RESPONSE OF DUNG BEETLE COMMUNITIES (COLEOPTERA: SCARABAEIDAE) ACROSS GRADIENT OF DISTURBANCE IN THE TROPICAL LOWLAND FOREST OF BUTON, SULAWESI

RESPONS KOMUNITAS KUMBANG TINJA (COLEOPTERA: SCARABAEIDAE) PADA GRADIEN GANGGUAN DI HUTAN DATARAN RENDAH BUTON, SULAWESI

Mariana Silvana Moy^{1,2}, Ani Mardiastuti³, Sih Kahono⁴

¹Tropic Biodiversity Conservation Graduate School of IPB, Darmaga Campus, Bogor, 16680 ²Program Studi Agroteknologi, Fakultas Sains dan Teknologi, Universitas Kristen Wira Wacana Sumba, Waingapu, Sumba Timur ³Department of Conservation of Forest Resources and Ecotourism, Faculty of Forestry, IPB, Darmaga Campus, Bogor 16680 ⁴Research Center for Biology, Indonesian Institute of Sciences, Cibinong, Bogor e-mail: yanemoy@gmail.com

(diterima September 2015, direvisi April 2016, disetujui Juli 2016)

ABSTRAK

Informasi mengenai bagaimana gangguan antropogenik dapat meningkatkan hilangnya keanekaragaman serangga penting di sebuah pulau, seperti kumbang tinja (Coleoptera: Scarabaeidae) masih sedikit diketahui. Penelitian ini bertujuan untuk mempelajari respons kumbang tinja pada gradien gangguan habitat di hutan dataran rendah sekunder (Hutan Lambusango, Sulawesi, Indonesia). Dari bulan Juni sampai Agustus 2013, kumbang tinja telah dikoleksi dari hutan dengan gangguan rendah, sedang, dan tinggi Tiap level gangguan terpasang tiga transek berjarak 500 m(n=9) Sepuluh perangkap jebak per transek dengan umpan dari kotoran sapi terpasang sepanjang 100 m, selama 48 jam. Total 1710 individu dari 29 spesies kumbang tinja terkoleksi. 79% dari spesimen yang terperangkap dan 55% dari kekayaan spesies ditemukan di gangguan rendah daripada di gangguan sedang maupun tinggi, sedangkan indeks Shannon-Wienner sangat berbeda nyata di gangguan sedang. Ordinasi dua dimensi berdasarkan indeks Bray-Curtis menunjukkan perbedaan komposisi spesies kumbang tinja antar level gangguan. Penelitian ini menemukan komunitas kumbang tinja di hutan dataran rendah sekunder menunjukkan respons yang besar terhadap level gangguan.

Kata kunci: kumbang Scarab, keragaman, hutan sekunder, Sulawesi Tenggara

ABSTRACT

Little is known about how antropogenic disturbance triggered the biodiversity loss of functionally important insect groups in an island, including dung beetle (Coleoptera: Scarabaeidae). This study focused on the responses of dung beetle across gradient of disturbance in a secondary tropical lowland rainforest (Lambusango forest, Sulawesi, Indonesia). From June to August 2013, dung beetles were collected in the forest with low, intermediate, and high level of disturbances. Each disturbance level had three transects which were separated at least 500 m each other (n=9). Ten pitfall traps per transect baited with cattle dung were set, along 100 m transect for 48 hours. A total of 1.710 dung beetles, representing 29 species, were collected. Total 79% trapped specimens and 55% of species richness was found in the intermediate disturbance, which it was significantly differed compare to two other disturbances. Shannon-Wienner index was significantly higher in low disturbance. A two-dimensional scalling plot based on Bray-Curtis index indicated the different species composition of the beetles between disturbance levels. We concluded that dung beetle assemblages of secondary lowland rainforests appeared a robust respond to the disturbance levels.

Keywords: Scarab beetle, diversity, secondary forest, Southeast Sulawesi

INTRODUCTION

Inevitably, the alteration of the tropical rainforest has affected the rate and pattern of biodiversity loss over decades (Mace 2005). In general, a dramatically forest conversion has retreated the mosaic of species, either species richness or abundance has decreased due to habitat modification (Schulze et al. 2004). Moreover, it was not merely influenced the local diversity (α -diversity), but also triggered and accelerated the turn over of species per se (Kessler et al. 2009; Quintero et al. 2010). Nevertheless, some species has evolved and obtained benefit due to habitat pressures, including the diversity of the Sulawesi endemic bird species (e.g. Waltert et al. 2005). Despite this well-known trend of biodiversity, insect diversity in lowland forests on a remote island has been poorly understood (Abdulhadi et al. 2014).

