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ORIGINAL PAPER

Landscape diversity of pasture dung beetle communities in the central region of mainland Japan and implications for conservation management

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Abstract We studied the diversity of dung beetle communities in Japanese pastures to identify the factors that maintain or enhance the diversity of dung beetles at a landscape scale. We surveyed dung beetles from 17 pastures located in the northeastern part of Tochigi Prefecture, which is in the center of mainland Japan. From 1999 to 2001, surveys were conducted during the 6-month grazing period (May to October) by using dung baited basket traps. We also collected information about the environmental conditions and pasture management practices. Twenty-five dung beetle species belonging to Geotrupinae, Scarabaeinae, and Aphodiinae (including 13 tunneler and 12 dweller species) were recorded. The abundance of dweller species decreased with increasing elevation, possibly because of the effect of rainfall, whereas the species richness of tunneler species was affected by cattle disturbance and soil condition. Beetle species richness significantly increased with the number of years that the pastures had been grazed. Ivermectin administration did not appear to have any adverse effect on dung beetle abundance, species richness, or species diversity. The dung beetle datasets of the current study (including specific tunneler and dweller beetle groups) supported the widely documented positive relationship between local abundance and species distribution ranges. The within pasture, within area, and between area hierarchical additive partitioning of regional total diversity indicated that landscape-scale management should be implemented to conserve the regional diversity of the dung beetle communities inhabiting Japanese pastures.

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Introduction

Grasslands used for raising cattle, including grazing pastures and meadows, have multifunctional benefits. For instance, grasslands (1) conserve water, soil, biodiversity, and landscape features; (2) counteract global warming by absorbing greenhouse gasses and sequestrating carbons in the soil; and (3) provide opportunities for recreation and tourism (Gibon 2005; Hopkins and Holz 2006). Furthermore, many organisms depend on grassland habitats for food, reproduction, and survival; thus, grasslands are fundamental for the conservation of organisms (Tucker 1997; Kitahara and Sei 2001; Sala et al. 2001; Finck et al. 2002; Tsukada et al. 2004).

Biologically diverse communities have various functions in ecosystems (termed ecosystem functions) (e.g., Tilman 1999; Loreau et al. 2002; Hooper et al. 2005; Spehn et al. 2005; Gessner et al. 2010). Dung beetles (which are coprophagous insects belonging to Scarabaeoidea, Coleoptera) that inhabit cattle grazing pastures are important for facilitating the cycling of nutrients (Bornemissza 1960; Hosogi 1985; Bang et al. 2005; Yamada et al. 2007; Nichols et al. 2008), improving soil structure (Bornemissza 1960; Bang et al. 2005; Nichols et al. 2008), dispersal of plant seeds (Nichols et al. 2008), suppressing harmful flies and endoparasites of livestock found in animal dung (Bornemissza 1960; Blume et al. 1973; Fincher 1975; Hosogi 1985; Nichols et al. 2008), and reducing rank patches (i.e., the zone of rank growth around dung pads that cattle avoid grazing) (Bornemissza 1960). Such beneficial functions to ecosystems are termed ecosystem services (Costanza et al. 1997; Daily et al. 1997; Sala and Paruelo 1997; Millennium Ecosystem Assessment (ed.) 2005). In USA, the economic value of eco~~logical~~ system services provided by dung beetles is estimated to be around 380 million US dollars annually (Losey and Vaughan 2006).

However, the number and diversity of dung beetles has recently declined, because of a reduction in grazing areas, changes in pasture management (Lumaret and Kirk 1991; Lobo et al. 2001; Tsukamoto 2003; Carpaneto et al. 2007; Escobar et al. 2008; Nichols et al. 2008), and habitat fragmentation (Klein 1989; Estrada et al. 1998; Nichols et al. 2007). Consequently, many dung beetle species have become listed as threatened on national or local Red Lists (Vessby and Wiktelius 2003; Imura 2010). In addition, it has been predicted that the rapid extinction of dung beetles would cause the loss of ecosystem functioning (Larsen et al. 2005; Nichols et al. 2008). Therefore, studies about the diversity and conservation of dung beetles are of increasing importance (Hortal et al. 2001; Lobo 2001; Martín-Piera 2001; Hutton and Giller 2003; Chefaoui et al. 2005; Davis and Philips 2005; Lobo et al. 2006; Nichols et al. 2007; Jay-Robert et al. 2008b; Navarrete and Halffter 2008).

Here, we studied the regional diversity of dung beetle communities in pastures at a landscape scale, to identify the factors that maintain or enhance dung beetle diversity, which would be required to establish ecosystem-service-facilitated sustainable cattle farming. Over a 3-year period, we surveyed dung beetles from 17 pastures in a region of northeastern Tochigi Prefecture, which is located in the central part of mainland Japan. In a

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previous study, Imura et al. (2011) selected 10 major land-use elements that might influence the suitability of habitats used by dung beetles from the GIS DATA. The prediction model for dung beetle species richness generated by the authors indicated broad-leaved deciduous forests and pastures as positive land-uses elements, whereas artificial forests represented a negative element. Furthermore, the model indicated that areas of high pasture density might serve as hotspots for dung beetle diversity. However, the model only explained 65 % of the variability in dung beetle diversity; hence, other factors might also influence the diversity of dung beetle communities. Thus, the current study focused on evaluating environmental factors (such as physical, vegetation, and cattle management factors) that might influence the diversity of dung beetle communities in pastures. We also performed macroecological analyses to determine the regional structure of dung beetle diversity, to develop suggestions to improve the conservation management of dung beetle communities.

