

Contribution of Alpha and Beta Diversity Across Land-Use Type to the Regional Diversity of Dung Beetles in Central Sulawesi

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The importance of spatial scale has been acknowledged as one of determining factors of species diversity in local and regional diversity. The aim of this study was to evaluate contribution of alpha (α) and beta (β) diversity across land-use type to gamma (γ) diversity at the margins of tropical forest in Central Sulawesi using dung beetles (Coleoptera: Scarabaeidae) as a focal group. Baited pitfall traps set in four land-use types ranging from natural forest through cacao agroforestry systems to open areas during two years of sampling (2009 and 2012). A total of 28 dung beetle species belonging to four genera were captured during the study period. The results showed that contribution of β diversity was higher than that of α diversity of dung beetles. Each land-use type contributed about 56.5 to 62.5% of the total species richness (γ diversity). The similar pattern of biodiversity between each spatial scale and during the two sampling years emphasized the large contribution of each land-use type to maintaining a high portion of the regional species richness. It suggests the importance of managing other land-use types, such as secondary forest and agroforestry as well as protecting the remaining natural forests.

Keywords: dung beetles, diversity, spatial scales, additive partitioning, tropical forests

INTRODUCTION

Anthropogenic changes to tropical landscapes have been reported as major drivers of the global biodiversity crisis (Chapin *et al.* 2000; Sala *et al.* 2000). However, species diversity is influenced by a suite of factors that may affect species differently at different spatial scales. The driving factors behind biodiversity loss may work either at a small spatial scale, such as habitat type and management intensity (Klein *et al.* 2002; Shahabuddin *et al.* 2005; Shahabuddin *et al.* 2010) or at a larger scale such as land-use changes at the landscape or regional level (i.e. Tylianakis *et al.* 2006; Rizali *et al.* 2012). During the last decade, biodiversity conservation programs have shifted from the management of individual species within habitats to the preservation of entire communities within ecoregions (Gaston *et al.* 2001; Summerville *et al.* 2003). This paradigm shift has required greater attention to how patterns of biodiversity vary across spatial scales.

Generally, landscapes are composed of a mosaic of different land-use types. Regardless of how a landscape is partitioned, different components of a landscape typically vary in their contribution to the species diversity of the landscape as a whole. For example, some locations may have relatively high

species richness or relatively high concentrations of rare species, while other locations may have relatively low species richness or be inhabited mostly by ubiquitous species. The fact that landscape components vary in their contribution to species diversity has important consequences for efforts to understand and conserve biological diversity (Underwood & Chapman 1996; Fleishman *et al.* 2003). By knowing the influence of each component on species diversity at the landscape level, we may be able to predict how perturbations to one component will affect the diversity in the system as a whole.

Assessing diversity at multiple scales can be done using the additive partitioning approach (Lande 1996; Veech *et al.* 2002). Lande (1996) demonstrated that regional species diversity (γ diversity) can be calculated as the sum of alpha (α) and beta (β) diversity, where α is the average within-sample diversity and β is the average of among-sample diversity, or the average diversity not found in a single, randomly chosen sample. This approach can help to determine the relative contribution of α and β diversity on the total diversity across spatial scales (Lande 1996). For example, Wagner *et al.* (2000) used additive partitioning and concluded that β diversity among land-use types is more critical than β diversity between patches of the same land-use type in generating plant species richness in agricultural landscapes. Additive partitioning has been applied to

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several taxa, such as vegetation associations (Wagner *et al.* 2000), birds (Fleishman *et al.* 2003), beetles (Gering *et al.* 2003), moths (Summerville & Crist 2005), and aquatic macroinvertebrate assemblages (Stendera & Johnson 2005), and spiders (Garcia *et al.* 2010). However, the contribution of α and β diversity to regional diversity across a range of spatial scales remain unclear (Loreau 2000; Gering & Crist 2002). Moreover, although it has been previously reported in some studies (e.g. Rizali *et al.* 2012), the effect of sampling time or seasonality on diversity patterns across spatial scales are rarely investigated.