Dung beetles (Coleoptera: Scarabaeidae) were an excellent provider of ecosystem service due to their function as megafauna detritivore of dung and carrion (Begon et al. 2006) and their behavior that supported the ecological process, such as nutrient recycling, dispersal of seeds, and soil perturbation (Estrada & Coates-Estrada 1991; Hanski & Cambefort 1991; Nichols et al. 2008, Scholtz et al. 2009). The taxon also has well understood in taxonomy (Hanski & Cambefort 1991). All traits have emplaced the dung beetle as an invertebrate main bioindicator for examining the relationship between biodiversity and forest conversion (Davis et al. 2001; Spector 2006). In tropical rainforest, many studies documented that dung beetle displayed rapid and graded responses to many kinds of natural and anthropogenic disturbance (e.g. Barragan et al. 2011; Davis 2000; Hanski & Krikken 1991; Jankielsohn et al. 2001; Kahono & Ubaidillah 2003; Nichols et al. 2008; Shahabuddin et al. 2005). Hallfter & Arellano (2002) addressed that forest-restricted species reduced significantly due to deforestation and replaced by open-area species, further the habitat modification likely influenced the functional loss of dung beetle (Braga et al. 2013). In addition, due to their dependences on vertebrate dung, the beetle assemblages were used to predict the distribution and population of mammals (Estrada et al. 1993).

In lowland rainforest, the diversity of dung beetle was enormous. Davis (2000) identified 97 species of dung beetle inhabit evergreen dipterocarp forest in Sabah, Malaysia in 1992. In contrast, recently, the asset of dung beetle diversity in there has declined sharply because of forest logging (Slade *et al.* 2011). All facts showed that indeed lowland forest likely facing similar trend of diversity due to habitat alteration.

Here we provided the first recorded of dung beetle response to habitat disturbance in a secondary lowland rainforest on Sulawesi Islands. The synthesis of dung beetle diversity in this secondary rainforest addressed the following questions:

- Did the dung beetle community present a responds across gradient of habitat disturbances?
- 2. Did the species community responds to disturbance in a specific composition?

RESEARCH METHODS

Study Site

The study area located in Lambusango Forest, Buton Island, Southeast Sulawesi (5° 24'S, 123°07'E) (Figure 1). The secondary lowland rainforest covered the 65.000 ha area. The diversity of dung beetle was studied in three locations with different levels of disturbances (low (undistubed forest, 5°27'S, 122°95'E), intermediate (disturbed forest, 5° 18'S, 122°88'E) and high (cashew plantation, 5° 18'S, 122°89'E) (Table 1). For each location, three transects were selected for replication. Basically, the forest sites with low and intermediate level of disturbances have selected based on transect and grid that established by Operation Wallacea (Seymour 2004). The plantation sites with high level of distubarnces

were selected irrespective of Operation Wallacea.

Sampling

Dung beetles were collected at each site by using baited pitfall traps on June (intermediate disturbance) to July (low and high level of disturbance), 2013. The pitfall traps were made from a transparent plastic cups, with a diameter of 6.5 cm and a height of 9 cm. Each trap was baited with ca 20 g of fresh cattle dung (*Bos taurus*). We followed Shahabuddin *et al.* (2005) in setting the bait. Three transect with ten pitfall traps along a 100 m per transect were set up in each disturbance levels.. The interval between transects were 500 m. All traps were exposed for 48 hours without baited replacement.

Specimens were stored in 96% alcohol and later identified using Balthasar (1963), Boucomont (1914), and the works on Scara-

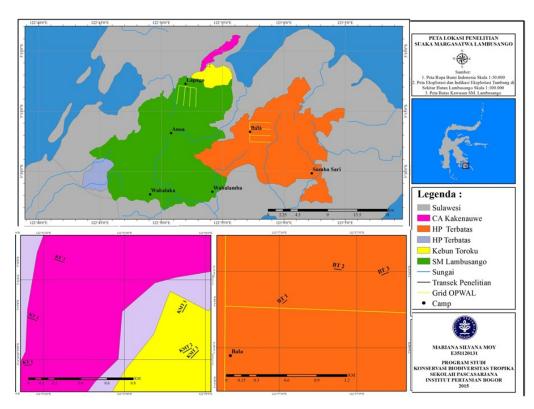


Figure 1. Location of study sites in Lambusango Forest, Buton Island Tenggara.

