 0.1 – 0.05 were discussed as the trend. Since the PG1kmR and PG5kmR are strongly correlated, these two covariates were not used together in any of the models.

The models listed in the Table 4 are the five models, which was tested for all the response variables mentioned in the Table 3. The significance of the model containing the habitat alone, determines that habitat management measure influenced the response variable. The positive or negative effect/slope of the significant response variable is discussed in the results as effect in restored pastures. Positive slope is considered as that the restoration measure carried out has increased the abundance of the response variable tested and vice versa for the negative slope. In the model that contains both fixed factor "habitat" and covariate "proportion of grassland", the significance of the covariate means that, this specific response variable's abundance is influenced by the proportion of grassland in specific radius of landscape matrix. The final model which contains, fixed factor, covariate and their interactions in which the significant interaction between covariate and fixed factor indicates that, the habitat management measure has the effect on the abundance of the response variable in the presence of influence from grassland proportion at the specific radius of the landscape matrix.

Table 4. *Models list for general linear model (GLM)*

Response Variable	=	Random variable + Fixed Factor + Covariates + Fixed FactorXCovariates
ln(ES Total Abundance)	=	Site Pair + Habitat + Grassland Proportion + HabitatXGrassland Proportion
Y	=	Site Pair + Habitat
Y	=	Site Pair + Habitat + PG1kmR
Y	=	Site Pair + Habitat + PG5kmR
Y	=	Site Pair + Habitat + PG1kmR + PG1kmRXHabitat
Y	=	Site Pair + Habitat + PG5kmR + PG5kmRXHabitat

Regression analysis (Crawley, 2012b) between the predictor variable (i.e. natural log transformed) "time since restoration" and response variables were done using the R version 3.1.3 (Team, 2015) From the obtained results the p-values less than 0.05, were taken as significant values and p-values between 0.1 and 0.05 is interpreted as a trend in the discussion. The significance of the regression analysis between the Time since restoration and the abundance indicate that, whether the duration of restoration management in the restored pastures is influencing the increase or decrease of the dung beetle populations in local habitat.

The graphical scatterplot presentations (Crawley, 2012a) of the statistically significant or marginally non-significant (>0.1) response variables of GLM and regression analysis were made using the R version 3.1.3 (Team, 2015).

3 Results

3.1 Response of total abundance and species richness to habitat management and grassland proportion

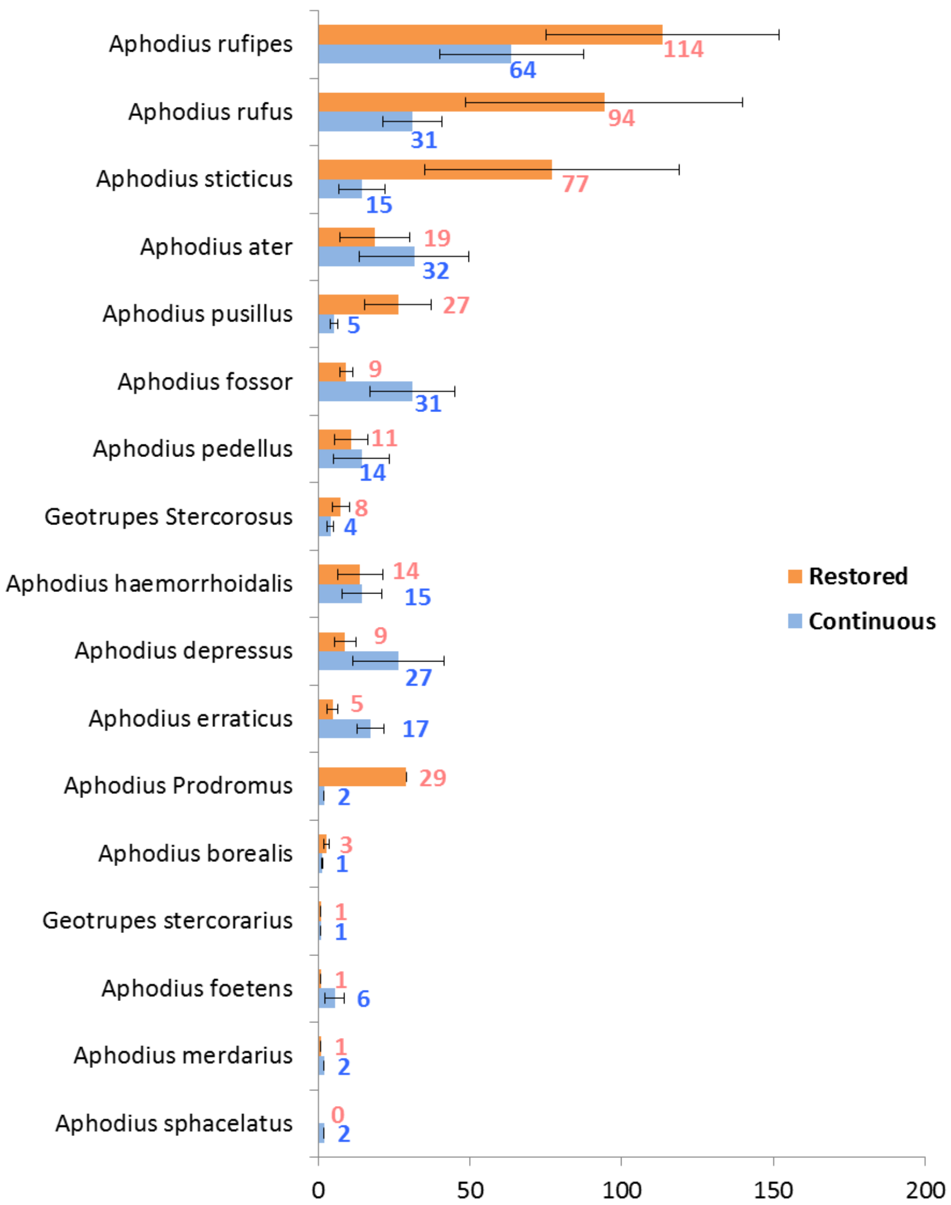

Figure 3. Mean abundance of dung beetle species per pasture

The sampling of the total 10 "Site Pairs" conducted at the respective semi-natural grasslands yielded 4784 beetles from 200 pats in which continuous & restored pastures had 2014 & 2770 individuals respectively (See Figure A17 & A18). The species richness of the continuously managed pastures is 17 and for the restored is 16, i.e. totally 17 species were identified in this study (See Figure A19) belonging to two different genera (*Aphodius* and *Geotrupes*). Out of these seventeen species, *A. merdarius* is a rare species. And among the total abundance, exceptionally the two-generalist species *A. rufipes* and *A. rufus* (See Figure 3) made up more than half of the total abundance (2664 individuals).

Table 5. *GLM for total abundance and species richness (The response variables "Species Richness" and "Total Abundance" tested against the Habitat Management (Fixed Factor), Grassland Proportion (Co-Variates) and their interaction. The significant values [i.e., < 0.05] &trend values [i.e., 0.05 to 0.1] are highlighted by marking it bold)*

Response Variable (Y)	Predictor: Habitat R/C		Co-variates: Grassland Proportion				Interaction: Grassland Prop.*Habitat			
			PG1kmR		PG5kmR		PG1kmR		PG5kmR	
	F	P	F	P	F	P	F	P	F	P
ln(Total Abundance ES)	3.73	0.193	123.26	**0.008***	–	–	–	–	–	–
ln(Total Abundance ES)	159.30	**0.050**	–	–	130.81	**0.056**	–	–	145.28	**0.053**
ln(Species Richness ES)	0.00	0.992	2.95	0.228	–	–	–	–	–	–
ln(Species Richness ES)	6.11	0.245	–	–	2.43	0.363	–	–	4.50	0.281
ln(Total Abundance HS)	3.59	0.155	3.33	0.165	–	–	1.43	0.318	–	–
ln(Total Abundance HS)	2.30	0.204	–	–	2.18	0.213	–	–	–	–
ln(Species Richness HS)	0.76	0.448	–	–	0.68	0.471	–	–	0.80	0.437

"– "= Not Included, *= <0.05

The total abundance and species richness of both early summer and high summer samples were tested and among them only early summer total abundance shows strong statistical significance for PG1kmR covariate (F= 123.26, P= 0.008), in the non-interaction model. This indicates that the early summer local habitat abundance of dung beetles is influenced only by the dispersal from surrounding grassland habitat at 1km radius rather than habitat management type. The type of influence by the surrounding grassland habitat is shown by the slope of regression line in scatterplot (See Figure 4) as a positive effect of higher grassland proportion on local habitat dung beetle abundance. Whereas for the same early summer total abundance data, the interaction model containing covariate PG5kmR shows a trend of significance for all the model components such as Habitat management (F= 159.30, P= 0.050), 5km radius grassland proportion (F= 130.81, P= 0.056) and their interaction (F= 145.28, P= 0.053). This indicates that there is a possibility of dung beetle dispersal from the grassland habitats at 5 Km radius into the local habitat in the presence of specific type of habitat management.

On the other hand, the other response variables namely, high summer total abundance or early & high summer species richness are not statistically significant with any GLM's (see Table 5).

The linear regression of all the response variables i.e., ES-total abundance (F= 0.23, P= 0.682) and ES-species richness (F= 0.75, P= 0.478), HS-total abundance (F= 0.20, P= 0.677) and HS-species richness (F= 0.03, P= 0.864), was also tested against the predictor variable "time since restoration" of restored pastures, neither of them was statistically significant.

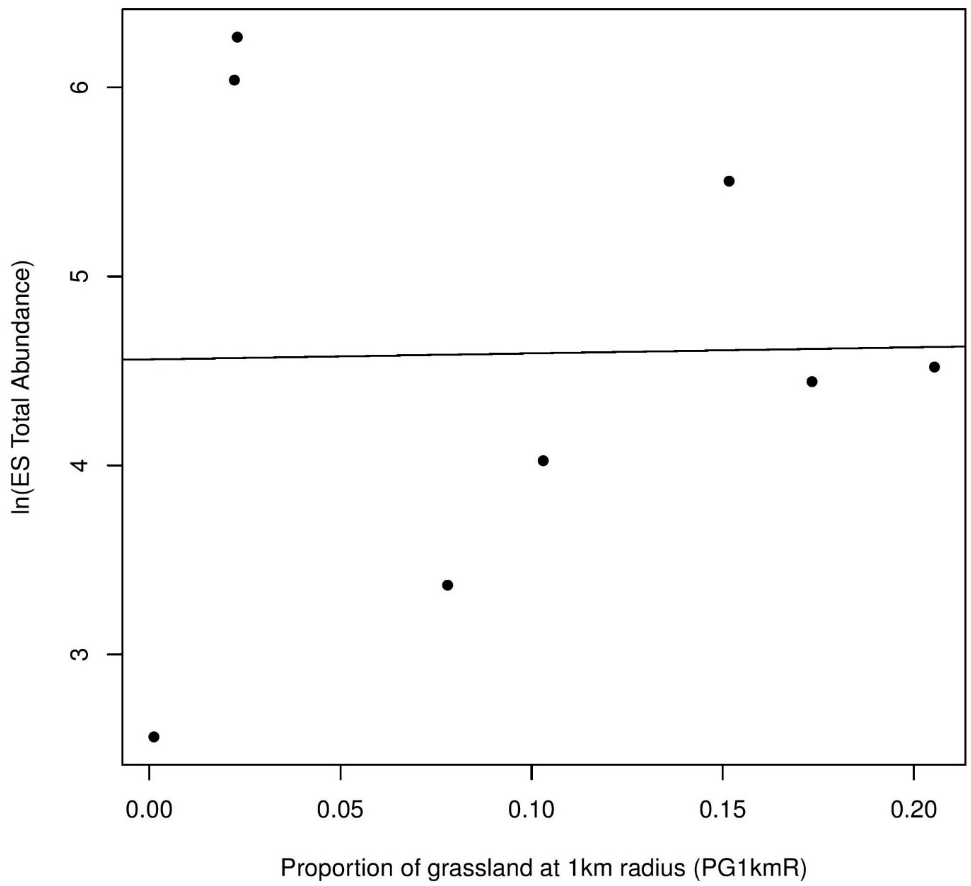

Figure 4. Scatterplot showing effect of covariate PG1kmR on ES total abundance

3.2 Response of species specific abundance to habitat management and grassland proportion

Overall only 7 species (See Figure 5) among the total 17 species showed either strong statistical significance or marginally non-significant results for GLM analysis. Whereas for the linear regression analysis of "time since restoration", none of the species were statistically significant.