Dung beetles are an ideal group for testing the effects of spatial scale and sampling period on biodiversity due to their sensitivity to habitat disturbance and changes in vegetation structure, particularly in tropical forests (Scheffler 2005; Shahabuddin *et al.* 2005; Shahabuddin *et al.* 2010), and because their community structure is affected by local and regional processes (Davis *et al.* 2000). In addition dung beetles contribute significantly to functional processes in most terrestrial ecosystems (Nichols *et al.* 2008; Shahabuddin 2011; Slade *et al.* 2011; Beynon *et al.* 2012). Dung burial activity by dung beetles is important for maintaining and increasing soil fertility, enhancing the total nitrogen and phosphorus available for plants and increasing yield, enhancing plant regeneration through dung beetle related seed dispersal and control of flies and controlling of vertebrate parasites (Nichols *et al.* 2008 and references therein).

This study evaluated the contribution of a landscape composed of various land-use types on the regional diversity of dung beetles. In particular, the following questions were addressed: (i) how does α and β diversity contribute to the regional (γ) diversity of dung beetles?, (ii) does sampling time

have a significant effect on the diversity pattern?, and (iii) how important are individual land-use types for maintaining dung beetle diversity at the tropical forest margin in Central Sulawesi?

MATERIALS AND METHODS

Study Area. This study was carried out at the northern margin of the Lore Lindu National Park (LLNP) in Central Sulawesi – Indonesia. The Lore Lindu National Park is a local biodiversity hotspot, covering an area of 229,000 ha and located southeast of Palu, the provincial capital of Central Sulawesi. All study sites were in the surrounding of the Palolo Valley in the vicinity of the villages of Bobo (01°07'0.46" S - 119°59'702" E), and situated at an altitude between 790 and 985 m asl (Table 1) and in a distance at least 50 m each others. Dung beetle communities were studied in four land-use types: natural forest (NF); secondary forest (SF); cacao plantation under a mono-specific shade tree *Gliricidia sepium* (CP); and open areas (OA), cultivated either by *Zea mays* or *Morus alba*. Three replicate sites for each land-use type were selected with the distance at least 50 m each others.

Specimen Collection. Dung beetles were sampled at the 12 sites using dung-baited pitfall traps as described in Shahabuddin *et al.* (2010). Six traps were set up in the centre of a 50 x 50 m plot and placed in a distance 10 m each. Traps were baited with ca. 30 g of fresh cattle (*Bos taurus*) dung and exposed six times (April to July in 2009 and March to June in 2012). Besides abundant and easy to collect in the study area, cattle dung attracts the dung beetles in similar species composition with the feces of anoa (*Bubalus depressicornis*), an endemic herbivore in Sulawesi (Shahabuddin *et al.* 2010). Specimens were

Table 1. Observed (Obs.) and estimated (Est.) dung beetle species richness from 12 studied sites in the study area. Estimated number of species from the Jack-2 estimator. %, sampled species as a percentage of predicted number of species

Land- use type	Site	Geographic position		Altitude (m a.s.l)	Total species					
		Longitude (S)	Latitude (E)		2009			2012		
					Obs.	Est.	(%)	Obs.	Est.	(%)
Natural forest (NF)	NF1	01°07.05'	119°59.16'	985	9	12.43	(72.41)	9	11.93	(75.44)
	NF2	01°06.91'	119°59.17'	945	10	13.97	(71.58)	10	12.90	(77.52)
	NF3	01°07.37'	119°59.33'	856	10	14.95	(66.89)	11	13.29	(82.77)
Secondary forest (SF)	SF1	01°07.05'	119°59.22'	808	8	10.50	(76.19)	12	14.50	(82.76)
	SF2	01°07.18'	119°59.33'	812	9	11.97	(75.19)	10	12.92	(77.39)
	SF3	01°07.17'	119°59.45'	844	9	10.30	(87.38)	11	12.91	(85.25)
Cacao plantation (CP)	CP1	01°07.23'	119°59.63'	831	9	12.70	(70.87)	10	13.91	(71.89)
	CP2	01°07.25'	119°59.64'	803	12	13.55	(88.56)	8	10.90	(73.39)
	CP3	01°07.29'	119°59.67'	811	10	13.90	(71.94)	12	15.99	(75.05)
Open area (OA)	OA1	01°07.20'	119°59.67'	786	7	10.93	(64.04)	7	9.90	(70.71)
	OA2	01°07.22'	119°59.63'	794	8	9.70	(82.47)	6	8.93	(67.19)
	OA3	01°07.21'	119°59.58'	790	7	9.72	(72.02)	7	9.89	(70.78)
Total for alls 12 sites					23	27.73	(82.94)	20	23.73	(84.28)

removed from the traps after two days and preserved in *Scheerpelz* solution as recommended by Krell (2007). Samples were later identified in the laboratory using Balthasar (1963) and the reference collection of the Center for Biodiversity Research Tadulako University. Individuals which could not be identified were sorted to morphospecies. A reference collection is deposited in Center for Biodiversity Studies, University of Tadulako.