Level of disturbance	Habitat type	Habitat description*		
Low	Undisturbed	Secondary forest with an area of 1,200 hectare (total area		
	forest	35,000 ha), elevation 345-431 m asl, trunk diameter of breast		
		height (DBH) up to 30 cm and tree height up to 20 m, rattan		
		covering forest floor, low accestability (5.14 km from the near-		
		est village and 3-4 hours by walking to reach from the village)		
Intermediate	Disturbed for-	Secondary forest with an area of 100 hectare (total area 810		
	est	ha), located in 172-259 m asl. DBH up to 10 cm and tree		
		height up to 20 m, logging and rattan harvest countinously,		
		<1.0 km from nearest village, <100 m from the mainroad		
		road, 45 minutes by walking to reach from the village		
High	Cashew plan-	Unmanageable garden with an area of 2 hectare, located at 86-		
	tation	172 m asl. dominated by cashew plantation and grasses, 1.0 km		
		from village, close to main road, cattle grazing		

Tabel 1. Habitat characteristic for sampling sites of dung beetle in Lambusango forest.

*Seymour (2004)

baeidae by Krikken and Huigbregts (e.g. Krikken & Huijbregts 2008). Identification was up to species level. If there were uncertainty about the species name, they were sorted to genus. Voucher collections were deposited at the Entomology Museum of Indonesian Institute of Science, Bogor.

Data Analysis

The R-Statistic (R Development Core Team 2011) was used to calculate both parametric and non-parametric analysis. Species richness and abundance of the beetles were compared between levels of disturbances with using ANOVA test, while the confirmation of the significant difference by Tukey's HSD Test (Gotelli & Ellison 2013). Shanon-Wiener Index (H'=- Σ p_i ln p_i) was used to assess the local diversity, Simpson Index to measure species dominance (D= Σ [n_i(n_i-1)/N(N-1)], and Shannon-Wiener Eveness to measure species eveness [J'=H'/ln(S)] (Magurran 2004). Significancy of species richness was analyzed used t test (t= $[H_1' - H_2']/[var H_1' + var H_2']^{1/2}$ with variance (Var H'= $[(\Sigma p_i(\ln p_i)^2 - (\Sigma p_i \ln p_i)^2)/$ N]-[(S-1)/2N²)] and degrees of freedom (df= $(Var H'_1 + Var H'_2)^2 / \{ [(Var H'_1)^2 / N_1] + [(Var H'_1)^2 /$ $H'_2)^2/N_2$ (Maguran 1988). Estimator Chao₁ was used to estimate species richness through singletons species (f_1) and doubletons species (f₁) at each sites with equation: $S_{est}=S_{obs}+[f_1^2/$ $(2f_2)$], if $f_2>0$, and $S_{est}=S_{obs}+[f_1(f_1-1)/2(f_2+1)/$ 1)] if $f_2 = 0$ (Chao *et al.* 2009). Species composition of each site was ordinated by Non -Metric Multidimensional Scaling (NMDS) (Clarke 1993) using Bray-Curtis Index as distance measure. Analyse of Similarity (ANOSIM) was used to test significances test of similarities.

RESULTS AND DISCUSSION

Abundance and species richness

A total of 1.710 dung beetle belongings to 29 species, 3 genera (*Copris, Onthophagus,* and *Paragymnopleurus*) was collected in the present study (Table 2). The mean from total of trapped individual dung beetles (N) did not differ in the two level of disturbance (low and high), but was significantly higher at intermediate level of disturbance compared to all other sampled habitat (Figure 2 (a)). The mean from total number of individual dung beetle specimens (N) at intermediate level of disturbance (33.17 \pm 2.82) was ca. two times higher than in the low level of disturbance (12.70 \pm 1.60). The lowest abundance (11.13 \pm 2.54) was in the high level of disturbance.

Similarly, the mean of number of species (S) did not differ in the two level of disturbance (low and high), but was significantly higher at intermediate level of disturbance compared to all other sampled habitat (Figure 2 (b)). The mean number of species (S) in the three level of disturbance respectively was 5.30 ± 0.75 (low), 7.67 ± 0.44 (intermediate),

 3.9 ± 0.52 (high). Only 41% of the total of species richness occurred in all disturbance levels. Additionally, based on study literature, we discovered 23 endemic species, 12 species categorized as forest species, and eight of 29 species have functions as detritivore of anoa dung. The distribution of those species was fluctuated among all sites.