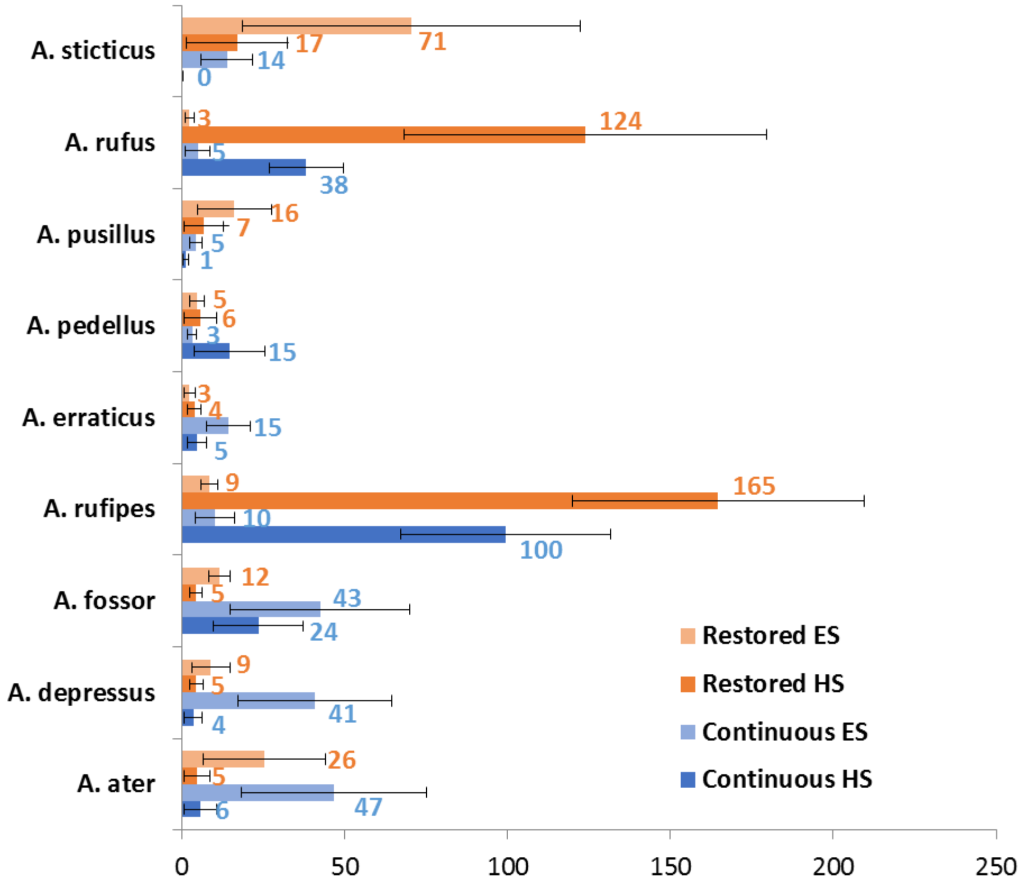

Figure 5. Sub-seasonal mean abundance for species-specific GLM

The abundance data of various relatively abundant large-bodied species (See Figure 3) such as *G. stercorosus*, and *A. haemorrhoidalis* was not responsive to any model containing main factors or interactions, in both GLM analysis as well as the linear regression analysis. Some more species such as *A. prodromus*, *A. borealis*, *A. foetens*, *A. merdarius*, *A. sphacelatus* and *G. stercorarius* were also not responsive to GLM models or regression analysis in this study, which could be reasoned to either lack of power in sample size of these species in the collected samples or the focused landscape variables didn't explain the spatial pattern of these specific species.

3.2.1 Species specific GLM models

Abundance of each species was tested individually with GLM, among them only statistically significant and marginally non-significant results were included in the Table 6.

Among the total 17 species only 5 species (4 HS & 1 ES and 5 PG5kmR) showed statistical significance to the GLM analysis (Table 6) (Figure 5) and 2 other species *A. depressus* and *A. pusillus* shows a trend of statistical significance. Among the total 7 species, some had statistical significance/trend only to the habitat management, some only for the influence of grassland proportion (at 1km radius or 5km radius) i.e. covariate and some only for interaction between the habitat management type and grassland proportion (Table 6).

Table 6. *GLM for species-specific abundance (The response variables "Species-Specific Abundance" tested against the Habitat Management (Fixed Factor), Grassland Proportion (Co-Variates) and their interaction. The significant values [i.e., < 0.05] &trend values [i.e., 0.05 to 0.1] are highlighted by marking it bold)*

Response Variable (Y)	Predictor: Habitat R/C		Co-variates: Grassland Proportion				Interaction: Grassland Prop.*Habitat			
			PG1kmR		PG5kmR		PG1kmR		PG5kmR	
	F	P	F	P	F	P	F	P	F	P
A. ater										
ln(*A. ater ES*)	6742.92	**0.008***	NA	NA	2362.20	**0.013***	NA	NA	4967.10	**0.009***
A. depressus										
ln(*A. depressus ES*)	40.55	**0.099**	NA	NA	17.39	0.150	NA	NA	33.45	0.109
A. rufipes										
ln(A. rufipes ES)	2.48	0.256	15.79	**0.058**	NA	NA	NA	NA	NA	NA
ln(*A. rufipes HS*)	3.39	0.139	NA	NA	12.59	**0.024***	NA	NA	NA	NA
A. pusillus										
ln(*A. pusillus HS*)	2.47	0.214	NA	NA	6.90	**0.079**	NA	NA	3.13	0.175
A. fossor										
ln(*A. fossor HS*)	6.19	**0.055**	NA	NA	NA	NA	NA	NA	NA	NA
ln(*A. fossor HS*)	10.76	**0.031***	NA	NA	2.87	0.166	NA	NA	NA	NA
A. erraticus										
ln(*A. erraticus ES*)	6.41	**0.085**	NA	NA	NA	NA	NA	NA	NA	NA
ln(*A. erraticus ES*)	17.79	**0.052**	4.31	0.173	NA	NA	NA	NA	NA	NA
ln(*A. erraticus HS*)	23.95	**0.016***	NA	NA	15.43	**0.029***	NA	NA	19.54	**0.021***
A. pedellus										
ln(*A. pedellus HS*)	5.20	**0.085**	NA	NA	22.33	**0.009***	NA	NA	NA	NA

NA=Not Applicable, *= <0.05

Among the 7 species listed in Table 6 its only two species, that atleast had a statistical trend for fixed factor (Habitat management) only model, they are domestic feeder species *A. fossor* HS (F= 6.19, P= 0.055) and *A. erraticus* ES (F= 6.41, P= 0.085). However, the statistical significance of habitat management (fixed factor) relatively increased in the presence of co-variates PG5kmR and PG1kmR for *A. fossor* HS (F= 10.76, P= 0.031) and *A. erraticus* ES (F=

17.79, P= 0.055) respectively. Also the sub-seasonal mean abundance (figure 5) of these species shows that the mean abundance of continuously managed pastures is higher than the restored pastures. This indicates that the local abundance of these species in their specific sub-seasons (HS *A. fossor* and ES *A. erraticus*) depends on the continuous habitat management and this effect further gets enhanced in the presence of higher proportion (See Figure A20) of surrounding grassland habitats. *A. depressus* abundance at early summer, shows a trend of statistical significance in the interaction model, for the influence of habitat management (fixed factor F= 40.55, P= 0.099) alone, this indicates probably the interaction between habitat management & 5km radius grassland proportion may increase its population at the local pastures. Also ES mean abundance of *A. depressus* shows that there is relatively higher abundance in the continuously managed grassland. Invariably every species that has either strong statistical significance or a trend of statistical significance have relatively higher abundance in the continuously managed grassland.

In high summer sub-season, *A. rufipes* (F= 12.59, P= 0.024), *A. pedellus* (F= 22.33, P= 0.009), and *A. pusillus* (F= 6.90, P= 0.079) shows either strong statistical significance or a trend of significance for the covariate PG5kmR. This indicates that there is dispersal or possibility of dispersal of these dung beetles from the 5km radius surrounding grassland habitats into local pastures through metapopulation dynamics. However, for these strongly significant first two species, the slope has contrasting pattern in their response to the grassland proportion gradient, while *A. rufipes* abundance increases as the grassland proportion increases (See Figure A21), the abundance of *A. pedellus* decreases with increase in proportion of grassland (See Figure A22). Finally, ES *A. rufipes* shows also a trend of statistical significance for covariate PG1kmR thereby implying the possibility of dispersal from the surrounding grassland habitats at 1km radius.

Two domestic feeders namely ES *A. ater* and HS *A. erraticus* has strong statistical significance for all the factors (fixed, covariate and interaction) in an interaction model (See Table 6) containing the PG5kmR covariate. The slope of these two species are in opposite direction as the grassland proportion increases. In the scatterplot, abundance of the early summer *A. ater* decreases (See Figure A23) and high summer *A. erraticus* increases (See Figure A24) with increase in proportion of surrounding grassland habitats.

To summarise, among the 7 species tabulated (Table 6), it's only *A. rufipes* that shows just a trend of statistical significance for the covariate PG1kmR, whereas all other species (except *A. depressus*) shows either a strong or a trend of statistical significance for the covariate PG5kmR and for some species in the presence of covariate PG5kmR in the model, that enhanced the statistical significance for habitat type (Fixed factor). Thus the grassland proportion at 5 km radius has relatively higher influence for the population dynamics of these specific species.

3.3 Response of functional guild specific abundance to restoration & grassland proportion

The abundance of each and every guild was tested with GLM and regression analysis. The results that were strongly significant and marginally non-significant (p<0.1) was included in the table 8. Among the total 14 functional guilds, there were species belonging to 13 guilds that had been collected in this sampling, and the missing stenotopic guild species restricted to forest habitats. Among the collected 13 functional guilds, it was only 6 guilds (5 ES & 1 HS and 5 PG1kmR & 1 PG5kmR) that had strong statistical significance, and 5 other guilds had a trend for statistical significance. As species specific models, none of the functional guild models were statistically significant for test of variables "Time Since Restoration".