Methods

Surveyed pastures

We surveyed 17 grazing pastures in the northeastern part of Tochigi Prefecture, which is located in the central part of mainland (Honshu) Japan. The study pastures were distributed across an area of about 50 km (along longitude) × 70 km (along latitude) (3,150 km^2) (Fig. 1; Table 1). This region has a history of horse and cattle stock farming dating back several 100 years, with many operational cattle ranches.

Dung beetle survey

For the survey, we separated the region into three areas according to its geographical and topographical conditions, with each area containing 5–6 pastures (Table 1; Fig. 1). Area 1

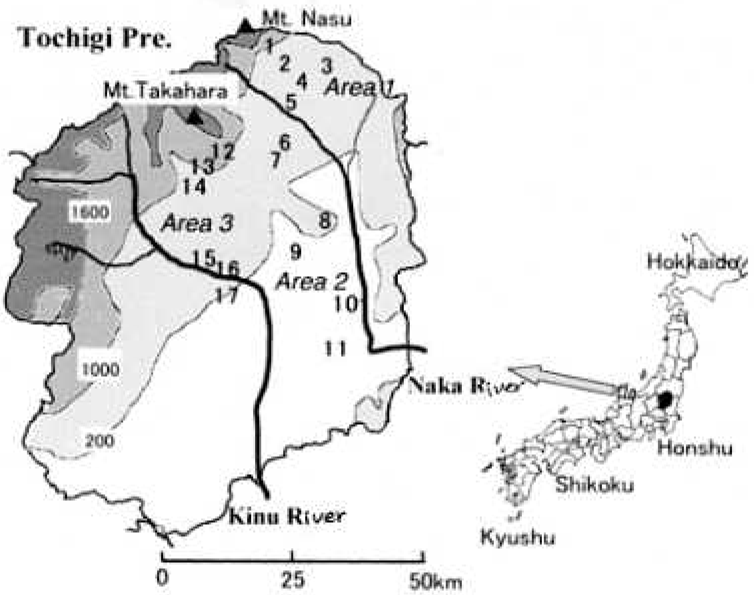

Fig. 1 Locations of pastures surveyed in the Tochigi Prefecture. The numbers correspond to the pasture numbers presented in Table 1. The *contour lines* indicate the altitude in meters

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was located on a hillside at the foot of Mt. Nasu, area 2 was situated on the alluvial fan of River Naka, and area 3 was located on a hillside at the foot of Mt. Takahara in the River Kinu basin. We surveyed 5–6 pastures in each area within a 1-week period, with the survey lasting three successive weeks for the three areas combined. From 1999 to 2001, we surveyed dung beetles once a month between May and October, which was the period during which cattle grazed the pastures. We established a survey site in the center of each pasture. Since the Nasumohan pasture covered a large area, we established two sites in paddocks of different altitudes (Nasumohan-U and Nasumohan-L, see Table 1) for the survey. At each site, beetles were trapped using three dung-baited basket traps (Hayakawa et al. 1976), which were placed at approximately 10-m intervals along a transect line. The trap consisted of a plastic basket (20 cm in diameter and 8 cm deep), which contained andosol on which 400 g of fresh cattle dung had been placed. The cattle dung was collected from dairy cattle fed with hay. The dung, 400 g in weight, was stored until use in polyethylene bags in a freezer. We buried the traps to the rim in the soil. The trap mimics cattle dung (feces) on the ground of pastures. Thus, the trapping technique was regarded as a quantitative sampling method of the dung beetles that colonize cattle droppings. After 24 h of deployment, we transferred the traps to the laboratory and separated the beetles from the dung and soil in the traps. The beetles were stored in 75 % alcohol until identification. Voucher specimens were deposited in the Nasu Research Station, NARO and in the Nasunogahara Museum, Nasushiobara, Tochigi, Japan.

Environmental and management measures

We measured the height and species richness of vegetation in four quadrats (1 m × 1 m) that were randomly placed at each survey site. Vegetation height was calculated as the average height measured at 5 random points within a quadrat. We also measured soil hardness (kg cm^{-2}) at five points in each quadrat by using a soil hardness tester (Nakayama type handy model, Fujiwara Scientific Co., Tokyo), and averaged the measurements after excluding the minimum and maximum values. Vegetation and soil hardness were measured during June of 2000 and 2001. The measurements were averaged across the 2 years for the data analyses.

The longitude–latitude coordinates at each survey site were recorded using a handheld GPS device (Model-FG-212/210, Empex Co., Tokyo). The altitude of the survey sites was determined from comparing the GPS location with the databases of the National Land Agency of Japan. We obtained climatic variables of annual average temperature (°C), annual precipitation (mm), and annual solar radiation (J cm^{-2}) for the sites from GIS Mesh Data (1 km × 1 km), according to the Automated Meteorological Data Acquisition System provided by the Japan Meteorological Agency (Seino 1993). The climatic variables were averaged over the 3-year survey period.

Through interviews with farmers, we collected information about each study pasture, including details of the grazing area, grazing years, grazing period, and administration of ivermectin (an anthelmintic drug that is known to have adverse effects on dung beetles) (e.g., Wall and Strong 1987; Lumaret et al. 1993; Krüger and Scholtz 1997).