Species index and estimation

Sites with low level of disturbance owned the most diverse in the Shannon-Wiener Index (H') and the Index of Evenness (J'). There was a significant different in H' between intermediate disturbance and both low and high disturbance. The Index of dominance species (D) in the intermediate level of disturbance was the lowest (Table 3). The species estimator (Chao₁) displayed that based on the total number of rare dung beetle species (singletons and doubletons), all habitat types owned a possibility to obtain more species (Table 4). In total, approximately 2 to 25 new

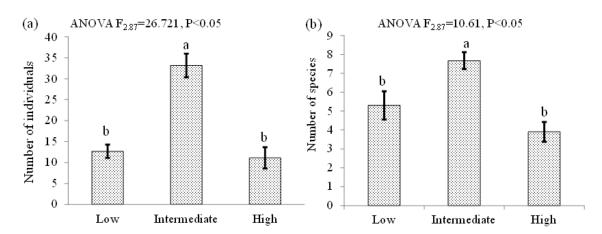


Figure 2. Mean number of individuals (a) and species richness (b) of dung beetle across gradient of three disturbance levels. Bars on each histograms indicate SE and the result of ANOVA are given. Different letters on top of the bars indicate significant differences between habitats.

Sub family Coprinae	Tribe Coprini	Species	Leve	l of habitat bance	distur-	Description	
		Species	Low	Interme- diate	High	- Description	
		Copris celebensis	11	3	0	Endemic in Sulawesi (ES) ^	
		Copris erratus masayu- kii	38	40	32	ES	
	Ontho- phagini	Onthophagus ambang morowali	0	3	0	ES; Forest Species (FS) **	
	1 6	Onthophagus ambang ambang	0	0	1	ES; FS**	
		Onthophagus aper	3	1	0	ES	
		Onthophagus aureopilo- sus	18	14	1	ES; FS**, <i>AD</i>	
		Onthophagus chandrai	0	1	0		
		Onthophagus curvicari- natus	24	42	10		
		Onthophagus discedens	1	0	0		
		Onthophagus fulvus	21	5	11	ES	
		Onthophagus fuscos- triatus	0	6	0	ES; FS-open area**, AD	
		Onthophagus griseoae- neus	54	12	82	ES; FS lowland-open area**	
		Onthophagus holos- ericeus	2	39	2	ES, AD	
		Onthophagus limbatus	0	0	1	ES; open area* AD,	
		Onthophagus matanyo	0	2	0	ES; FS lowland*	
		Onthophagus mekara	0	0	1	ES; FS lowland*	
		Onthophagus ribbei	94	78	15	ES, AD	
		Onthophagus rosen- bergi divergens	1	50	89	ES; FS**	
		Onthophagus rosen- bergi rosenbergi	20	22	1	ES; FS**	
		Onthophagus sarasi- norum	0	0	3	ES; FS**	
		Onthophagus sembeli	0	0	1	ES; FS**	
		Onthophagus schwaneri	0	1	0	ES	
		Onthophagus scrutator	3	51	16	ES, AD	
		Onthophagus sugihartoi	2	1	0		
		Onthophagus toraut	0	5	3	ES: FS**	
		Onthophagus vander- blomi	0	3	1	ES; FS lowland*	
		Onthophagus wallacei	12	34	32	ES, AD	
		Onthophagus sp 1.	0	2	0		
Scara- baeinae	Gymno- pleurini	Paragymnopleurus planus	77	580	32	AD	
	F 21	r	381	995	334		

Table 2. Diversity of dung beetle across gradient of habitat disturbance.

Source: ^(Balthasar 1963; Boucomont 1914; Krikken dan Huijbregts 2008,2009, 2011), * (Krikken dan Huijbregts 2009), ** (Krikken dan Huijbregts 2011), ^{AD} anoa dung (Shahabuddin *et a.* 2010)

species expected across gradient of disturbance. The number of expected species at high level of disturbance (25 species) was ca. 6 times higher than in the intermediate level of disturbance (4 species). The lowest of expected species (2 species) was in the low level of disturbance. The estimator of Chao₁ also forecasted that to fulfill the target, it needed an additional number of individual, i.e. for high level of disturbance, to reach out the asymptote of 100 % of total new species (g=1) needed 6631 individual, and around 2021 individual was needed to complete 90% of estimation target (g=0.90).

Community composition

Two-dimensional scaling based on Bray-Curtis similarity index displayed a clear separation of community of dung beetle among all type of disturbance (Figure 3). The similarity value in each type of disturbance successively 65.7% in low disturbance, 80.1% in intermediate disturbance, and 66.5% in high disturbance. The highest similarity occurred between site with low and intermediate disturbance (64.9%), while the lowest degree of similarity appeared between site with the intermediate and high level disturbance (59.0%). There was a significant difference among similarity of species composition along gradient of disturbance levels (R = 0.8272, P = 0.005).