Table 7. *GLM of functional guild specific abundance (The response variables "Functional Guild Specific Abundance" tested against the Habitat Management (Fixed Factor), Grassland Proportion (Co-Variates) and their interaction. The significant values [i.e., < 0.05] &trend values [i.e., 0.05 to 0.1] are highlighted by marking it bold)*

Response Variable (Y)	Predictor: Habitat R/C		Co-variates: Grassland Proportion				Interaction: Grassland Prop.*Habitat			
			PG1kmR		PG5kmR		PG1kmR		PG5kmR	
	F	P	F	P	F	P	F	P	F	P
HABITAT GUILD										
ln(Generalist Habitat ES)	0.16	0.729	59.93	**0.016***	NA	NA	NA	NA	NA	NA
ln(Generalist Habitat ES)	68.75	**0.076**	NA	NA	49.08	**0.090**	NA	NA	56.53	**0.084**
ln(Pasture Specialists HS)	4.58	**0.099**	NA	NA	2.29	0.205	NA	NA	NA	NA
ln(Pasture Specialists HS)	0.51	0.528	NA	NA	6.15	**0.089**	NA	NA	3.05	0.179
ln(Forest Specialist ES)	2.07	0.387	429.93	**0.031***	NA	NA	144.54	**0.053**	NA	NA
ln(Forest Specialist ES)	103.59	**0.062**	NA	NA	78.31	**0.072**	NA	NA	128.82	**0.056**
DIET GUILD										
ln(Domestic Feeder ES)	5.79	**0.095**	NA	NA	NA	NA	NA	NA	NA	NA
ln(Domestic Feeder HS)	8.23	**0.045***	NA	NA	2.39	0.197	NA	NA	NA	NA
ln(Domestic Feeder HS)	0.49	0.534	NA	NA	9.85	**0.052**	NA	NA	5.27	0.106
ln(Generalist Feeder ES)	1.83	0.309	26.47	**0.036***	NA	NA	NA	NA	NA	NA
MICROCLIMATE GUILD										
ln(Eurytopic ES)	4.35	0.172	58.05	**0.017***	NA	NA	NA	NA	NA	NA
ln(Eurytopic ES)	59.84	**0.082**	NA	NA	64.99	**0.079**	NA	NA	61.80	**0.081**
ln(Oligotopic ES)	0.15	0.735	26.07	**0.036***	NA	NA	NA	NA	NA	NA
SEASON GUILD										
ln(Generalist Season ES)	0.10	0.786	14.02	**0.065**	NA	NA	NA	NA	NA	NA
ln(Summer Species HS)	9.53	**0.091**	NA	NA	2.71	0.242	NA	NA	NA	NA
SIZE GUILD										
ln(Big ES)	0.55	0.535	16.10	**0.057**	NA	NA	NA	NA	NA	NA
ln(Big ES)	7.78	**0.068**	NA	NA	0.49	0.536	NA	NA	9.01	**0.058**
ln(Small ES)	0.60	0.520	8.74	**0.098**	NA	NA	NA	NA	NA	NA

NA=Not Applicable, *= <0.05

3.3.1 Habitat guild

The habitat functional guild is the most widely used tool in studying the landscape population structure of the temperate dung beetles. In this study there were samples belonging to all the four guilds (see Graph 3). Among the habitat guilds the generalist guild was most dominant in the pastures both restored and continuously managed. Restored pastures harbor higher abundance of dung beetles in all functional habitat guilds, than the continuously managed pastures, however the exception is pasture specialist guild. While the generalist species was higher in abundance during high summer season, all other habitat guilds had relatively higher abundance in early summer sub-season. Except pasture preferring intermediate species guild, all other guilds show response for GLM analysis (see Table 8).

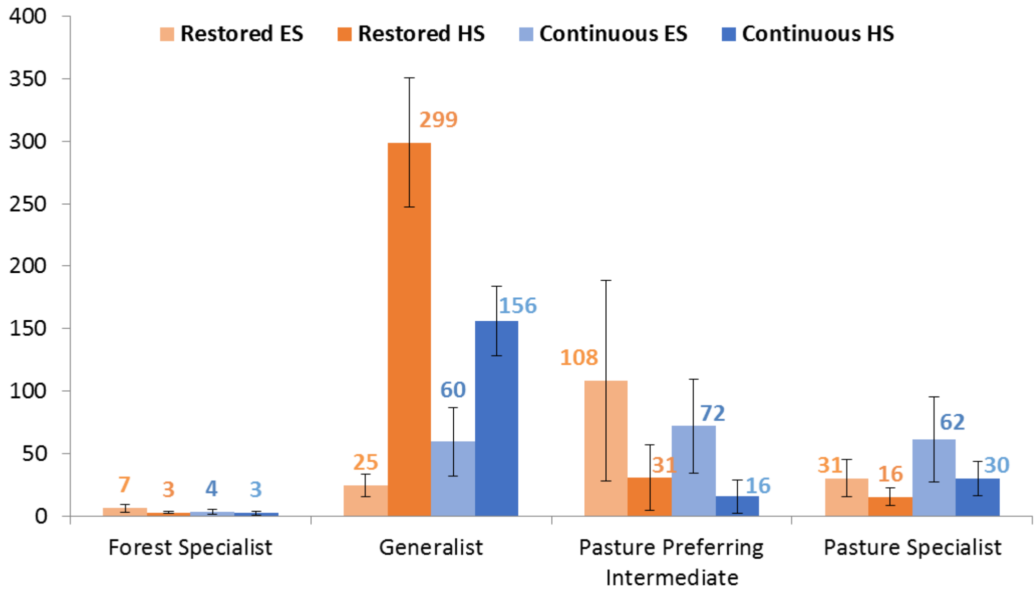

Figure 6. Sub-Seasonal mean abundance chart of habitat guild

GLM analysis of generalist habitat guild

Only ES samples of the generalist habitat guild was responsive to the GLM analysis. The model of this ES abundance with habitat and proportion of grassland as the main factors had statistical significance for the covariate PG1kmR (F= 59.93, P= 0.016). The scatterplot of the ES generalist species guild against the variable PG1kmR shows that the abundance of generalist species increases as the proportion of the grassland increases (see Figure 7). This indicates that the abundance of the ES generalist dung beetles in local pasture is influenced by the proportion of grassland at 1km radius of the surrounding landscape. Among species-specific GLM analysis, only ES *A. rufipes* (F= 15.79, P= 0.058) a generalist habitat species, showed similar response for the influence of PG1kmR covariate, however with weak statistical significance i.e. as a trend.

Interestingly the same ES generalist habitat guild also shows a statistical trend for all the factors in an interaction model containing PG5kmR as the covariate (See Table 8). Indicating that there is possibility of generalist dung beetle dispersal from the surrounding grassland habitat at 5km radius is as an influence of habitat.

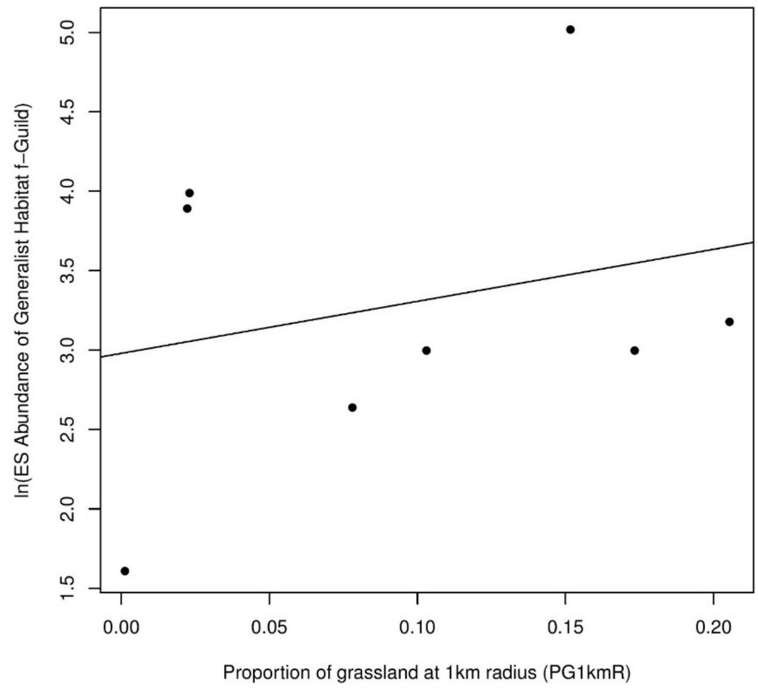

Figure 7. Scatterplot of ES generalist species guild abundance against the PG1kmR

GLM analysis of pasture specialist guild

The habitat management (F= 4.58, P= 0.099) had a statistical trend for HS abundance of pasture specialist guild, only in the non-interaction model that included covariate PG5kmR. And to the same model when interaction factor is included, the statistical trend had shifted to the covariate PG5kmR (F= 6.15, P= 0.089). Also this indicates that there is possibility for the influence of both habitat type and 5 km radius surrounding grassland proportion on the local pasture abundance.

It's also important to note that the species namely *A. pusillus*, *A. fossor* and *A. erraticus* constitutes the pasture specialist guild, and specifically high summer abundance of all these species had showed similar trend of or strong statistical significance for GLM analysis with covariate PG5kmR or its interaction factor. Probably the distinctness of *A. pusillus* from the other two species, contributes to the weaker statistical trend of high summer pasture specialist guild. The distinctness is that, while pusillus mean abundance is higher in restored habitats, the other two pasture specialists had higher abundance in continuously managed grassland with strong statistical significance for the habitat management only in the presence of covariate PG5kmR (Refer section 3.2.1).

GLM analysis of forest specialist guild

In the interaction model, the abundance of ES forest specialist guild was strongly significant for the covariate PG1kmR (F= 429.93, P= 0.031) and a statistical trend for interaction factor

(F= 144.54, P= 0.053). Also the scatterplot (See Figure 8) shows negative slope, as the proportion of the surrounding grassland habitat increases, there is a decrease in abundance of these species. This indicates that the, forest specialist species might depend on the dispersal from the other landscape components such as forest land proportion surrounding the local pastures.

The same ES abundance shows a statistical trend for all the factors in the interaction model containing the covariate PG5kmR. This again indicates the possibility of dispersal of ES forest specialist guild population into the local pastures only in the presence of specific type of habitat management. The response of the ES forest specialist for both the covariates PG1kmR and PG5kmR could be attributed to the dispersal behavior of *G. stercorosus* big species, and *A. borealis* small species, which has common trait of dispersal from forest habitats to pastures.

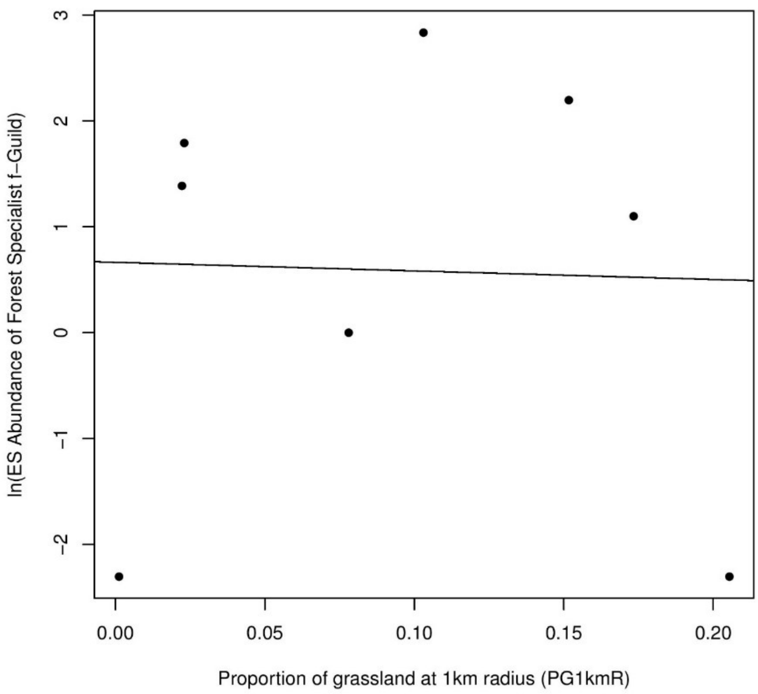

Figure 8. Scatterplot of ES forest specialist guild abundance against the PG1kmR

3.3.2 Diet guild

Among the two diet guilds, the domestic feeder abundance is lesser than the generalist feeder (See Figure 9). In the domestic feeder guild, the restored pasture abundance is lesser than the continuously managed pastures, whereas the generalist feeder abundance was higher in the restored pastures than the continuously managed pastures. Also sub-seasonal mean abundance is higher in early summer for the domestic feeder guild and for the generalist feeder mean abundance is higher for high summer season.