Data analyses

We estimated the expected species richness by using a nonparametric method of the bias corrected Chao2 (Chao and Shen 2012), based on the presence–absence data of dung beetle species. The estimator Chao2 provides the least biased estimate for small numbers of

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Table 1 Pastures surveyed for dung beetles in the northeastern part of Tochigi Prefecture and their attributes related to topography, climate, soil, grazing, and vegetation

Pasture (survey site)	Area[a]	Altitude (m)	Area(ha)	Temperature (°C)[b]	Precipitation (mm)[c]	Soil hardness (kg cm^{-2})	Cattle type[d]	Grazing years[e]	IVM treatment[f]	Vegetation type[g]	Vegetation height (cm)	Vegetation diversity[h]
1. Nasumohan-U[i]	1	867.6	185.0	8.7	2,202	4.81	DC	31	Y	A	50.7	6.5
2. Nasumohan-L[i]	1	813.9		9.1	2,206	3.87	DC	31	Y	A	54.3	7.6
3. Ohsawa	1	538.9	18.0	10.7	1,973	3.89	BC	37	N	A	55.8	6.0
4. Ohfukabori	1	616.5	35.0	10.3	1,980	5.71	BC	38	Y	A	53.7	6.1
5. Ikeda	1	532.7	15.0	10.9	1,920	4.95	BC	38	N	A	39.1	7.5
6. Fujinita	2	311.1	41.6	12.3	1,803	2.93	BC	57	N	SN	57.7	11.3
7. NILGS-West	2	314.8	9.1	12.3	1,883	7.44	DC	57	N	A	18.7	7.1
8. Ohya	2	173.4	25.0	13.2	1,503	6.59	DC	33	Y	A	18.0	8.4
9. Nakamura	2	196.8	9.7	12.9	1,579	9.09	BC	1	N	A	7.0	7.8
10. Minaminasu	2	164.1	36.8	13.2	1,446	16.49	DC	21	N	A	22.4	3.8
11. Fureai	2	147.3	9.5	13.2	1,383	7.29	DC	20	Y	A	56.5	4.1
12. Happo	3	1,011.0	104.0	8.0	2,326	6.15	BC	37	N	SN	7.9	8.1
13. Dojodaira	3	962.5	119.0	8.3	1,977	5.01	DC	35	N	A	26.8	6.1
14. Hohzukidaira	3	698.8	33.4	9.9	1,947	6.32	DC	27	N	A	41.3	3.5
15. Kawamura	3	265.0	10.5	12.5	1,821	7.81	BC	28	Y	A	27.3	5.9
16. Uwasawa	3	246.6	20.5	12.7	1,735	6.09	BC	26	Y	A	26.7	6.3
17. Kobayashi	3	228.6	22.0	12.8	1,645	6.74	DC	49	Y	A	24.8	5.1

[a] The three survey areas separated according to the geographical and topographical conditions (see Fig. 1)

[b] Annual mean temperature

[c] Annual precipitation

[d] *DC* dairy cattle, *BC* beef cattle

[e] Grazing years until 1999

[f] Ivermectin (an anthelmintic) treatment; *Y* administrated, *N* not administrated

[g] *A* artificial grassland, *SN* semi natural grassland

[h] Average number of plant species per m^2

[i] The upper and lower paddocks of the same ranch

samples (Colwell and Coddington 1994). We also estimated species diversity measured by 1-D (Pielou 1969; Hurlbert 1971), where D was the Simpson's measure of concentration (Simpson 1949) based on the minimum variance unbiased estimator (MVUE) (Magurran 1988), by using the software SPADE (Chao and Shen 2012).

We analyzed the relationship between interspecific distribution and local abundance (Gaston et al. 1997; Holt et al. 2002) of dung beetle species. We defined distribution as the frequency at which the species occurred among the pastures, and we defined abundance as the average number of individuals per year per pasture where the species occurred (i.e., abundance-when-present), to avoid the detection of a spurious positive relationship between distribution and abundance (Gaston and Lawton 1990; Wright 1991).

To examine the spatial structure of dung beetle diversity in the pastures of the surveyed landscape, we partitioned regional total diversity (γ) into hierarchical diversity components (Allan 1975). Partitioning of β diversities was performed based on the three areas that were separated according to their geographical and topographical conditions for the survey (Fig. 1). We used the PARTITION software (ver. 3.0) for the hierarchical additive partitioning of regional total diversity γ with respect to within pasture (α) diversity, within area (β_1) diversity, and between area (β_2) diversity (Crist et al. 2003; Veech and Crist 2009), based on the numbers equivalent (i.e., the true diversity), which makes diversity components α and β independent (Lande 1996; Jost 2007). We selected the Simpson's diversity index, with the parameter q being set to 2 (Jost 2007). The diversity components and their significance test were calculated using no sample weighting based on the relative number of individuals in each sample and the individual-based randomization that randomly reassigns each individual in the data set to the lowest hierarchical level of analysis (Veech and Crist 2009), by running 1,000 iterations.

The relationship between two variables was analyzed using Spearman's rank correlation. The effect of nominal pasture variables on dung beetle diversity was analyzed using the Wilcoxon's rank sum test. For all statistical tests, * indicates p (probability of significance) ≤ 0.05, ** indicates $p \leq 0.01$, and *** indicates $p \leq 0.001$.