Discussion

In lowland rainforest of Buton, both species richness and abundance of dung beetle assemblages increased in intermediate level of disturbance and decreased in high level of disturbance. The emergence response of dung beetle assemblages due to habitat modification displayed a different pattern with previous research in Sulawesi (Shahabuddin *et al.* 2005) and in others rainforest disturbance that located outside of Sulawesi (Davis *et al.* 2001; Filgueras *et al.* 2015; Halffter & Arrelano 2002; Nichols *et al.* 2007).

Although, no difference in species richness and abundance of dung beetles be found between low disturbance and high disturbance, the structure of dung beetle communities changed between low disturbance and high disturbance. In the intermediate level of disturbance, the site was not merely divers of species but also their structure more rich than two other sites. Statistically, only 41% of the total species occurred in each site, thereby indicating that each level of disturbances shaped and enriched more than 50% of dung beetles diversity. The variation of species was

Table 3. Alpha diversity index of dung beetle in three level of habitat disturbance.

Indices	L	р			
Indices	Low	Intermediate	High	Р	
Species number	16	23	19		
Shanon-Wienner Index (H')	2.182 ^a	1.709 ^b	2.111 ^a	0.05*	
Eveness (J')	0.787	0.545	0.717		
Dominance (D)	0.854	0.642	0.835		

expected due to different characteristics of each habitat. The intermediate disturbance located in disturbed forest that fragmented by permanent road and plantation, while the high level of disturbance covered by different vegetation (cashew plant) and also fragmented by permanent road. In contrast, the low level of disturbance located in intact forest.

Those facts similar with previous studies which explained that the characteristic of habitat supported the environmental carrying capacity and edge effect for species diversity. According to Connell (1978), the intermediate disturbance supported the highest of diversity due to more tolerant resources that benefit for refugee species. Previous work on species diversity in different forest structure and distance from road has revealed different results. Carpio *et al.* (2009) reported several rare species respond to road construction within an incredible rapid timeframe. While Shahabuddin *et al.* (2005) found that both species richness and abundance diminished along change of rainforest towards agroforestry systems and annual culture. Forest fragment and human made habitat provided horizontal and vertical diversity of the vegetation that influence significantly on the distribution of non-flying mammals, a producer of dung (Estrada *et al.* 1998).

The probability of species expansion in lowland forest still higher due to a massive environmental carrying capacity (Davis *et al.* 2001; Hanski 1983;), e.g. types of dung (Estrada & Coates-Estrada 1991; Estrada *et al* 1993; Tshikae *et al.* 2008) and the numbers of mammals (Nichols *et al.* 2009). In other hand, Shahabuddin *et al.* (2010) stressed on the body

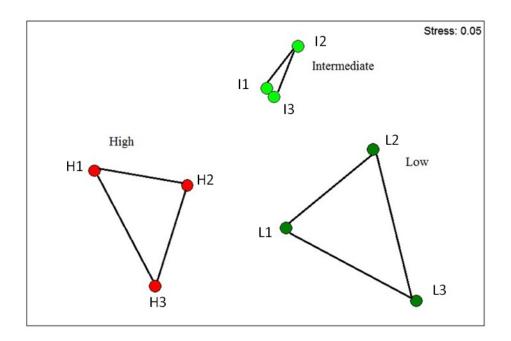


Figure 3. Two dimensional scaling of fauna similarity based on Bray-Curtis index for dung beetle communities in the three types of disturbance (stress=0.05). Line connect site belonging to the same type of disturbance.

Level of disturbance	n	S _{obs}	Chao ₁	\mathbf{f}_1	\mathbf{f}_2	\mathbf{q}_0	n*(g=1)	n*(g=0.95)	n*(g=0.90)
Low	381	16	18	2	1	0.005	1026	304	40
Intermedi- ate	995	23	27	4	2	0.004	3589	1081	391
High	334	19	44	7	1	0.021	6637	2831	2021

 Table 4. Asymptotic estimator for individual-based sampling of dung beetle.