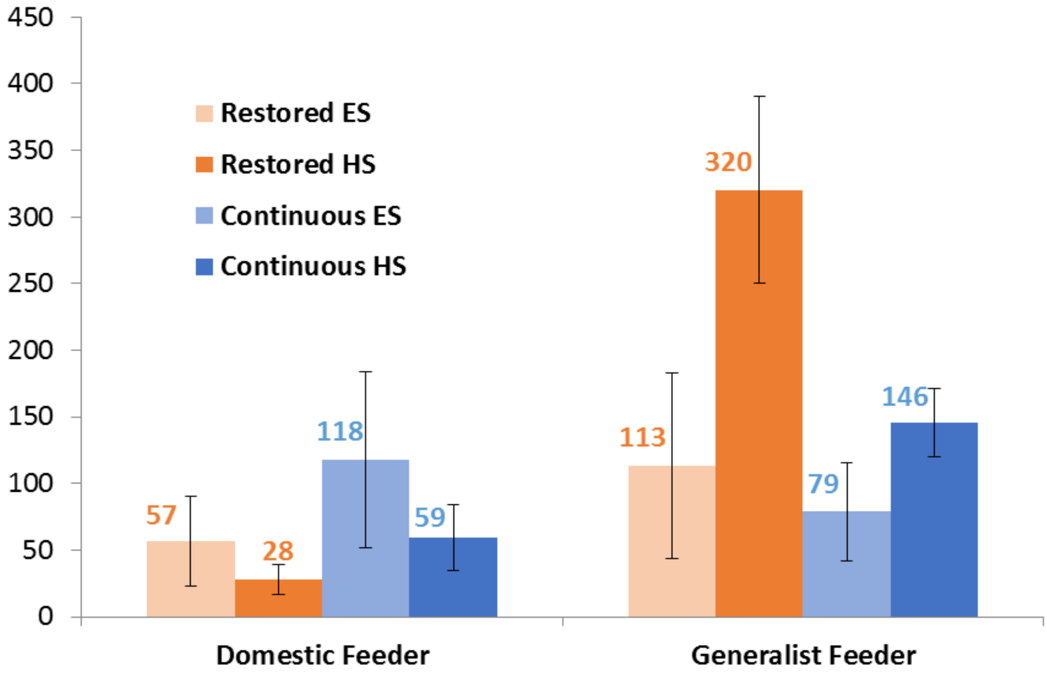

Figure 9. Sub-seasonal mean abundance chart of diet guild

GLM analysis of domestic feeder guild

The HS domestic feeder abundance was best predicted by the main factor habitat type (F = 8.23, P = 0.045), when covariate PG5kmR was also present in the model (See Table 8). And further when interaction factor is introduced to the same model, the habitat type is not statistically significant, whereas the covariate PG5kmR (F= 9.85, P= 0.052) shows a statistical significance trend. The scatterplot of high summer domestic feeder guild against the covariate PG5kmR has negative slope due to decrease in abundance as the proportion of grassland increases (See Figure 10). Even the ES domestic feeder guild has a trend of statistical significance for habitat type (F= 5.79, P= 0.095) in the simple model containing fixed factor alone. This indicates that in general the abundance of this guild at high summer season depends on the continuous habitat management type, and the presence of grassland habitats surrounding the local pasture has an effect on the local population.

GLM analysis of generalist feeder guild

The early summer generalist feeder abundance shows strong statistical significance to the covariate PG1kmR (F= 26.47, P= 0.036) in the model without the interaction factor (See Table 8). The scatterplot of the generalist feeder against the PG1kmR shows, the abundance in the local pastures increases with increase in the proportion of grassland at 1km radius of the surrounding landscape (see Figure 11). This indicates that the proportion of grassland in 1km radius of surrounding landscape influences the abundance of the generalist feeder.

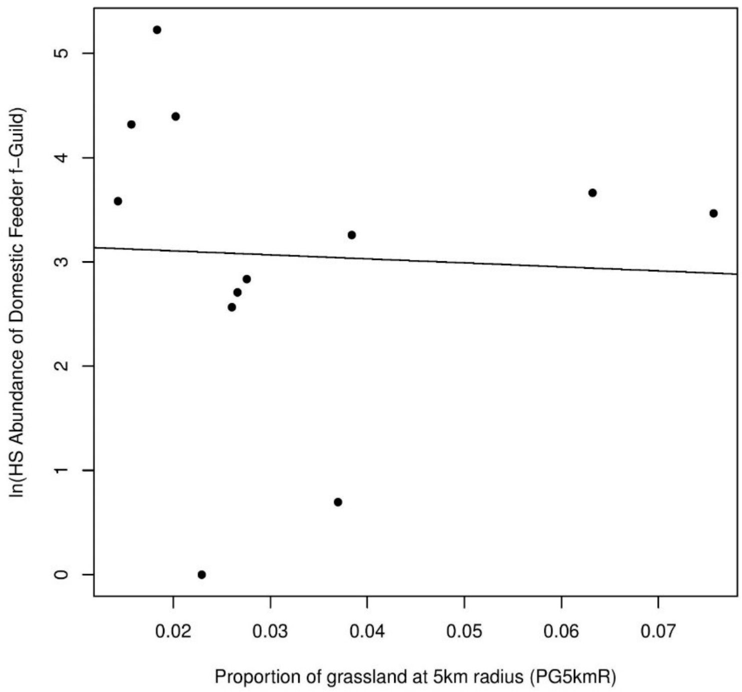

Figure 10. Scatterplot of HS domestic feeder guild abundance against PG5kmR

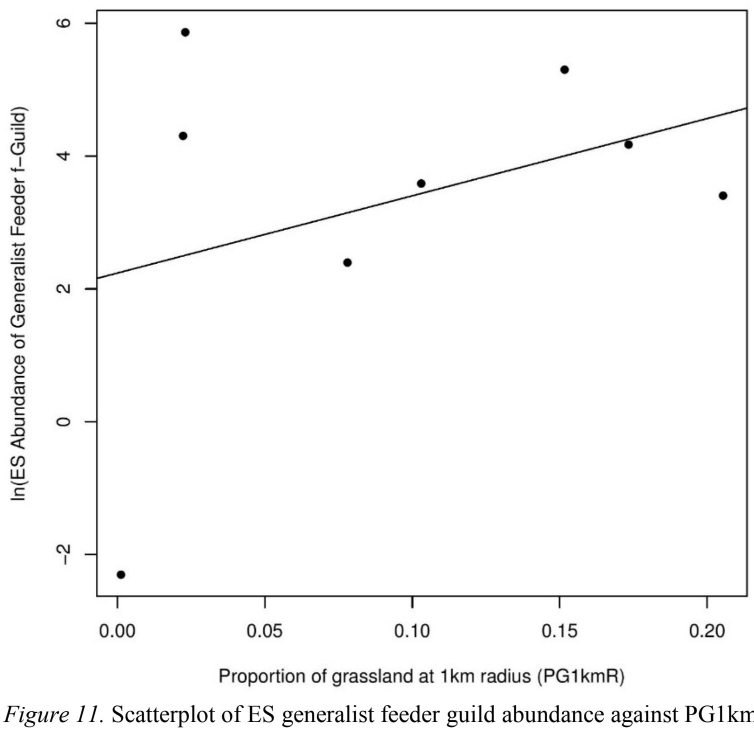

Figure 11. Scatterplot of ES generalist feeder guild abundance against PG1kmR

3.3.3 Microclimate guild

In comparison to the oligotopic guild, the eurytopic guild is highly abundant and also it has higher abundance in the restored pastures (See Figure 23), whereas the oligotopic guild has relatively higher abundance in the continuously managed pastures. For eurytopic guild higher abundance is at the high summer season and for the oligotopic guild it is at early summer season. Only the early summer abundance was responsive to the GLM analysis.

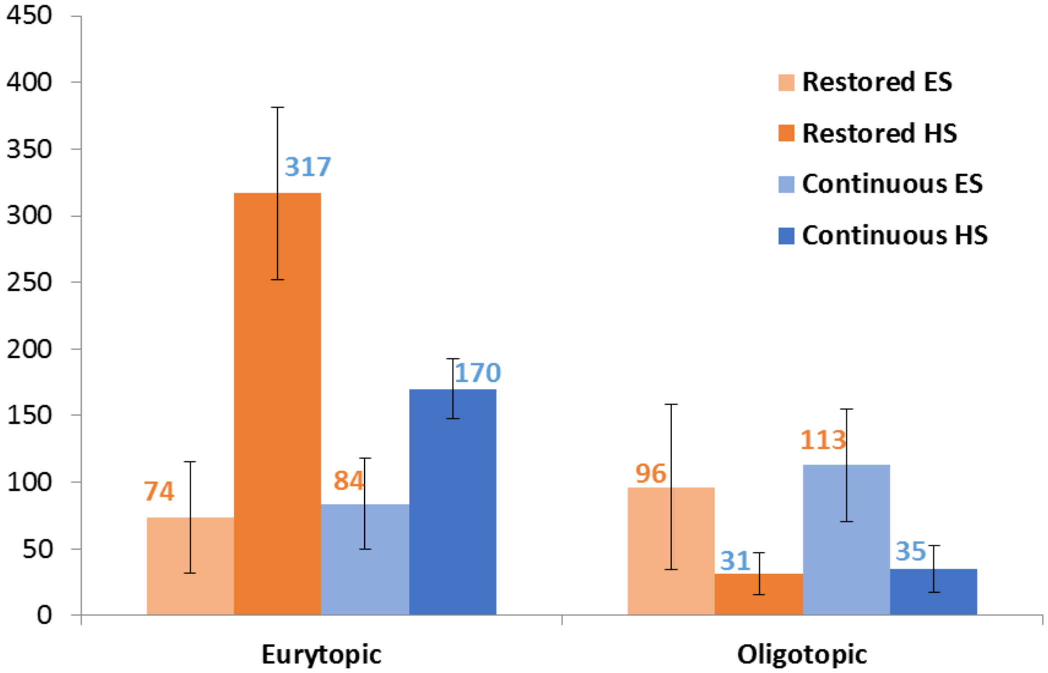

Figure 12. Sub-seasonal mean abundance chart of microclimate guilds

This pattern in abundance between the continuously managed and restored pastures is similar to the habitat and dung feeder guilds (cf. Figure 6, 9), i.e. eurytopic guild is similar to the generalist habitat & feeder guild, oligotopic guild is similar to pasture specialist and domestic feeder guild's abundance pattern.

When the ES eurytopic ($F= 58.05$, $P= 0.017$) and ES oligotopic ($F= 26.07$, $P= 0.036$) guild's abundance were analysed with GLM, both had statistically significance to the covariate PG1kmR, in the model without interaction factor (See Table 8). The scatterplots for these two guilds against the PG1kmR covariate, has contrasting slope, while the ES eurytopic has negative slope and the ES oligotopic has positive slope (See Figure 13 & 14). This indicates that both the ES eurytopic and ES oligotopic species has the effect of surrounding grassland habitat, on the local pasture abundance, and with increasing grassland proportion the abundance of former decreases and the latter increases.

The ES eurytopic guild also had shown a statistical trend for all the factors in the interaction model (See Table 8) containing PG5kmR covariate. This indicates that there is a possibility of surrounding grassland habitat at 5km radius having an effect on local pasture ES eurytopic population.