Data Analysis. Alpha diversity was calculated as the number of species of dung beetle recorded at each trap, site or land-use type. The second-order Jackknife estimation was calculated from observed values per trap/site/land-use type to estimate total species richness of a trap/site/land-use type by using EstimateS v7.00 (Colwell 2004). To estimate the total species richness of traps, sites land-uses and the study area, samples were pooled for individual sample times ($n=6$ trap replicates). Because observed species richness and estimated species richness was strongly correlated ($r = 0.92$, $P < 0.0001$, in 2009; $r = 0.96$, $P < 0.00001$ in 2012), only observed species was used for statistical analysis, however acknowledge that actual species richness was presumably higher. A two-way ANOSIM was calculated using PRIMER version 5 to analyze the significance of effects of land-use and sampling time on species composition with 1000 random permutations of the data matrix (Clarke & Warwick 2001). Differences in species richness at the trap and site level in two sampling years were tested by ANOVA (Zar 1999).

The contribution of spatial scale and land-use type on regional (γ) diversity of dung beetles was measured using the additive partitioning approach based on the values of α , β and γ (Lande 1996; Veech *et al.* 2002). Between each of the spatial scales the β -diversity (among-scale richness) was calculated as the difference between total species richness (γ) and mean species richness (α) within one spatial scale. The scales in this study were: sampling unit (trap), study sites, land-use types and study area. Therefore α diversity in this study consisted of species richness per trap (α_1), study site (α_2), land-use type (α_3), and total (regional) species richness (α_4 or γ). Beta (β) diversity indicated differences (the change) of species composition between each spatial scale, and it was measured by calculating the change in species richness from trap to study site (β_1), from study site to land-use type (β_2), and from land-use type to total species richness within the study area (β_3). Mathematically, species richness at a spatial scale

' n ' equals $\alpha_n = \alpha_{n-1} + \beta_{n-1}$, in which the highest possible α_n equals total species richness γ (Wagner *et al.* 2000; Gering *et al.* 2002; Summerville 2003).

RESULTS

General Patterns of Dung Beetle Diversity.

A total of 28 dung beetle species from four genera were captured across the four land-use types in Palolo region. The number of species recorded in 2009 and 2012 was 23 and 20, respectively. The four most dominant species in both sample times were represented by *Onthophagus wallacei*, *O. ribbei*, *O. fuscostriatus*, and *O. rudis* (Table 2). The jack-2 Estimate showed that the number of species observed for each plot was ranged from 64 to 87% in 2009 and 67 to 85% to the estimated species, while the estimated species for all 12 sites accounted 83 and 84% in 2009 and 2012, respectively (Table 1).

Species composition between the first and the second sampling period was similar. However, the dung beetles communities differed greatly across land-use type. There was a significant effect of land-use type, but not of sampling year on species composition (*land-use type*: ANOSIM statistic $R = 0.57$ $P = 0.001$; *sampling year*: ANOSIM statistic $R = 0.17$, $P = 0.171$). The species richness but not abundance of dung beetles changed significantly from natural forest to agroforestry cacao to open area both at the site and trap levels (Table 3). However there was only a significant decrease in species richness in the open areas, and surprisingly, the species richness of dung beetles in cacao plantations was similar to that of natural forest and higher than that of the open area in both years studied (Figure 1).

Contribution of α and β Diversity. Additive partitioning of the total diversity (γ diversity) into α and β diversity showed the contribution of each spatial scale on the regional diversity of dung beetles in each year of sampling (Figure 2). In general, in both regions the α diversity component was lower than the β diversity component. The contribution of α diversity (α_i) to the total diversity was 14.8 and 19.6% in 2009 and 2012, respectively. The fraction of the total diversity represented by β diversity ($\beta_1 + \beta_2$), was about 41.7% in 2009 and 39.8% in 2012. Each land-use type (α_3) supported about 56.5% (2009) and 62.5% (2012) of the total diversity, while variability of land-use type in the Palolo landscape (β_3) contributed 43.5% of the total diversity in 2009 and 32.6% in 2012 (Figure 2).