Notes: n=no.individuals collected; S_{obs} =observed species richness; S_{est} =estimated asymptotic species richness based on the Chao₁ index; f_1 =the no.species represented by exactly one ind. (singletons); f_2 =the no.species represented by exactly two ind. (doubletons); q_0 = the probability of next ind. sampled represents a previously undetected species, calculated as (f1/n); n*=estimated no additional ind. needed to be sampled to reach 100% of Chao₁(g=1), 95% of Chao₁ (g=0.95), and 90% of Chao₁ (g=0.90).

size boosted the mobility and dispersal of species which large-bodied species supported the mobility of dung beetle for food hunting at different scale of distance, but it more sensitive to habitat disturbance and the ratio of large to small-sized dung beetles declined with land-use intensity. Nonetheless, some large species showed their dominance in natural open area than disturbed habitat (Jankielsohn *et al.* 2001). Recently, Viegas *et al.* (2014) presented that dung beetle diversity correlated positively with both coverage and density of leaf litter and canopy cover.

The robust response of new species indicated that the anthropogenic habitat transformation in the high level of disturbance provided benefit for the diversity of dung beetle, with the following assumption, e.g. 1) the availability of dung resource was sufficient, due to the habitat also used for cattle grazing, therefore the dung reservoir was adequate for resource partitioning, 2) the distance of cashew plantation was closed to the forest, then the site was suitable for buffer area for dung beetle, especially for the large-body species. In contrast, both in the low and interme-

diate le-vel of disturbance, the number of expected species diminished due to the community in both site has succeeded achieved their population stability. Hanski (1991) mentioned that both type and size of dung was the micro habitat of dung beetle that supported the diversity of dung beetle. Additionally, Estrada et.al (1993) stated that in rainforest, both herbivore and omnivore mammals were the important resource producer in providing dung to the assemblage. Similarly, coolbeetle in temperate forests, most of 14 species collected possessed the ecological characteristic of selecting specific mammalian feces (Japanese macaques, Asiatic black bears, Japanese serows, and cattle) (Enari et al. 2013).

The similarity in species composition may supported by different type of niche and guild of dung beetle. In Lambusango rainforest, species composition of Scarab beetle separate into three niches (generalist, forest specialist, and synanthropogenic species) and two guilds (roller and tunneller). Variation of spatial process, resource partitioning, and flight activity played the important rules in shaping niche and guild (Hanski & Cambefort 1991).

From northern temperate to tropical, dung beetles are classified into grassland species and forest species, and in the tropics, grassland and forest own the different diversities of dung beetles distinctly each other and there is no overlap in species composition between them (Hanski and Cambefort 1991). However, some forest dung beetles are synanthropogenic species that have strong adaptation with human modified landscape and such species make the differences (Horgan 2007). The different composition of dung beetle assemblage from natural forest to man-made habitat also found in Shahabuddin *et al.* (2005).

CONCLUSION

In conclusion, dung beetle assemblages of the lowland rainforest of Buton Island presented a rapid response across gradient of habitat disturbances. The pattern of response was unique which it sharply increased in the intermediate level of disturbance and diminished in high level of disturbance. There was a distinct dissimilarity of species composition among all type of disturbance. Furthermore, upcoming studies may focus on (1) the diversity of dung beetle in omnivore dung, (2) the relationship between body size and habitat gradient, and (3) how the relationship between dung beetle diversity and its ecological roles in lowland rainforest.

ACKNOWLEDGMENTS

We thank to Balai Konservasi Sumber Daya Alam Kendari and Department of Forestry-Buton District, who kindly provided all necessary permission to conduct our field research. We are grateful to Operation Wallacea Management, Dr. David Tosh and Dr. Nancy Priston, as field head scientist, who kindly encouraged and support us in the field. We are grateful to La Alinudin who assisted us in the field. Speciall thanks to Darren Mann who assisted us in all specimen identification, Jan Krikken who provide us for additional identification and excellent articles, and Ilka Hanski who supported us in discussion and articles. We thank to Laboratory of Biological Control, IPB, who provided equipments for identification. The field research was funded by the Operation Wallacea in 2013.

REFERENCES

- Abdulhadi, R., Widjaja, E. A., Rahayuningsih, Y., Ubaidillah, R., Maryanto, I. & Rahajoe, J. S. (Editor.) (2014). Kekinian keanekaragaman hayati Indonesia. Jakarta: LIPI-BAPPENAS-KLH.
- Balthasar, V. (1963). Monographie der Scarabaeidae und Aphodiidae der palaerktischen und orientalischen region Coleoptera: Lamellicornia Volume 1-2. Czechoslovakian Academy of Science.
- Barragán, F., Moreno, C. E., Escobar, F., Halffter, G. & Navarrete, D. (2011). Negative impacts of human land use on dung beetle functional diversity. *PLoS-One*, 6(3), e17976.
- Begon, M., Townsend, C.R., & Harper, J.L. (2006). Ecology from Individuals to Ecosystems, Fourth Edition. (pp 330). UK: Blackwell Publishing.
- Braga, R. F., Korasaki, V., Andresen, E. & Louzada, J. (2013). Dung beetle community and functions along a habitatdisturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. *PloSOne*, 8(2), e57786.
- Boucomont, A. (1914). Les Coprophages de l'Archipel Malais. Annales de la Societe

entomologique de France Paris, 83, 238-350.