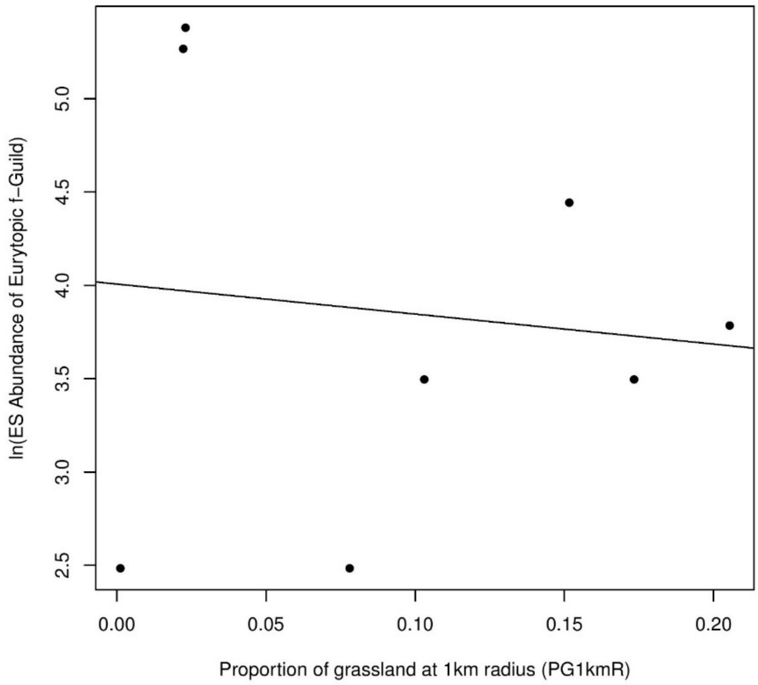

Figure 13. Scatterplot of ES eurytopic guild abundance against the PG1kmR

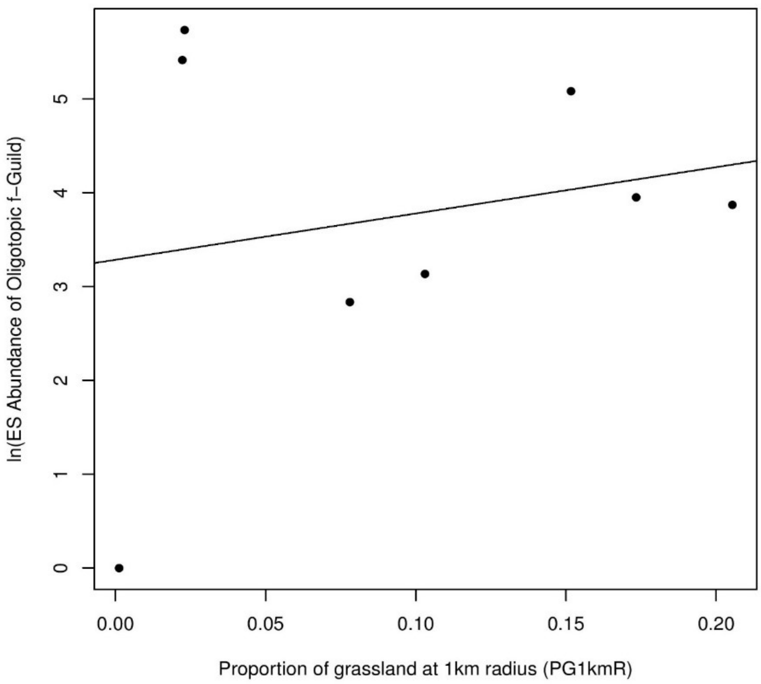

Figure 14. Scatterplot of ES oligotopic guild abundance against the PG1kmR

3.3.4 Season guild

Among the three season guilds summer species guild is the least in abundance (see Graph 4) also the same summer species guild has exceptionally lesser abundance in restored pastures, whereas the other two guilds have higher abundance in restored pastures (See Figure 25). GLM analysis of summer species guild was not statistically significant with any models as opposed to generalist and spring species guild.

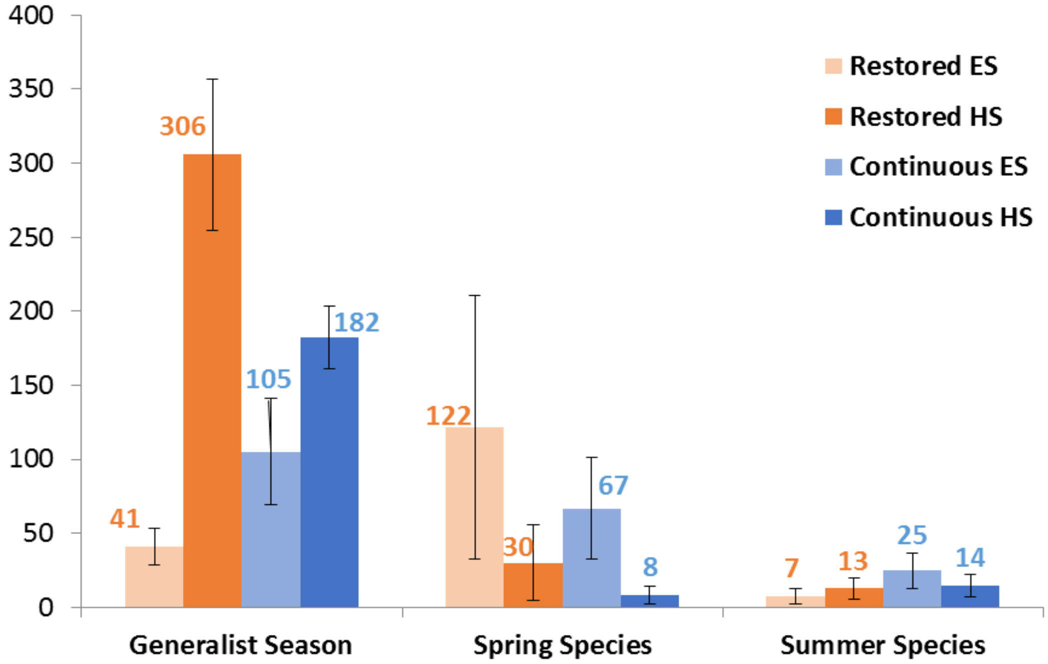

Figure 15. Sub-seasonal mean abundance chart of season guild

GLM analysis of generalist season guild

The ES generalist season guild has shown a statistical trend for the covariate PG1kmR (F= 14.02, P= 0.065) in the model without interaction factor (See Table 8). This indicates that the abundance of the generalist season guild abundance is possibly influenced by the proportion of grassland in 1km radius of the surrounding landscape.

GLM analysis of summer species guild

The HS summer species guild shows a statistical significance trend to the fixed factor i.e. habitat management type (F= 9.53, P= 0.091) in the model containing only the covariate PG5kmR without interaction model (See Table 8). This guild constitutes of only three species (namely *A. haemorrhoidalis*, *A. erraticus*, *and A. foetens*) among which probably HS *A. erraticus* contributes to this trend. The HS *A. erraticus* (F= 23.95, P= 0.016) had similar response to the species-specific GLM analysis in the presence of covariate PG5kmR in an interaction model (See Table 6). Overall the habitat management type could be influencing the HS summer species guild abundance in local pastures in the presence of dispersal from the surrounding grassland habitats at 5km radius.

3.3.5 Size guild

The abundance of small dung beetle is lesser than the large dung beetles (See Figure 28). The restored pasture abundance is higher in the small species guild. Both the small and big species guild has higher relatively higher abundance in the high summer sub-season.

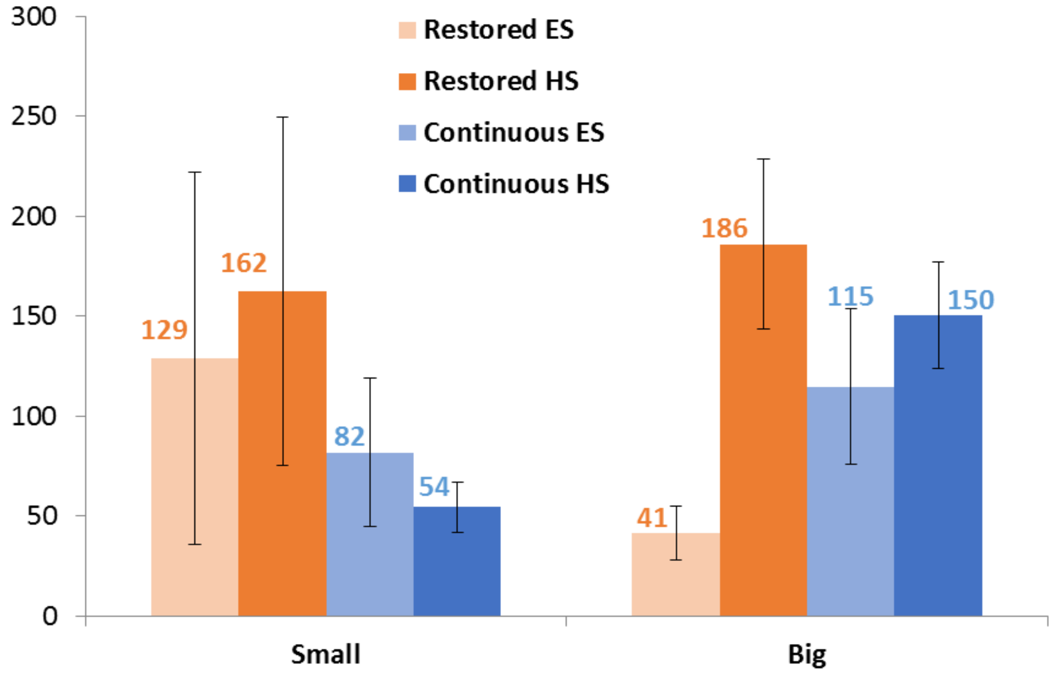

Figure 16. Sub-seasonal mean abundance chart of size guild

GLM analysis of big and small species guild

The Table 8 shows that there is a trend of statistical significance for the covariate PG1kmR in the abundance pattern of both big species guild (F= 16.10, P= 0.057) and small species guild (F= 8.74, P= 0.098), in a model without interaction factor. Possibly the abundance of both small and big species guild is influenced by the proportion of grassland at 1km radius of the surrounding landscape.

In the presence of PG5kmR covariate in an interaction model, both the interaction factor and fixed factor show a trend of statistical significance for the abundance of ES big species guild. This implies that, the habitat management type could be influencing the effect of surrounding grassland habitat at 5km radius over the local pasture big species population abundance.

4 Discussion

Dung beetles are recognised as a candidate study taxon of applied biodiversity research in various biomes across world, mainly in forest biomes (Kanda *et al.*, 2005; Kunz & Krell, 2011; Nichols & Gardner, 2011). Importantly, studying the landscape scale dynamics of dung beetles in semi-natural habitats and cultural landscapes (Eriksson, 2013) could be much more helpful for guiding conservation practitioners to assess the restoration efficiency of these co-evolved management practices in recovery and persistence of co-adapted & coevolved species-pool in respective cultural landscapes. Thus dung beetles in the cultural landscapes rely upon spatially and temporally stochastic behaviours of two ecosystem engineers, i.e. humans and domestic herbivores (Wright & Jones, 2006). Especially in the case of the semi-natural grassland restoration it is very important to measure how far the fragmented habitat interacts with the grassland proportion in surrounding landscape and its effect on the restoration measures as well as how this shapes the persistence of the organisms targeted for conservation such as pasture specialists & their preferred local microclimatic conditions. In this section I discuss, how the habitat management type and surrounding landscape grassland proportion influenced the local population of specific-species & functional guilds. The variable time-since restoration was not statistically significant for any response variable possibly due to lack of power in sample size, hence was not discussed.

Almost in the same study region (Uppsala county) in the year 1996 extensive dung beetle study done by Vessby, (2001) had recorded 13 *Aphodius* species and 2 *Geotrupes* species; whereas the present study had showed totally 15 *Aphodius* (See Table 2) species and 2 *Geotrupes* species. Although there is minor methodological difference between the studies (i.e. the previous study sampled 7 full sized dung pats and this study sampled 10 full sized dung pats), the important differences between these studies are that the 1996 study was conducted only in continuously managed semi-natural grassland and the present study conducted in both restored & continuously managed pastures together as a pair. This study's continuously managed pasture had all the 15 *Aphodius* species whereas in restored pasture there were 14 species excluding *A. sphacelatus*. The same two species of the genus *Geotrupes* were found in both studies, whereas the *Aphodius* species composition differed, with addition of four species *A. borealis* (FS), *A. sphacelatus* (PPIS), *A. foetens* (PPIS) & *A. merdarius* (PS) and absence of *A. distinctus* (PPIS) and *A. tenellus* (FS) in the present study. The recently resolved cryptic species complex (Miraldo *et al.*, 2014), of *A. pedellus* and *A. fimetarius*'s abundances were treated as single species in both these studies. However, this comparison between the species composition of these two studies could not be used to derive any broader conclusion regarding species richness, due to limitation that both these studies differ in their patch locations, especially this study's sites were more spatially segregated.