Results

Pastures

Information about the attributes in relation to the topography, climate, soil, grazing, and vegetation of each pasture survey site are shown in Table 1. The altitude of the pastures represented by the site values ranged from 147 to 1,011 m. Annual mean temperature ranged from 8.0 °C (Happo) to 13.2 °C (Ohya, Minaminasu and Fureai). Annual precipitation was fairly high, ranging from 1,383 mm (Fureai) to 2,326 mm (Happo). Annual solar radiation (omitted from Table 1) ranged from 3,830 MJ m^{-2} (Nasumohan-L) to 4,636 MJ m^{-2} (Minaminasu). The distribution of the pastures with respect to the environmental gradients of altitude, temperature, and precipitation is shown in Fig. 2. Soil hardness was the lowest at Fujinita (2.93 kg cm^{-2}), and exceptionally high at Minaminasu (16.49 kg cm^{-2}). The pastures were grazed by dairy or beef cattle. Except for the recently established pasture at Nakamura (1 year before), pastures had been grazed for longer than 20 years. Ivermectin was administered to cattle at 8 pastures. Other pesticides including insecticides and herbicides were not applied to the pastures. The pastures of Fujinita and Happo had a seminatural vegetation type dominated by Japanese lawn grass *Zoysia japonica*. The vegetation type at all other pastures was artificial grassland dominated by

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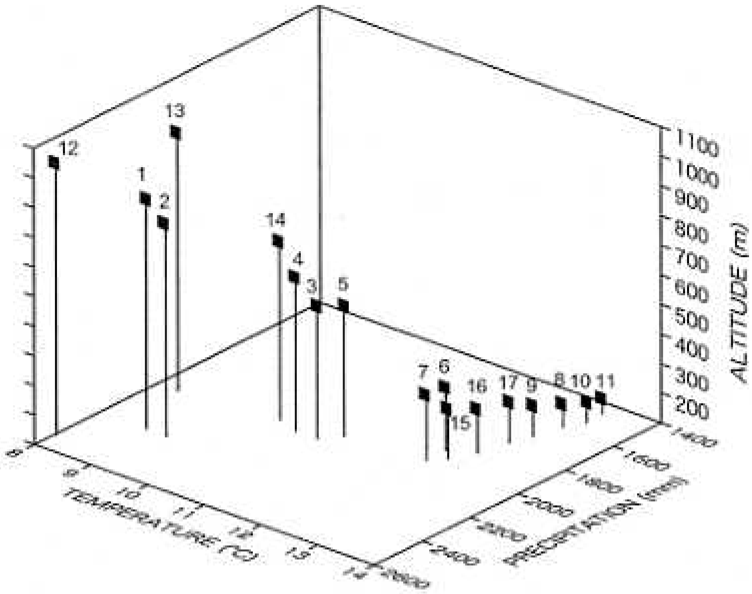

Fig. 2 Distribution of pastures (survey sites) in relation to the environmental gradients of temperature, precipitation, and altitude. The *numbers* correspond to the pasture numbers presented in Table 1

Lolium perenne, *Dactylis glomerata*, *Poa pratensis*, and *Trifolium repens*. Vegetation height ranged from 18 to 58 cm, except for the Nakamura and Happo pastures, where it was less than 10 cm. Vegetation diversity exceeded 11 species per m^2 at the Fujinita pasture, which ranged from 4 to 9 species per m^2 at all other pastures.

Dung beetles and influencing factors

In total, 47,387 individuals belonging to 25 dung beetle species were collected (Table 2). Two species belonged to the Geotrupinae subfamily, 9 belonged to Scarabaeinae, and 14 belonged to Aphodiinae. All Geotrupinae and Scarabaeinae species and 2 Aphodiinae species were tunnelers (13 species), while all other Aphodiinae species were dwellers (12 species). Tunnelers and dwellers are functional groups of dung beetle species that are classified depending on their reproductive behaviors (Cambefort and Hanski 1991); tunnelers dig tunnels in the ground under dung and bury dung mass for egg laying, and dwellers lay eggs and breed in dung on the ground. Cambefort and Hanski (1991) misinterpreted *Aphodius elegans* and *A. quadratus* as dwellers. *A. urostigma* was the most abundant species, followed by *A. rectus*, *Onthophagus lenzii*, *A. quadratus*, *A. sublimbatus*, *A. pusillus*, and *A. uniplagiatus*. *Copris pecuarius* and *Myrhessus samurai* were only captured once. *A. quadratus* was present in all pastures, while *O. lenzii*, *A. urostigma*, *A. pusillus*, *A. rectus*, *A. sublimbatus*, and *O. ater* were present in most pastures. Except for *O. ater*, these species represented the dominant species of this region.

The total number of beetles captured per year, the number of species collected (observed species richness), the expected species richness estimated by Chao2, and species diversity (1-*D*) of the pastures are shown in Table 3. A large variation was observed in the total number of beetles (abundance) among the pastures. A 30 times higher beetle abundance was observed in the largest pasture (Fureai) compared to the smallest (Dojodaira) pasture. Although beetle abundance was significantly correlated with altitude, temperature, and precipitation ($p < 0.01$ or $p < 0.05$), only the abundance of dwellers contributed to these relationships ($\rho = -0.640$**, $\rho = 0.635$**, and $\rho = -0.561$*, respectively).