- Carpio, C., a NDonoso, D., Ramón, G. & Dangles, O. (2009). Short term response of dung beetle communities to disturbance by road construction in the Ecuadorian Amazon. Ann. la Société Entolomologie. Fr., 45(4), 455–469.
- Chao, A., Colwell, R. K., Chih-Weilin. & Gotelli, N. J. (2009). Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, *90*(4), 1125–1133.
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117-143.
- Connel, J. H. (1978). Diversity in tropical rain forest and coral reefs. *Science*, *199*, 1302-1310.
- Davis, A. J. (2000). Species richness of dungfeeding beetles (Coleoptera: Aphodiidae, Scarabaeidae, Hybosoridae) in tropical rainforest at Danum Valley, Sabah, Malaysia. *The Coleopterists Bulletin*, 54(2), 221-231.
- Davis, A. J., Holloway, J. D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A. H. & Sutton, S. L. (2001). Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology*, 38, 593-616.
- Enari, H., Koike, S. & Sakamaki, H. (2013). Influences of different large mammalian fauna on dung beetle diversity in Beech forests. *Journal of Insect Science*, *13*(54), 1–13. dx.doi.org/10.1673/031.013.5401.
- Estrada, A. & Coates-Estrada, R. (1991). Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, 7, 459-474.
- Estrada, A., Halffter, G., Coates-Estrada, R. & Meritt, D. A. (1993). Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, 9, 45-54.
- Estrada, A., Coates-Estrada, R., Dadda, A. A. & Cammarano, P. (1998). Dung and carrion beetles in tropical rainforest fragment and agricultural habitat at Los

Tuxtlas, Mexico. *Journal of Tropical Ecology*, 14, 577-593.

- Gotelli, N. J. & Ellison, A. M. (2013). *A* primer of ecological statistica 2nd edition: new chapters estimating species diversity-estimating species abundance. Massachuset: Sinauer Associates.
- Halffter, G. & Arellano, L. (2002). Response of dung beetle diversity to human induced-change in a tropical landscape. *Biotropika*, 34, 144-154.
- Hanski, I. & Niemelä, J. (1989). Elevational distributions of dung and carrion beetles in northern Sulawesi. In *Royal Entomological Society symposium on project wallace expedition*. 1989 (pp. 145-152). United Kingdom: Royal Entomological Society London.
- Hanski, I. & Krikken, J. (1991). Dung beetles in tropical forest in South-East Asia. In I. Hanski & Y. Cambefort (Editor), *Dung beetle ecology* (pp. 179-197). New Jersey: Princeton University Press.
- Hanski, I. & Cambefort, Y. (1991). Resource partitioning. In I. Hanski & Y. Cambefort (Editor), *Dung beetle ecology* (pp. 330-349). New Jersey: Princeton University Press.
- Horgan, F. G. (2007). Dung beetles in pasture landscape of Central America: proliferation of synanthropogenic species and decline of forest specialists. *Biological Conservation, 16*, 2149-2165.
- Jankielsohn, A., Scholtz, C. H. & Louw, S. Vdm. (2001). Effect of habitat transformation on dung beetle assemblages: a comparison between a South African nature reserve and neighboring farms. *Environmental Entomology, 30*, 474-483.
- Kahono, S. & Ubaidillah, R. (2003). Diversity and abundance of dung beetle (Scarabaeidae: Coleoptera) in the tropical rainforest around Pa'raye village, Kayan Mentarang National Park East Kalimantan. In A. Mardiastuti, & T. Soehartono (Editor), *Joint biodiversity expedition in Kayan Mentarang National Park*, (pp. 248-258). Jakarta: Ministry of Forestry-WWF Indonesia-ITTO.
- Kessler, M., Abrahamczyk, S., Bos, M., Buchori, D., Putra, D. D., Gradstein, S. R., Hohn, P., Kluge, J., Orend, F., Pitopang, R., Saleh, S., Schulze, C. H., Sporn, S. G., Steffan-Dewenter, I.,

Tjitrosoedirdjo, S. S. & Tscharntke, T. (2009). Alpha and beta diversity of plants and animals along a tropical land-use gradient. *Ecological Application*, *19*, 2142-2156.