4.1 Effect of habitat type

Semi-natural grassland's restoration management is aimed at the restoration of the species richness and abundance in the local habitats by reviving the abandoned habitats through recovering management practices of the respective cultural landscapes. In general, the species richness and abundance of various organism groups showed the positive effects of habitat management in various grassland restoration studies (Mortimer *et al.*, 1998; Rosén & Maarel, 2000; Hellström *et al.*, 2003; Pykälä, 2003, 2005; Pöyry *et al.*, 2004).

In this study both species richness and total abundance had no explicit effect of restoration management, however restoration management is successful, i.e. evident from the fact that restored pasture species richness almost equals that of the continuously managed pastures. The lack of habitat type effect on the species richness, is due to fast colonisation ability of dung beetles in general, into the restored habitat patches (Roslin, 2001a; Roslin & Koivunen, 2001; Reigada *et al.*, 2015). On the other hand the lack of habitat type effect on the total abundance could be attributed to the confounding effect (Ewers & Didham, 2006) of the generalist dung beetles that have similar or even slightly higher abundance in the restored grasslands, whereas the specialist dung beetles show lower abundance in the restored landscapes than the continuously managed grasslands probably due to time-lag in establishment at gradually improving habitat quality (Andersson *et al.*, 2010; Jonason *et al.*, 2011), which is masked by the effect of highly abundant generalist species.

Among the species specific models, it's only HS *A. fossor* and in functional guilds "HS Domestic feeder" guild which are influenced by the habitat management, with higher abundance in the continuously managed pastures (See figure 3, 5 and Table 6 & 7). Semi-natural grasslands belong to group of "cultural landscapes" which were subjected to human-mediated niche construction that resulted in the contiguous open landscapes creating ecological opportunities to subset of forest species pools that shifted its realized niche or species that co-evolved the traits that increase its fitness into the stable open pastures (Eriksson, 2013). The species belonging to the pasture specialist & domestic feeder guild represent the species pool which completely specialised & adapted respectively for the biotic/abiotic niche provided by the open pastures, very importantly pasture specialist depend upon the three major elements of cultural landscapes as described by (Eriksson, 2013) namely sustained openness, interconnectivity and spatial stability. Under the present habitat fragmentation and land use change, all these three elements are constrained, which lead to increased vulnerability of pasture specialist species. Also these pasture specialist species pool exhibit interspecies variation in the dispersal and size traits. Such interspecies difference contributes for the varying response to the covariates PG1kmR & PG5kmR among the species, but invariably every sub-seasonal abundance that has higher population in the continuously managed grassland has either strong or a trend of statistical significance for the main factor "habitat type" in the models containing covariate only or interaction factor also. The HS *A. fossor*, ES *A. erraticus*, ES *A. ater*, ES *A. depressus*, HS *A. pedellus*, and functional guilds constituting these species namely, ES Generalist Habitat, HS pasture specialist, ES & HS Domestic Feeder, ES Eurytopic, HS Summer Species and ES big species guild show response to main factor habitat type in the presence of covariate PG5kmR, except *A. erraticus* that responds in the presence of both covariates PG5kmR & PG1kmR. There is presence (Strong Significance) or possible (A trend of significance) presence of the influence of continuous habitat management on the local pasture population abundance, with probable influx of individuals from 5km radius surrounding grassland habitats or interaction between continuous management and 5km radius surrounding grassland habitat.

Therefore, it's also important to explore in future studies, how the gradient of surrounding grassland "habitat types (Restored & Continuous)" contributes to the variability in the local pasture abundance. The lack of response for surrounding grassland proportion by *A. fossor*, reaffirms the conclusion by Roslin (2001a), that highly mobile specialists are not sensitive for landscape structure.

The population of Domestic feeder guild species namely *A. ater* and *A. pedellus* adheres to the predictions of landscape-moderated concentration hypothesis which says that habitat specialists respond to habitat destruction by population concentration in the remnant habitat (Tscharntke *et al.*, 2012). The transient positive trend in *A. ater* and *A. pedellus* abundance at isolated continuously managed pastures is either due to the crowding effect (Ewers & Didham, 2006) or due to dung habitat "space opportunity" created by decrease in dispersal of generalists from the surrounding landscape grasslands which enables specialists to escape competition for space (Finn & Gittings, 2003).

The *A. merdarius* (small size pasture specialist) population suspected to be crashed due to metapopulation-level processes (Roslin, 1999) is recovering from the endangered status (Gärdenfors, 2005, 2010) due to the renewed habitat management i.e. horse grazing, which is the source of specialised dung resource for this species (Personal communication with Håkan Ljungberg, Artdatabanken).

4.2 Effect of grassland proportion

Grassland proportion does not influence the total species richness of the local habitat, which is consistent with previous dung beetle study (0.5 km radius Matrix) reported from Uppsala's semi-natural grasslands habitats (Söderström *et al.*, 2001). The reason why the species richness is not sensitive to the grassland proportion gradient is because, the dung beetles in general are relatively good dispersers that enables them to occupy even isolated pastures (Roslin, 2001a; Roslin & Koivunen, 2001; Reigada *et al.*, 2015). However, this study very interestingly documents, how much does the surrounding grassland proportion at much higher (1km & 5km) spatial scale determine the abundance of various species and functional guilds in local habitats, indeed it's also being increasingly emphasized that the understanding about dynamics of "population abundance" is of key importance in furthering the understanding about the various dimensions of biodiversity -besides commonly focused species richness- in retaining the biosphere's integrity (Mace *et al.*, 2014; Steffen *et al.*, 2015). Through recent advances in landscape ecology, the landscape matrix surrounding the local habitat was found to be important determining factor of insect population abundance in crop lands surrounded by natural and semi-natural habitat matrix (Elliott *et al.*, 1999, 2002; Gardiner *et al.*, 2009).

The ES total abundance is highly influenced by the dispersal of dung beetles from the surrounding grasslands at 1km radius. In general, dung fauna exhibit pulsed dispersal pattern to exploit the highly ephemeral dung resources in the pasture landscapes which is also facilitated by the short life history of the dung beetle community (Reigada *et al.*, 2015) . Insects which depend on the pulsed dispersal are relatively more active dispersers, however among this dung beetle community, the generalist habitat guild species are the ones which evolved preference for diverse habitats through their higher dispersal ability thereby exploiting the dung resources in the broader landscapes. The proportion of grassland at 1km radius had higher influence on the total abundance than any other species-specific or functional guild models, which shows that there is higher immigration of diverse trait of dung beetle species from the surrounding grassland landscapes.

The dominant species in this study, i.e. HS *A. rufipes* has higher dispersal to the local pastures from the grasslands of surrounding landscape at 5km radius, in search of supplementary resources, with relatively higher abundance in the restored pastures (See Figure 3). Additionally, *A. rufipes* is distinct from the other *Aphodius sp*. because of their nocturnal behaviour, which is consistent with the recent studies concluding that nocturnal species are in general larger in size probably as an adaptation to escape visual predators such as birds (Guevara & Avilés, 2013) thereby possibly leading to dominance in the community structure.

The HS *A. pedellus* was significant only for the covariate PG5kmR in a model without interaction factor. Interesting niche dimension about these two species i.e., HS *A. rufipes* & HS *A. pedellus* species are that they both belong to the same generalist habitat guild and almost similar size (Hanski, 1991a), this remarkable niche overlap makes these two populations to have such a wide spatial distribution, and this suggests that *A. pedellus* having distinct diet specialization & distinct bivoltine development behavior is possibly to ensure efficient resource partition, by occupying only the isolated restored pastures where dispersal of dominant species *A. rufipes* is relatively lesser. *A. pedellus* is so much sensitive to the presence of the dominant pair to the extent, if not competition for space (Finn & Gittings, 2003), by evolving habitat selection cue of avoiding the restored pastures (infested with dominant species) located at higher grassland proportion landscapes.

The other possibility is that late-successional adults (Lee & Wall, 2006) such as *A. fossor* and *A. pedellus* compete for the space (Finn & Gittings, 2003) or density dependent competition for dung resource is probably translating into the mode of escaping competition by discrimination in habitat selection by choosing the isolated restored pastures (See Figure 9 & 10), by *A. pedellus*. Pre-emptive interspecific competition leading to pre-emptive habitat selection by *A. pedellus* species to avoid the competition with *A. fossor* species (Finn & Gittings, 2003). It's likely that this *A. pedellus* species discrimination of grasslands dominated by either dominant pair or *A. fossor* and selecting the isolated restored landscapes could be recent exploitation of ecological opportunity provided by the restoration efforts (Storch & Frynta, 1999; Shreeve & Dennis, 2010). However, it's also important to take note of the fact that still the full dimensions or types of competitive behaviour in northern temperate dung beetles is not conclusive (Finn & Gittings, 2003).

In the case of *A. erraticus* and *A. fossor* (big size pasture specialists) Roslin and Koivunen (2001) argued that their relatively higher dispersal ability among the pasture specialist makes them insensitive to the surrounding grassland proportion, whereas data in this study confirms their prediction for *A. fossor* but not for *A. erraticus*. The HS *A. erraticus* species, had higher sensitivity to both surrounding grassland proportion at 5km radius as well as the continuous habitat management type. Therefore, further focused study of the sub-seasonal population dynamics might unravel important dispersal behaviours among dung beetle species.

The metapopulation (Roslin & Koivunen, 2001) characteristic of *A. pusillus* is reflected in the trend of colonisation from 5km scale surrounding grassland proportion, further it shows there is influence of PG5kmR not only on the generalist species but also a trend of influence on the pasture specialist species like *A. pusillus* (Roslin, 2001a; Roslin & Koivunen, 2001*)*. This means there is efficient migration and retention of local population turnover, in the restored pastures, therefore it's not only the size of the dung beetles which determine the colonisation ability, also the preference for the specific microclimatic condition, determines the colonisation through habitat selection process of this species from surrounding grasslands. Inter-patch/pasture dispersal among pasture specialists due to patch/pasture quality (Haynes & Cronin, 2004) is seems to be more evident in the case of *A. pusillus* than the *A. fossor* which is probably not experiencing any type of stress for the need of much more narrow specialised micro-climate like *A. pusillus*.

The interspecies successional difference among these two pasture specialist species is that *A. pusillus* an early successional species (Rainio, 1966) and *A. fossor* a late successional (Lee & Wall, 2006). Thus the species *A. pusillus* that depends on "more ephemeral resource" base (Sensu Holland *et al.*, 2005) i.e. relatively narrow niche of *A. pusillus* makes it dependent on active exploration of resources, unlike the broader niche bigger species *A. fossor* belonging to the same pasture specialist guild. However, the statistical confirmation of long distance dispersal behaviour in the less abundant species like *A. pusillus* suffer due to sample bias which should be tested with landscape scale units investigated under regional scale.

While most species-specific models show higher significance for the covariate PG5kmR, the functional guilds show higher significance for the influence of the PG1kmR, mostly the guilds, which contain the species which where responsive to the species-specific models, such as generalist species *A. rufipes*, *A. rufus* and *A. pusillus* possibly due to the confounding effect of these species (Ewers & Didham, 2006). The generalist species guild because of their higher dispersal abilities they could have spill-over effect on local populations (Roslin & Koivunen, 2001). But these significant results showing the influence of the proportion of grasslands in the surrounding landscape has high influence on the generalist population abundance is contradicting the argument of Roslin (2001a), that the generalists are not sensitive to the landscape characteristics. To conclude, the generalists' distribution may be a causal mechanism of despotic distribution pattern (Horne, 1983) by other specialist species that has inverse relationship with generalists, due to their similar successional niche owing to the competition for space (Finn & Gittings, 2003), this needs further investigation focusing on collecting data of habitat use and habitat availability.

4.3 Effect of interaction by habitat type & surrounding grassland proportion

Among the species-specific models, it's only ES *A. ater* and HS *A. erraticus* that show, response for the interaction model, but with contrasting pattern in their slope against grassland proportion gradient irrespective of their habitat type. This contrast is probably due to different mechanisms that control the population abundance, i.e. ES *A. ater* abundance seems to be higher in the isolated remnant patches either as a crowding effect (Ewers & Didham, 2006) or competition for space (Finn & Gittings, 2003) with other species that occupy similar successional niche and the HS *A. erraticus* abundance is higher in contiguous landscapes, probably due to its dispersal efficiency higher in landscapes where grassland proportion is more. Overall these two specie's population abundance is determined by the interaction between the habitat type and surrounding grassland proportion at 5 km radius.