Table 2 Dung beetle species collected from the pastures in northeastern Tochigi

Family	Subfamily	Species	FG[a]	Number of individuals[b]	Number of pastures[c]
Geotrupidae	Geotrupinae	*Phelotrupes auratus* (Motschulsky)	T	167	7
		Phelotrupes laevistriatus (Motschulsky)	T	36	4
Scarabaeidae	Scarabaeinae	*Copris acutidens* Motshulsky	T	8	2
		Copris pecuarius Lewis	T	1	1
		Liatongus minutus (Motschulsky)	T	569	11
		Caccobius jessoensis Harold	T	435	7
		Onthophagus ater Waterhouse	T	135	14
		Onthophagus atripennis Waterhouse	T	161	11
		Onthophagus fodience Waterhouse	T	155	12
		Onthophagus lenzii Harold	T	5,860	16
		Onthophagus nitidus Waterhouse	T	6	5
	Aphodiinae	*Aphodius breviusculus* (Motschulsky)	D	284	2
		Aphodius comatus Ad. Schmidt	D	359	5
		Aphodius eccoptus Bates	D	133	5
		Aphodius elegans Allibert	T	65	11
		Aphodius pratensis Nomura et Nakane	D	587	8
		Aphodius pusillus (Herbst)	D	2,564	16
		Aphodius quadratus Reiche	T	4,311	17
		Aphodius rectus (Motschulsky)	D	8,484	15
		Aphodius rugosostriatus Waterhouse	D	347	5
		Aphodius sordidus (Fabricius)	D	184	7
		Aphodius sublimbatus Motschulsky	D	3,051	14
		Aphodius uniplagiatus Waterhouse	D	910	11
		Aphodius urostigma Harold	D	18,574	16
		Myrhessus samurai (Balthasar)	D	1	1

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Table 2 continued

Family	Subfamily	Species	FG[a]	Number of individuals[b]	Number of pastures[c]
Total				47,387	

[a] *FG* functional groups (Cambefort and Hanski 1991), *D* dweller, *T* tunneler

[b] Total number of individuals captured

[c] Number of pastures where the species occurred

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Table 3 Abundance and diversity measures of dung beetle communities in the pastures

Pasture	Number of beetles[a]	Observed species richness[b]	Expected species richness[c]	s.e.	Species diversity 1-D[d]	s.e.
1. Nasumohan-U	696	14 (7)	15.7	2.5	0.667	0.127
2. Nasumohan-L	844	15 (8)	15.0	0.2	0.681	0.086
3. Ohsawa	450	17 (9)	17.6	1.1	0.657	0.101
4. Ohfukabori	782	17 (9)	18.7	2.5	0.638	0.137
5. Ikeda	822	16 (7)	16.4	1.0	0.778	0.066
6. Fujinita	704	17 (9)	17.0	0.2	0.822	0.046
7. NILGS-West	1262	14 (6)	15.0	1.8	0.605	0.148
8. Ohya	2348	14 (7)	15.0	2.3	0.606	0.141
9. Nakamura	1619	16 (7)	20.7	4.9	0.395	0.346
10. Minaminasu	1511	13 (6)	13.1	0.6	0.747	0.085
11. Fureai	3119	13 (7)	13.0	0.2	0.647	0.147
12. Happo	116	7 (6)	7.7	1.5	0.327	0.414
13. Dojodaira	93	11 (7)	12.3	2.3	0.571	0.154
14. Hohzukidaira	431	13 (8)	13.0	0.2	0.739	0.065
15. Kawamura	450	9 (4)	9.1	0.6	0.542	0.262
16. Uwasawa	319	9 (7)	9.1	0.6	0.408	0.350
17. Kobayashi	232	8 (1)	8.3	1.3	0.703	0.075

[a] Total number of individuals collected per year

[b] Figures in parentheses indicate the number of tunneler species

[c] Expected species richness estimated by a bias-corrected form for the Chao 2 estimator (Chao and Shen 2012)

[d] 1-D, where D is Simpson's species diversity index estimated by the minimum variance unbiased estimator (MVUE) (Magurran 1988)