Table 2. Numbers of dung beetles in land-use type for each species recorded in 2009 and 2012 across land-use type. NF, Natural Forest; SF, Secondary Forest; CP, Cacao plantation; OA, open area

Species	Sampling time and land-use type							
	2009				2012			
	NF	SF	CP	OA	NF	SF	CP	OA
<i>Copris macacus</i> Lansberge	64	18	24	0	2	0	2	0
<i>C. punctulatus</i> Wiedemann	2	4	5	0	0	3	2	0
<i>C. saundersi</i> Harold	21	3	0	0	9	3	0	0
<i>Onthophagus fulvus</i> Sharp	0	0	0	0	17	7	24	31
<i>O. holosericeus</i> Harold	1	1	11	0	0	0	0	0
<i>O. limbatus</i> (Herbst)	0	3	1	130	0	0	0	14
<i>O. trituber</i> Wiedemann	0	0	5	65	1	0	1	5
<i>O. wallacei</i> Harold	175	54	137	194	18	15	23	3
<i>O. forsteni</i> Lansberge	0	0	2	0	0	1	2	0
<i>O. fuscotriatus</i> Boucomont	223	198	4	0	2	7	4	0
<i>O. mentaveiensis</i> Boucomont	0	0	0	0	0	1	0	0
<i>O. rectecornutus</i> Lansberge	0	0	2	0	0	0	1	0
<i>O. ribbei</i> Boucomont	53	33	8	1	4	14	12	0
<i>O. rudis</i> Sharp	1	3	11	10	36	117	106	36
<i>O. scrutator</i> Harold	0	0	0	0	9	15	18	0
<i>O. aureopilosus</i> Boucomont	0	1	0	0	0	0	0	0
<i>Onthophagus</i> sp.1	0	0	0	0	9	18	0	3
<i>Onthophagus</i> sp.2	27	25	14	5	0	0	1	0
<i>Onthophagus</i> sp.3	0	0	4	0	98	160	119	77
<i>Onthophagus</i> sp.4	1	0	0	0	0	0	0	0
<i>Onthophagus</i> sp.5	0	1	1	26	0	0	0	5
<i>Onthophagus</i> sp.6	26	0	4	6	2	3	0	0
<i>Onthophagus</i> sp.7	0	1	0	0	0	0	0	0
<i>Onthophagus</i> sp.8	1	0	0	0	0	0	0	0
<i>Onthophagus</i> sp.9	1	0	0	0	0	0	0	0
<i>Phaechrous emarginatus</i> Laporte	15	0	11	0	116	123	131	150
<i>Aphodius</i> sp.1	0	0	0	2	0	0	0	0
<i>Aphodius</i> sp.2	613	345	244	465	323	487	446	324
Number of individuals		13	16	10	13	14	14	9

Table 3. Effect of land-use change on species richness and abundance of dung beetles at the site and trap level in 2009 and 2012 tested by ANOVA

Dung beetles	Per site		Per trap	
	$F_{3,8}$	P	$F_{3,8}$	P
Species richness				
2009	6.13	0.018*	0.018*	0.001**
2012	6.6	0.015*	0.015*	0.035*
Abundance				
2009	1.92	0.205	0.205	0.141
2012	3.43	0.073	0.073	0.132

DISCUSSION

Species Richness Across Land-Use Types and Sampling Years. The species richness of dung beetles changed from natural forest, through agroforestry cacao to open areas. However a significant decrease in diversity was only detected in the open areas. Interestingly, the diversity of dung beetles in cacao plantations was similar to that of natural forest and much higher than the open areas (Table 2). Therefore, in contrast with other studies

reporting a negative effect of forest conversion on the species richness of tropical dung beetles (Arellano *et al.* 2005; Diaz *et al.* 2010; Barragan *et al.* 2011) this study showed that secondary forest and agroforestry systems may support a high portion of tropical dung beetles species, as has been suggested by Nichols *et al.* (2007) and a previous study in Central Sulawesi (Shahabuddin *et al.* 2010). The high similarity of vegetation structure and microclimate between the cacao plantation and forest sites may explain both the capacity of the cacao plantation to maintain dung beetle diversity, and the significant differences between these communities and those of the open areas (Shahabuddin *et al.* 2010).