The ES forest specialist guild consisting of *G. stercorosus* and *A. borealis* shows higher significance for PG1kmR in the model containing interaction factor that has a trend of statistical significance. The same ES forest specialist shows statistical trend for all the three factors in the interaction model containing PG5kmR as the covariate. Probably this is an effect of resource complementation and supplementation (Tilman, 1982) by highly dispersive *Geotrupes sp.*, and this could also be as the result of correlation between the grassland proportion and matrix forest habitat proportion.

4.4 Understanding from functional guilds

In the review about the North temperate dung beetle competition (Finn & Gittings, 2003) it was recommended that to increase the generality of the results functional grouping of dung beetle assemblage is necessary to understand the inter species competition, applying the same for understanding the landscape moderated species sorting in the local landscapes has given information about the possible pre-emptive competition for space leading to habitat selection discrimination by *A. pedellus* a generalist species against the similar late successional species pasture specialist *A. fossor*. As previous studies (Holland *et al.*, 2004) regarding differential spatial scale responses of organisms, this study also documents differential resource preference, nested under generalist habitat functional guild explains the resource preference as the possible cause for its spatial scale perception.

Among 14 different functional guilds investigated in this study, the two functional guilds namely "generalist habitat guild" and "domestic feeder guild" had helped applying the generality of landscape moderated species sorting. While generalist habitat guild characterises the dispersal behaviour from the surrounding grassland use, the domestic feeder guild has 7 out of 9 species with relatively higher abundance in the continuously managed pastures than the restored, hinting that restored pastures takes much longer period for recovery of specialised dung resource feeder abundance similar to reference habitats.

Habitat fragmentation seems to be influencing landscape scale selection of the dung beetle traits active dispersal and habitat generalism of species as the landscape-wide species sorting mechanism leading to homogenisation or dominance of the community composition by *A. rufipes* and *A. rufus*, this necessitates future investigation of shifts in community composition through the decades of dynamic land use changes.

The forest specialists, the generalist and pasture preferring intermediate species guild, constitute two third of the community composition, must be contributing an energy flux/subsidy between the human dominated landscapes and forest habitats due to cross habitat spillover of biomass. Summer species guild has relatively less abundance and narrow seasonal niche, which needs further investigation and management focus.

To summarise there is complete contrast between the species-specific models and functional guilds in their response to the covariate grassland proportion, while the most of the species-specific models had higher statistical confirmation for PG5kmR as the individual species that belongs mostly to domestic feeder guild, in the case of functional guild model (similar to total abundance) had higher statistical confirmation for PG1kmR, which shows the importance of functional guild based analysis.

4.5 Limitations of this study and suggestions for future research

This study was conducted with the systematic design for understanding the landscape structure moderated spatial population of dung beetles, however there are some limitations in the analysis included. Some of them are

a. Important habitat scale and landscape scale elements of landscape/habitat structure should be investigated, such as connectivity, habitat area, perimeter-area ratios, etc.
b. It could be interesting to test whether other matrix land use proportion has any influence on the species which were relatively abundant but does not respond to the variable surrounding grassland proportion included in this study
c. Possibly the sampling bias over the least abundant or rare species makes it difficult to investigate the influences of landscape structure and management type on these species.
d. Comparing the community structure similarity, co-occurrence across scales (Pat, patch and landscape), habitats types (“Restored” and “Continuously managed”) and landscape structure gradient would give valuable information about the extent of recovery of dung beetle community.
e. Quantitative statistical evaluation of the functional guilds such as season is not done in this study. And new guilds like succession, nesting, larval feeding and oviposition behaviour etc. could be included in further investigations.

Dung beetles in the cultural landscapes enable us to investigate the landscape moderated species sorting as the result of human-mediated niche construction behaviour spatially and temporally through this relatively simpler ecological system, since they do not influence their resource unlike other insects that feed on plants (Vessby, 2001).

a. It is important to test how colonization extinction dynamics differs through the landscape structure gradient at the regional scale so that the behaviour of even the rare species, narrow resource/seasonal/successional species pool could also be investigated (Hanski, 1991a).
b. Landscape complementation & supplementation could be studied in detail with the additional information about life-history traits and their preferences for respective habitats. For example, Soil type & moisture is an important factor for habitat selection by *Aphodius* assemblages (Vessby & Wiktelius, 2003), therefore information on soil type, vegetation structure etc., could be included in future studies which might help us to understand patterns and processes exhibited by the species which bury the dung resources in soil for their larvae such as *A. erraticus*.

c. Species successional sequence is conservative for dung beetle populations (Sladecek *et al.*, 2013), but the temporal optima of the species is plastic, non-random species sorting through the succession might differ between “landscape structure” gradients, hence to understand this there is a need for integrated analysis and interpretation of species-specific succession, oviposition, food/larvae relocation behaviour and it’s interacting habitat discrimination pattern evolution (Storch & Frynta, 1999) (of habitat types) to predict the future trajectories of dung beetle assemblages in fragmented semi-natural grasslands.
d. Investigation of the changes in the community composition or evenness of dung beetles through the decades of changes in land use is needed.
e. Though, the sampling of this study was planned to collect during species rich, sub-seasonal assemblage, some important and otherwise abundant species such as *A. sphacelatus* is not represented true to its relative abundance. To gain further understanding of the landscape moderated population dynamics of all species, it’s best to design sampling at peaks of all distinct sub-seasonal assemblage abundances (Finn *et al.*, 1998, 1999) and also including microhabitat specific environmental variables at the habitat level to account for population structure at all microhabitat types equally (Mehrabi *et al.*, 2014).
f. To understand the dynamic nature of population turnover synchronous with the seasons and ephemeral resource/habitat it’s important to focus together on the species specific pat residence time, dispersal behavior and longevity of their seasonal niche, which are more critical for predicting the efficiency of patch occupancy by dung beetle species which typically dependent on the pulsed dispersal behavior (Reigada *et al.*, 2015). Even though all dung beetle species are classified as pulsed dispersers the characteristic difference in the species-specific population turnover and life-history traits affect the colonization and extinction dynamics of these populations.
g. According to (Reigada *et al.*, 2015) the communities which are predominantly dependent on pulsed dispersal behavior would have metapopulation level persistence by ensuring minimum level of patch occupancy when the ephemeral resource availability is high, therefore population specialist’s seasonal and resource preference which drives the extinction of dung beetle populations rather than the dispersal limitation, therefore it becomes imperative to test the importance of resource diversity & narrow seasonal niche in landscape moderated colonization dynamics.
h. Quantitative investigation of the biological traits, such as body size/biomass through the landscape structure gradients could be investigated to understand the likely consequences of the matrix land use patterns over the dung beetle community. Also the recent advances in methodologies like Mesoclosure experiments (Lähteenmäki *et al.*, 2015), might help us explore the biodiversity ecosystem function mechanisms through landscape structure gradient to a greater detail.

5 Conclusion

Dung beetle persistence in the cultural landscapes depends on the two top ecosystem engineers engaged in niche construction through spatial and temporal stochastic process. Thus, the restoration of the dynamics of ecosystem engineers through restoration process resulted in successful recovery of dung beetles in the restored pastures, with similar species richness as continuously managed grasslands. This study mainly provides additional empirical evidence for metapopulation dynamics of dung beetle's total abundance, species specific abundance and functional guild specific abundance. However, the total abundance and functional guild specific metapopulation dynamics is driven by grassland proportion at 1km radius confounded mostly by generalist species dispersal behavior and whereas for certain individual species the metapopulation dynamics is at 5km scale radius due to their specialism for domestic feed and the resultant exploration for domestic feed resources at larger spatial scales relatively.

The highly dispersive pasture specialist *A. fossor* and domestic feeder guild persistence depends on the local habitat scale management practices. The investigation of the functional guild patterns, shows that the generalists are the dominant dung beetle population which depends on the metapopulation behavior, whereas the domestic animal dung feeding beetles depends on the resource facilitation at the local habitat scale with higher abundance in the continuously managed pastures than the restored pastures, the underlying mechanisms due to biotic and abiotic processes needs to be investigated further. The intra-guild difference in the successional, dispersal and resource preference behavior constrains gaining the generality across the pasture specialist guild hence it's important to have species specific understanding for poor dispersers whose local population resembles the classical metapopulation. Further refined analysis of functional guilds and landscape features would be helpful in understanding the landscape scale patterns and processes in the dung beetle guilds. Especially accounting for the dung beetle population variability contributed by the area, isolation, soil types, micro-climatic conditions and matrix land use types. The future studies on the dung beetle population patterns and processes, could include comprehensive data about the diverse domestic & wild feed availability in the landscape matrix and their impact on population persistence. Rare species that are elusive from yielding any understanding from observational studies due to low sample power, could explore metapopulation genetic approaches.

To increase the conservation potential of the dung beetles in the cultural landscapes it's important to focus research on the species which has narrow resource, season and successional niches and increasing the grazing regimes focused towards these species pool. Dung beetles could serve as a rapid "management quality" indicator species for the quality of management continuity sustained at local and landscape scale habitats.