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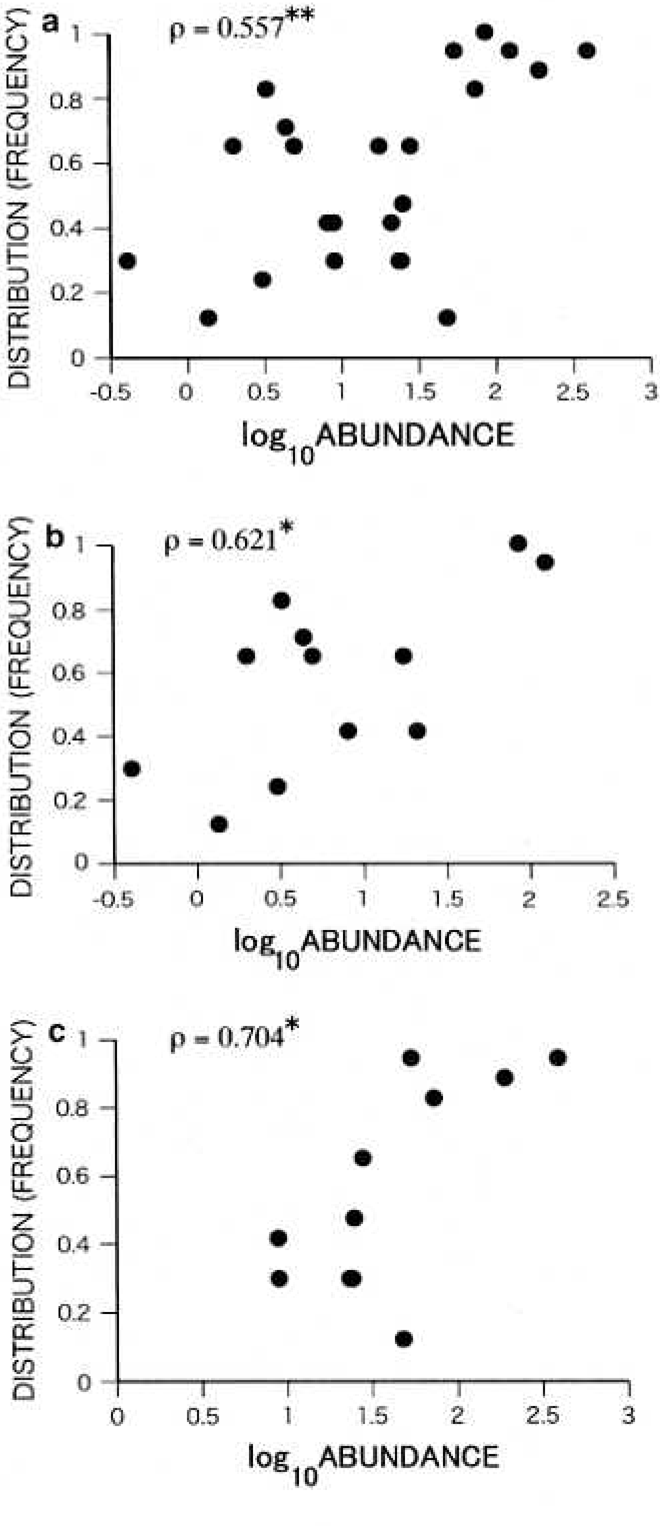

Fig. 3 Relationship between distribution (frequency of occupancy) and abundance (average number of individuals per year per site) for various dung beetle species. *a* all species; *b* tunneler species; and *c* dweller species

The figures showing the observed and expected species richness corresponded closely (Table 3). However, the expected species richness of the lately established Nakamura pasture had a large standard error (s.e.), which highly deviated from the observed species richness. Thus, the data by Nakamura were excluded from the subsequent analyses. The expected species richness was high at Ohsawa, Ohfukabori, and Fujinita, ranging from 17.0 to 18.7. In comparison, the expected species richness was low in the mountainous pasture of Happo and in the riverbed pastures of Kawamura, Uwasawa, and Kobayashi (7.7–9.1).

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The expected species richness significantly increased with the number of grazing years ($\rho = 0.691^{**}$). This relationship was recorded for the species richness of both tunnelers ($\rho = 0.572^{*}$) and dwellers ($\rho = 0.645^{*}$). The species richness of tunnelers also exhibited significant negative and positive correlations with soil hardness ($\rho = -0.741^{**}$) and vegetation height ($\rho = 0.728^{**}$), respectively; however, grazing years was not correlated with these two variables ($p > 0.05$). Species diversity (1-*D*) was the highest at Fujinita, followed by Ikeda, Minaminasu, Hohzukidaira, and Kobayashi, and was the lowest at Happo. Species diversity was not correlated with any climatic, vegetation, edaphic, or pasture management variables ($p > 0.05$). None of the nominal variables (i.e., cattle type, vegetation type, or ivermectin administration significantly affected the abundance, species richness, or species diversity of dung beetles (Wilcoxon's rank sum test, $p > 0.05$).

Distribution and abundance of dung beetles

Twelve dung beetle species were found in more than 10 pastures (Table 2), despite the survey pastures being distributed across a wide range of environmental gradients (Fig. 2). This observation indicated that these dung beetle species are euryokous.

We excluded *C. pecuarius* and *M. samurai* from the analysis of the relationship between interspecific distribution and local abundance, because these two species were only recorded once during the 3-year survey (Table 2). As local species abundance increased, the distribution range (frequency of occurrence in the pastures) significantly expanded ($\rho = 0.557^{**}$) (Fig. 3a). When tunnelers (12 species) and dwellers (11 species) were analyzed separately, the same relationship remained consistent for both groups (correlation for tunnelers and dwellers: $\rho = 0.621^{*}$ and $\rho = 0.704^{*}$, respectively; Fig. 3b, c).

Partitioning of species diversity

The survey was conducted in the different three areas that were separated according to the geographical and topographical conditions (Fig. 1), which were expected to influence the spatial structure of beetle diversity. Thus, we partitioned β-diversity into 2 hierarchical levels; within area β_1 and between area β_2 (Table 4). The results indicated that, while the contribution of observed α-diversity (within pasture) to regional γ-diversity was the largest (47 %), it was significantly smaller than the expected α-diversity ($p < 0.001$). In comparison, the observed β_1 (within area) and β_2 (between area) diversity (which contributed to 31 and 22 % of γ-diversity, respectively) was significantly larger than expected ($p < 0.001$).