Dung beetle species richness was significantly higher in natural forest and cacao agroforestry systems than in open area in both sampling years. In previous study, canopy cover, the number of tree species, and stem density decreased from natural forest to open areas in Palolo valley, while herb layer coverage and temperature showed a reverse pattern (Shahabuddin 2010). Habitats with a higher structural complexity of vegetation and a high canopy cover

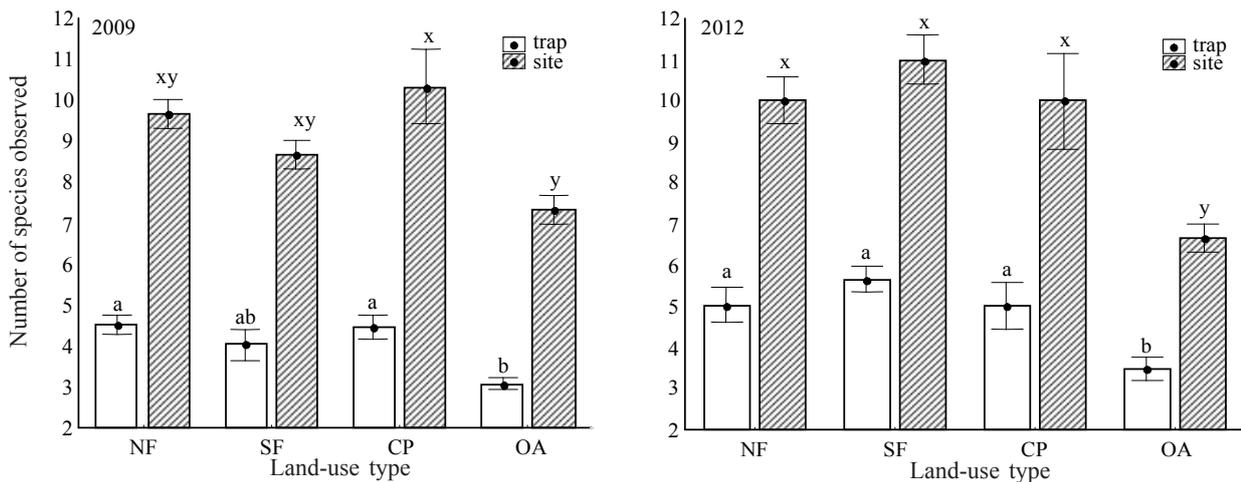


Figure 1. Effect of land-use type on mean (\pm SE) species richness of dung beetles per trap and site in two sampling years. NF = Natural Forest, SF = Secondary Forest, CP = Cacao plantation, OA = Open area. Letters over bars in the same years indicate significant differences at $P = 0.05$.

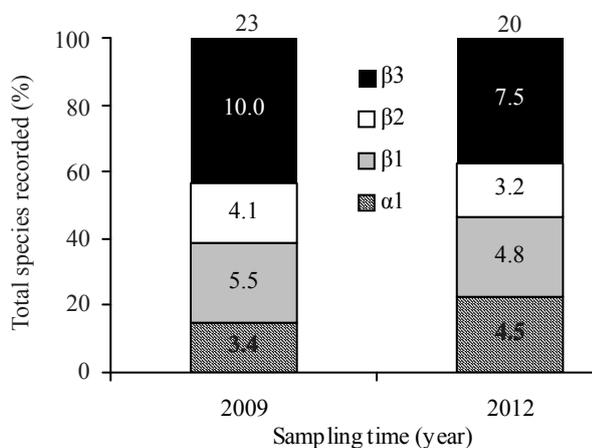


Figure 2. Contribution of each spatial scale (α and β diversity) to the regional species richness of dung beetles in the Palolo region. Species richness per trap indicated by α_1 ; change in species richness from trap to study site, from study site to land-use type and from land-use type to total species richness within study areas indicated by β_1 , β_2 , and β_3 , respectively. Total species richness (γ diversity) is indicated by the number over the bars in both sampling year.

thus appear to support higher dung beetle diversity (Arellano *et al.* 2005; Shahabuddin *et al.* 2010).