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Appendix

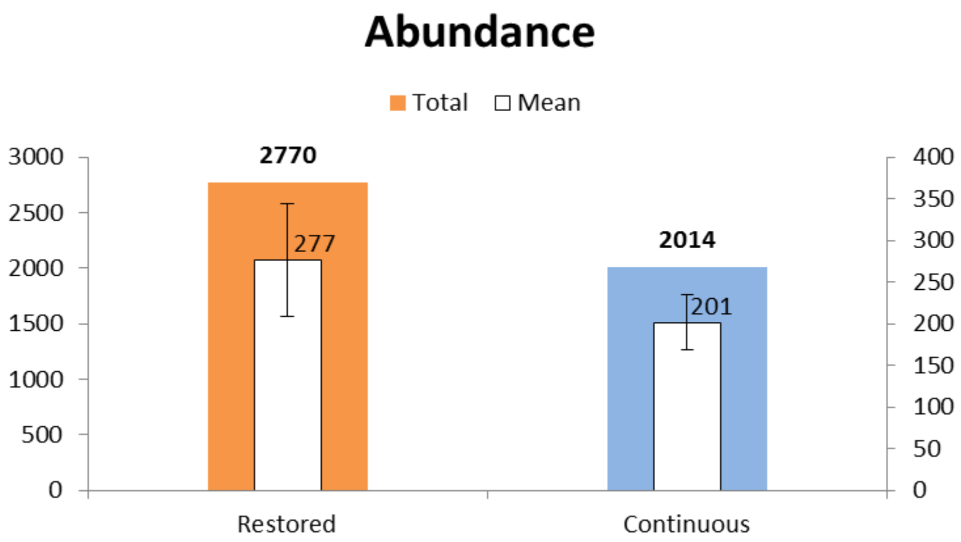

Figure A17. Abundance in grassland management types, restored and continuous

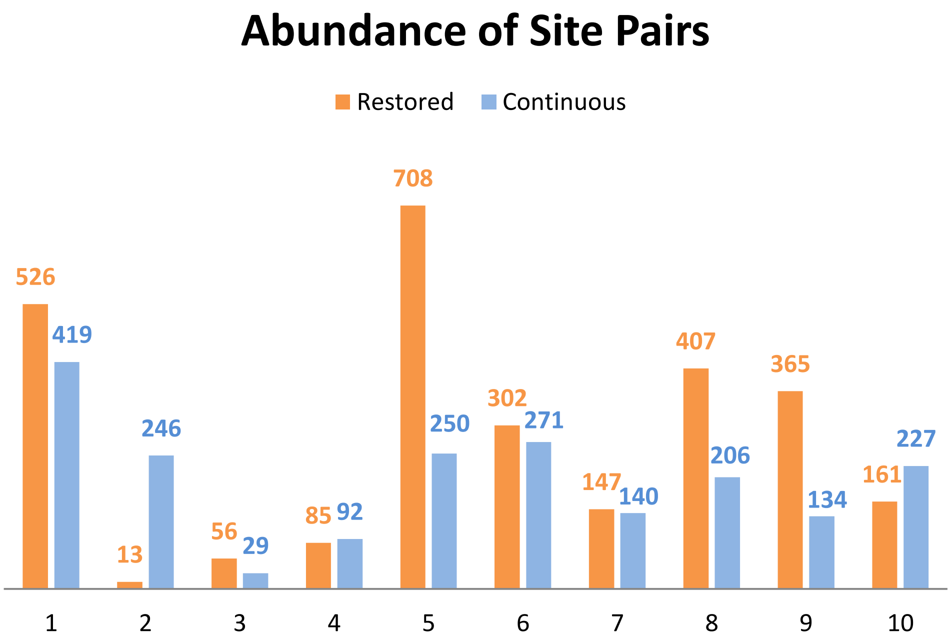

Figure A18. Abundance of site pairs

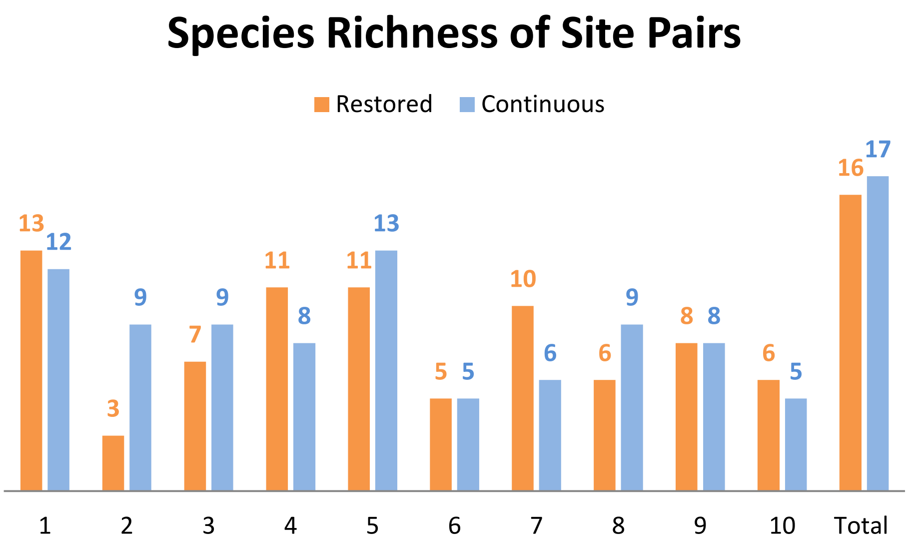

Figure A19. Species richness of site pairs

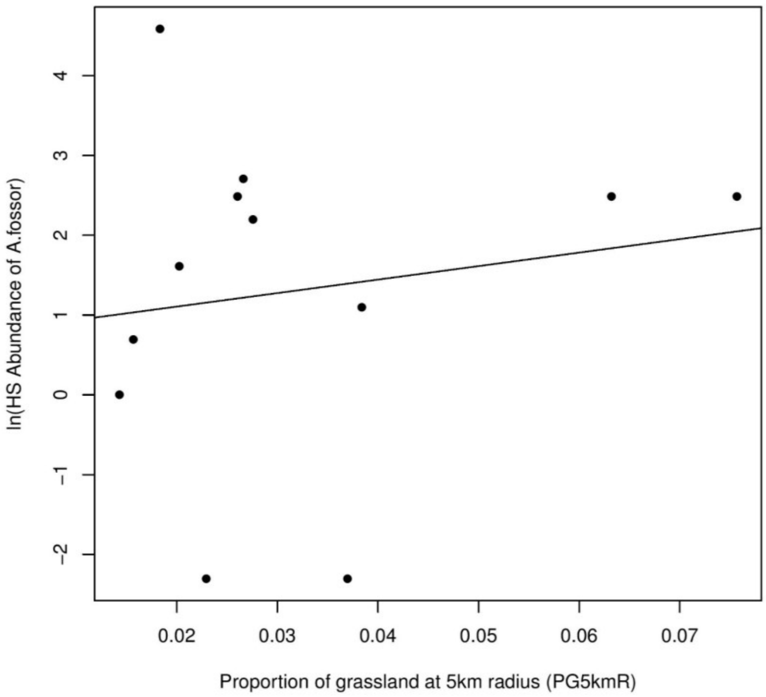

Figure A20. Scatterplot of HS *A. fossor* abundance against the PG5kmR

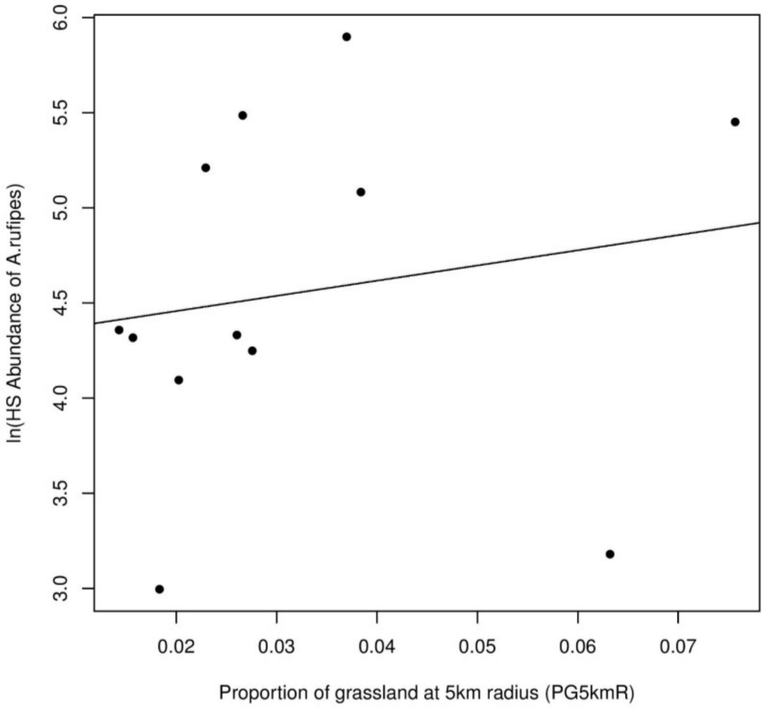

Figure A21. Scatterplot of HS *A. rufipes* abundance against the PG5kmR

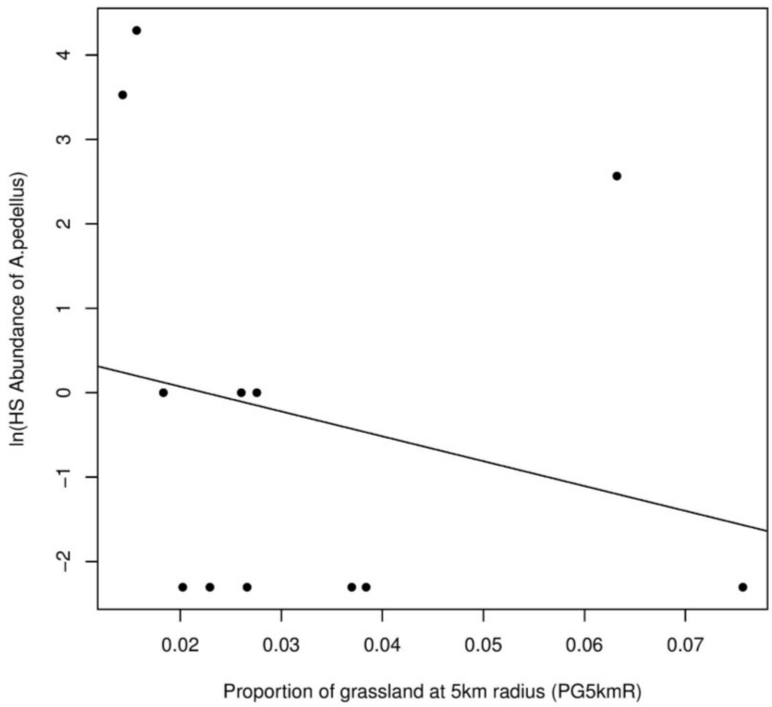

Figure A22. Scatterplot of HS *A. pedellus* abundance against PG5kmR

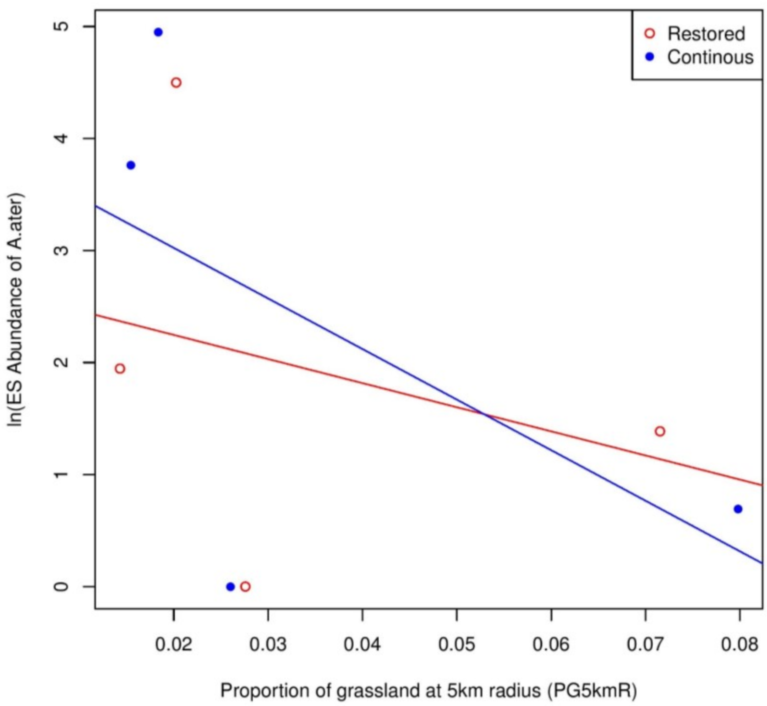

Figure A23. Scatterplot of ES *A. ater* abundance with habitat management against PG5kmR

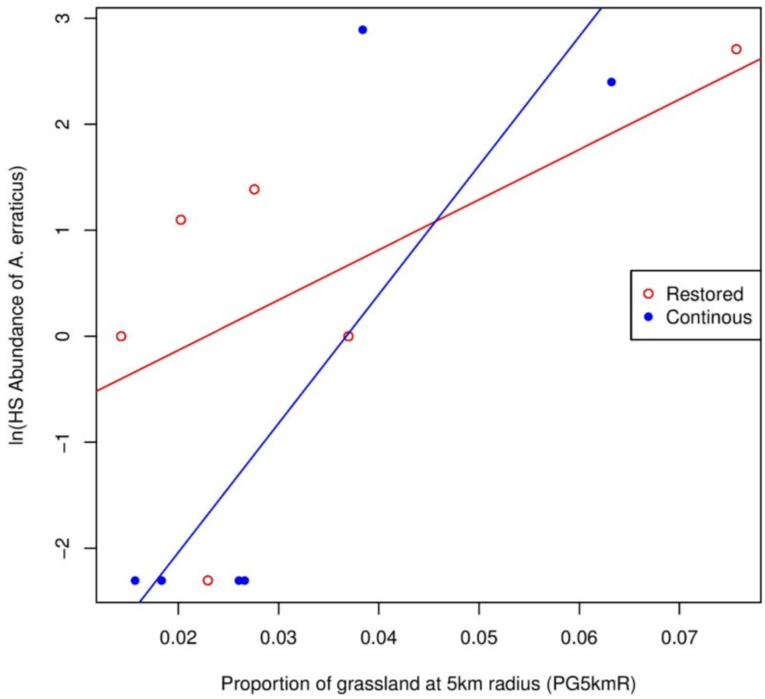

Figure A24. Scatterplot of HS *A. erraticus* with habitat management against the PG5kmR