Table 4 Hierarchical additive partitioning of regional γ-diversity in the pasture dung beetle communities

Diversity component[a]	Observed (%)[b]		Expected (%)[b]	Randomization test
α	2.62 (47.1)	<	4.59 (69.6)	$p < 0.001$
β_1	1.72 (30.9)	>	1.00 (15.2)	$p < 0.001$
β_2	1.22 (22.0)	>	1.00 (15.2)	$p < 0.001$
γ	5.56		6.59	

[a] True diversity component of the Simpson's index

α within pasture, β_1 within area, β_2 between area, and γ regional total diversity

[b] Figures in parentheses represent percentage occupied in the total diversity γ

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Discussion

In this study, 25 dung beetle species belonging to Geotrupinae, Scarabaeinae, and Aphodiinae were recorded. The number corresponded to 46 % of the species in these subfamilies that were found in Tochigi Prefecture (Tochigi Prefecture 2003), which is one of the most species-rich districts for dung beetles in Japan (Tukamoto 2003). This finding indicates that these pastures contain diverse dung beetle fauna. Pastures generally have high dung-beetle abundance and diversity, because they are rich in dung resources produced by large livestock, such as cattle and horses (Hanski and Cambefort 1991b; Barbero et al. 1999; Lobo et al. 2006; Zamora et al. 2007; Jacobs et al. 2010). In addition, the pastures in this landscape might have had high dung beetle diversity for historical, geographical, and landscape reasons. First, there is a long history of animal production in this region, where the grazing of horses and cattle has been actively and widely operated for hundreds of years; hence, this landscape probably conserves rich dung beetle fauna (Imura 2012). Second, the surveyed landscape is located at a temperate latitudinal region (36°30′–37°10′N, Fig. 1), with a broad altitude range (147–1011 m; Table 1; Fig. 2), which might facilitate the co-occurrence of cool-climate-adapted dwellers (12 species) and warm-climate-adapted tunnelers (13 species) (Table 2) (Hanski and Cambefort 1991b). Finally, the arrangement of many pastures surrounded by natural vegetation in this landscape might also contribute to the observed higher beetle diversity (Imura et al. 2011).

There was large variability in beetle abundance among the pastures (Table 2). The data also showed that beetle abundance declined with increasing altitude. A similar relationship was observed in the Iberian mountains of Spain (Martín-Piera et al. 1992; Romero-Alcaraz and Ávila 2000a) and the Slawesi mountains of Indonesia (Hanski and Niemelä 1990). However, when analyzed separately, dwellers showed this relationship, whereas tunnelers did not. Altitude was closely correlated with annual precipitation ($\rho = 0.975^{***}$) in this region (Fig. 2). The larval development and adult activity of Aphodiid dwellers mainly occurs in dung pats on the ground; hence, these species might be more adversely influenced by a greater amount of rain that washes away the dung on the ground at higher altitudes.

The observed and expected species richness corresponded closely, indicating that the 3-year survey period provided a good representation of the dung beetle fauna of pastures. Species richness was negatively correlated with annual solar radiation and soil hardness. Since the two variables were highly correlated ($\rho = 0.714^{**}$), increasing annual solar radiation might indirectly affect species richness by increasing soil hardness. Climatic factors are known to modify soil condition for dung beetles (Lumaret and Kirk 1991). When the functional groups were separated, the species richness of dwellers was not correlated with any environmental variables, whereas that of tunnelers was negatively correlated with soil hardness and positively correlated with vegetation height. Vegetation height indicates the extent of disturbance to pastures, such as grazing and trampling by cattle, which also cause soil compaction (Negro et al. 2011b). Thus, tunnelers are expected to be more sensitive to cattle disturbance (Jankielsohn et al. 2001; Negro et al. 2011b) through the effect of soil compaction compared to dwellers, as suggested in previous studies (Doube 1991; Davis 1996). Previous studies also support our finding that soil type and vegetation cover minimally influence dwellers (Hanski 1991; Hanski and Cambefort 1991a; Jay-Robert et al. 2008a). The present study indicated that environmental factors influenced the species richness of tunnelers and the abundance of dwellers.

Species richness significantly increased with an increase in the number of grazing years, with this relationship also being separately observed for both tunnelers and dwellers. According to the colonization theory (MacArthur and Wilson 1967; Simberloff and Wilson

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1969), isolated vacant habitats receive increasingly more species through colonization as time lapses. However, the observed species richness of the recently established Nakamura was exceptionally large, contradicting the species richness-grazing years' relationship. Surrounding land-use also influences the species richness of dung beetles. For instance, broad-leaved deciduous forests and pastures increase species richness, whereas artificial coniferous forests decrease species richness (Imura et al. 2011). The prediction model of species richness based on those land-use parameters indicated that the Nakamura area is a dung beetle hotspot in this region. Thus, the number of grazing years is expected to superimpose a long-term effect on the species richness of beetle communities, with the species richness also being influenced by the local conditions.

In this study, we could not detect any adverse effects of conventional ivermectin administration on the abundance, species richness, or species diversity of dung beetles. There have been extensive studies about the nontarget adverse effects of anthelmintics, including ivermectin, on dung beetles (e.g., Lumaret and Errouissi 2002; Suarez 2002; Floate et al. 2005). However, field assessments in which cattle are treated with anthelmintics on pastures remain rare, with variable outcomes (Krüger and Scholtz 1998a, b; Kryger et al. 2005; Römbke et al. 2010; Webb et al. 2010). The extent to which ivermectin affects dung beetle communities in the field possibly depends on a number of factors, including climatic conditions, the spatial scale of treatment, and the proportion of animals treated (Krüger and Scholtz 1998b; Kryger et al. 2005). Thus, large-scale and long-term field studies are required to confirm the effects of anthelmintics on dung beetle community structure and diversity in pastures (Lumaret and Errouissi 2002; Suarez 2002; Floate et al. 2005). In particular, species that are highly susceptible to ivermectin, such as *Copris* species (Iwasa et al. 2007), require careful assessment under actual grazing conditions.