- Krikken, J. & Huijbregts, J. (2008). Sulawesi large-eyed *Onthophagus* and their relatives: seven new species, with a key (Coleoptera: Scarabaeidae: Scarabaeinae). *Tijdschrift voor Entomologie, 151*, 155–171.
- Krikken, J. & Huijbregts, J. (2009). Sulawesi Onthophagus with paraocular protrusions: ten new species, with a key (Col.: Scarabaeidae: Scarabaeinae). Tijdschrift voor Entomologie, 152, 209–236.
- Krikken, J. & Huijbregts, J. (2011). Taxonomy of Sulawesi Onthophagus lacking a basal pygydial ridge (Col: Scarabaeidae: Scarabaeinae). Tijdschrift voor Entomologie, 154, 229–268.
- Mace, G., Masundire, H. & Baillie, J. (2005). Biodiversity. In R. Hassan, R. Scholes, & N. Ash (Editor), Biodiversity in ecosystems and human well-being volume 1: current state and trends, millenium ecosystem assessment, (pp. 77-122). USA: Island Press.
- Magurran, A. E. (2004). *Measuring biological diversity*, (pp. 108). Oxford: Blackwell Publishing Company.
- Magurran, A. E. (1988). *Ecological diversity and its measurement*, (pp. 35). Cambridge: Cambridge University Press.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S. & Favila, M. E. (2008). Ecological functions and ecosystem services providedby Scarabaeinae dung beetles. *Biological Conservation*, 141, 1461-1474.
- Nichols, E., Gardner, T. A., Peres, C. A., Spector, S. & The Scarabaeinae Research Network. (2009). Co-declining mammals and dung beetles: an impending ecological cascade. *Oikos*, *118*, 481-487.
- Quinterro, C., Morales, C. A. & Aizen, M. A. (2010). Effects of anthropogenic habitat disturbance on local pollinator diversity and species turnover across a precipitation gradient. *Biodiversity Conservation*, 19, 257-274. doi:10.1007/s10531-009-9720-5.
- R Development Core Team. (2011). R: a language and environment for statistical

computing. Vienna: R Foundation for Statistical Computing.

- Scholtz, C. H., Davis, A. L. V. & Kryger, U. (2009). *Evolutionary biology and conservation of dung beetle*. Moscow: Pensoft Publisher.
- Schulze, C. H., Waltert, M., Kessler, P. J. A., Pitopang, R., Shahabuddin., Veddeler, D., Mühlenberg, M., Gradstein, S. R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004). Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications*, 14(5):1321-1333.
- Seymour, A. (Editor) (2004). Operation wallacea report: monitoring forest degradation and animal populations in the forests of Central Buton: preliminary results from the pilot study. London: Operation Wallacea.
- Shahabuddin, Schulze, C. H. & Tscharntke, T. (2005). Change of dung beetle communities from rainforest towards agroforestry systems and annual cultures in Sulawesi (Indonesia). *Biodiversity and Conservation*, 14, 863-877. doi 10.1007/s10531-004-0654-7.
- Shahabuddin, Hidayat, P., Manuwoto, S., Noerdjito, W. A., Tscharntke, T. & Schulze, C. H. (2010). Diversity and body size of dung beetle attracted to different types along a tropical land-use gradient in Sulawesi Indonesia. *Journal of Tropical Ecology*, 26, 53-65.
- Slade, E. M., Mann, D.J., & Lewis, O.T. (2011). Biodiversity and Ecosystem Function of Tropical Forest Dung Beetles under Contrasting Logging Regimes. *Biological Conservation 144*: 166–174. doi:10.1016/j.biocon.2010.08.011.
- Spector, S. (2006). Scarabaeine dung beetles (coleoptera:scarabaeidae :scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Bulletin, Monograph Number,* 5, 71–83.
- Tshikae, B. P., Davis, A. L. V. & Scholtz, C. H. (2008). Trophic associations of a dung beetle assemblage (Scarabaeidae: Scarabaeinae) in a woodland savanna of Bostwana. *Environmental Entomology*, 37(2), 431-441.
- Viegas, G., Stenert, C., Schulz, U. H. & Maltchik, L. (2014). Dung beetles com-

munities as biological indicator of riparian forest widths in southern Brazil. *Eco-* *logical indicators, 36*, 703-710. http:// dx.doi.rog/10.1016/j.ecolind.2013.09.036