Contribution of α and β Diversity. By using the additive partitioning approach (Lande 1996), this study documented the importance of spatial scale for regional diversity. All land-use types contributed to the regional dung beetle diversity. Each type contributed on average 59.5% to the total species richness (γ diversity), while the landscape as a whole contributed about 38.1%. This indicates a strong effect of habitat heterogeneity, caused by a mosaic of various land-use types, on regional diversity.

A study in the Kublai region in the northern part of Lore Lindu National Park on solitary bees, parasitic Hymenoptera and canopy beetles also

reported a significant contribution of land-use systems to regional diversity. Each of land-use systems in the Kulawi landscape supported on average 45% of the total diversity of solitary bee and parasitic Hymenoptera and 58% of the total diversity of canopy beetles (Bos *et al.* 2007). Others authors have also noted the importance of land-use systems on regional diversity. For example, regional landscape heterogeneity contributed about 56% of regionally recorded plant species in central Switzerland (Wagner *et al.* 2000), 39% of regional solitary bee and wasp species in coastal Ecuador (Tylianakis *et al.* 2006), about 25% of regional beetle species in a conservation area in the USA (Gering *et al.* 2003), and 25% of regional butterfly species in deciduous forests of North America (Summerville *et al.* 2003).

The high contribution of beta (β) diversity to regional species richness is consistent with other studies on aquatic invertebrates (Stendera & Johnson 2005), and solitary bees, canopy beetles and ants (Bos *et al.* 2007), which found that β diversity increased with environmental heterogeneity between study sites. The *habitat heterogeneity hypothesis* states that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources, and thus increase species diversity (Tews *et al.* 2004). However, it is widely known that other ecological factors, such as dispersal ability and habitat isolation, can affect α and β diversity in a given landscape (Gering & Christ 2002).

The importance of α and β diversity on regional species richness is still unclear. Loreau (2000) stated that richness should decrease at fine spatial scales because the number of individuals is reduced and strong direct interactions could dominate the community, thereby increasing β diversity.

Contrastingly, it also can be argued that the importance of α diversity to overall regional richness should be more important at broader scales because local interactions are less important or undetectable (Loreau 2000; Gering & Crist 2002; Tylianakis *et al.* 2006). However, the contribution of different spatial scales on diversity also varies among taxa. For instance, Fleishman *et al.* (2003) found that α diversity was the most important component with respect to overall species richness of butterflies but less important to overall species richness of birds. Moreover, recent studies have shown that diversity patterns across spatial scales are not only taxon specific (i.e. mobile vs. sessile organism), but also dependent on the diversity measured (Ribeiro *et al.* 2008; Garcia *et al.* 2010; Flohre *et al.* 2011). For dung beetles a high interspecific competition for dung resources could be expected (Hanski & Cambefort 1991), which may reduce diversity at the scale of the dung patch. However, this competition is probably not so strong at broader spatial scales (e.g. sites within ecoregions), where processes such as dispersal and colonization–extinction dynamics structure the communities (Shmida & Wilson 1985; Viljanen *et al.* 2010). Dispersal ability may have strong effects on regional diversity since it may create a trade-off between local and regional diversity (Kneitel & Chase 2004). This is particularly true where organisms differ in their ability to utilize different habitat types and to disperse among habitats (Mouquet & Loreau 2003).

A high biodiversity at a landscape scale has the advantage that local disturbances are likely to be buffered by recolonization from diverse neighbouring communities, resulting in less vulnerable faunal communities (Tscharntke *et al.* 2005). The functional significance of biodiversity is most apparent at larger spatial and temporal scales, because spatial exchanges among local systems provide spatial insurance in heterogeneous landscapes when species may complement each other (Loreau *et al.* 2003). Recently, Tylianakis *et al.* (2005, 2006) suggest that conservation strategies need to follow a landscape scale approach in order to maximize beta diversity (species turnover) within and between habitat types. In conclusion, regional (γ) diversity of dung beetles in the Palolo region of Central Sulawesi was influenced by both α and β diversity where β diversity contributed the most to the total diversity of the region, indicating the importance of a high variety of land-use types to regional diversity. The similar pattern of biodiversity at each spatial scale

emphasizes the large contribution of each land-use type to maintaining a high portion of the regional species richness, and suggests the importance of managing other land-use types, such as secondary forest and agroforestry as well as protecting the remaining natural forests act as species source for adjacent land-use system.

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