A positive relationship between local abundance and the distribution range of species is a ubiquitously observed phenomenon in taxonomic assemblages (e.g., Hanski 1982; Brown 1984; Lawton 1993; Gaston 1996). In this study, all dung beetles combined demonstrated this relationship, as well as the specific tunneler and dweller functional groups. The present results, in combination with those of previous studies (Hanski and Koskela 1978; Hanski 1982; Lobo 1993; Romero-Alcaraz and Ávila 2000b), indicate that a positive distribution–abundance relationship is common in dung beetle communities. A number of hypotheses have been proposed to explain the causal mechanisms of this positive relationship, including sampling artifact, aggregated distribution, niche availability, habitat selection, and metapopulation dynamics, among others (Gaston et al. 1997; Holt et al. 1997; Borregaard and Rahbek 2010). While we did not investigate the causal mechanisms in this study, it is likely that several mechanisms jointly contribute to the relationship, with different relative importance depending on the circumstances (Gaston et al. 1997). Irrespective of the causal mechanisms, Lawton (1993, 1996) suggested that the positive distribution–abundance relationship is significant in the context of conservation. That is, species with a restricted distribution range also tend to have small local populations, which increase their vulnerability to human effects and risk of extinction (i.e., double jeopardy) (Lawton 1996). In fact, Freckleton et al. (2005) suggested that this relationship caused the decline in the regional tree sparrow population in Britain. Therefore, two coprid species *C. actidens* and *C. pecuarius*, which were particularly rare and locally restricted in this landscape, should be of significant conservation concern (note, the major habitat of *M. samurai*, which was rare in this study, is not pastures; Kawai et al. 2005). The results of this study also indicate that the continuous monitoring of the distribution and abundance of dung beetle populations at a landscape scale is necessary for effective conservation.

The regional structure of organism diversity at a landscape scale has been analyzed using within community (α) diversity and between community (β) diversity (Whittaker 1972; Magurran 1988; Southwood and Herderson 2000). To understand how ecosystems function for biodiversity conservation and ecosystem management, it is important to specify how species composition and distribution are determined (Legendre et al. 2005). Hence, the relative importance of diversity components should be tested by ensuring that the partitioning of the components allows them to be independent and additive (Jost 2007). The hierarchical additive partitioning of regional (γ) diversity into within pasture α, within area β_1, and between area β_2 diversity indicated that, while the contribution of the observed α-diversity to total (γ) diversity was largest, the observed β_1 (within area) and β_2 (between area) diversities were significantly larger compared to expected β_1 and β_2 values. The two observed β-diversity components contributed respectively to about 20–30 % of the regional γ-diversity. Analysis of dung beetle community structure through the additive partitioning of diversity components has also been carried out in heterogeneous landscapes containing pastures (Verdú et al. 2007; Numa et al. 2009; Negro et al. 2011a; 2011b). As found in the present study, α-diversity contributed to the largest part of γ-diversity, but not significantly, with hierarchically partitioned β-diversity components being significantly larger than expected by chance, irrespective of landscape scale (Numa et al. 2009; Negro et al. 2011a, b). The β-diversities of dung beetles indicated the presence of spatial heterogeneity that was associated with local and topographical conditions in this landscape; however, previous studies about dung beetles (Jay-Robert et al. 1997; Davis et al. 1999; Escobar et al. 2007) reported that β-diversity indicated species turnover along environmental gradients (such as altitude).

Legendre et al. (2005) proposed 3 hypotheses about the origin of β-diversity: (1) species composition is uniform over large areas; (2) species composition fluctuates in a random, autocorrelated way, with different parts of the ecosystem possibly sustaining different species compositions for historical reasons; and (3) species distributions are related to environmental conditions, with landscapes forming mosaics in which species composition is controlled by environmental site characteristics. The current study supported the second and third hypotheses, as β-diversities were significantly larger compared to those of neutral models. Hence, each area might have different exploitation and grazing history, such as cattle disturbance and grazing years, as indicated in the current study. The present results indicate that differences in climatic, edaphic, and pasture management conditions might also be responsible for the observed β-diversities of beetle communities. The second hypothesis implies that areas supporting different species composition large enough to minimize the risk of species extinction should be protected (Legendre et al. 2005). The third hypothesis implies that protected areas should represent the different types of habitat used by a given species, with each area being of sufficient size to be sustainable (i.e., prevent local extinction). Ultimately, habitats representing favorable dispersal routes (i.e., corridors) should be given special protection focus (Legendre et al. 2005).

Gering et al. (2003) concluded that regional conservation management programs targeted towards increasing hierarchical β-diversities of arboreal beetle diversity would be more effective than increasing α-diversity. Hence, based on these hypotheses, in combination with a recent decline and abandonment of pastures in this landscape, individual pastures and pastures encompassing certain areas should be maintained to conserve dung beetle diversity. Macagno and Palestrini (2009) also concluded that the maintenance of small pastures in a landscape mosaic of closed forests of the Alpine mountain belt would be effective towards conserving dung beetle diversity.

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