Effect of fragmentation of kerangas forest on small mammal community structure in Brunei Darussalam

Siti Salwa Abd Khalid[1] and T. Ulmar Grafe[1,2]*

[1]*Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Jalan Tungku Link, Gadong, BE 1410, Brunei Darussalam*
[2]*Faculty of Science, Universiti Brunei Darussalam, Jalan Tungku Link, Gadong, BE 1410, Brunei Darussalam*

**corresponding author email: salwa.khalid@ubd.edu.bn*

Abstract

Widespread and rapid forest loss and disturbance have resulted in increased fragmentation of tropical forests. The impacts of forest disturbance and fragmentation on small mammals have been widely studied across the tropics and these studies have highlighted the detrimental effects. However, there is limited understanding on the impacts on small mammals in Borneo. This study investigated the impacts of fragmentation on small mammal community structure in lowland coastal heath forests known as kerangas forests, in Brunei Darussalam. Twelve study sites were compared in three forest types: fragmented (2.07-17.6 ha), disturbed (443.55-483.79 ha) and undisturbed (>500 ha) forests. In addition, the correlations between species richness, abundance and biomass of small mammals, and forest size were investigated. There was a clear change in species composition in the different forest types. Fragmented forests had the lowest species richness but the highest pooled abundance and biomass compared with disturbed and undisturbed forests. Species richness increased with forest size as predicted by the theory of island biogeography. In contrast, abundance and biomass was negatively correlated to forest size. Factors that contribute to the pronounced decline in species richness in fragmented forests include loss of rare and native forest species, reduced forest size in fragmented forests and distance effect. We suggest that a release from top-down control by predators and favourable conditions as a result from forest fragmentation are responsible for higher abundance and biomass of small mammals in fragmented forests.

Index Terms: deforestation, extinction, landscape ecology, rodents, tropical rain forest

1. Introduction.

Forest disturbance including forest fragmentation is recognized as one of the major threats to biodiversity.[1-3] Forest fragmentation is of great concern especially in the tropics because tropical forests are among the most biodiverse places remaining on earth but also where the deforestation rate is highest.[4,5] Forests in Borneo in particular are continuing to decline at an accelerating rate, becoming increasingly fragmented and in many areas only small forest patches remain.[6] Small mammal communities show diverse responses to forest fragmentation, including changes in species richness and abundance,[7,8] loss or decline of species with specific requirements,[9,10] species invasions,[10] changes in community trophic structure,[10] and changes in movement patterns.[11]

The Island Biogeography theory[12] proposed that the number of species found in an island was determined by immigration and extinction. Immigration and extinction, in turn are influenced by distance and area. The two main predictions of island biogeography theory are that: (1) islands close to a source area should have a higher number of species than islands further from the source area; and (2) for islands located at similar distance from the source area, larger islands should have more species than smaller islands.[12] This theory can be adapted to habitat islands such as fragmented forests.

Forest fragmentation has been characterized by reduced patch size and increased patch isolation, each of which has distinctive impacts on biodiversity. The effects of forest fragmentation on small mammals have been widely studied in the tropics (e.g., Amazon,[7,9,13] Australia,[14] Madagascar,[15] Thailand[16]). Some studies found positive effects such as higher species richness, abundance and biomass of small mammals in fragmented forests compared with continuous forests.[7,13] Others reported negative results such as a decline in species richness and abundance with decreasing fragment size[14,15] and extinction of certain species.[9,16] Given that these studies have mostly highlighted the detrimental effects of forest fragmentation, we should expect a similar reduction in species richness and abundance of small mammals in fragmented forests on Borneo.
Studies on the effects of forest fragmentation in Borneo are limited. Previous studies on faunal communities were based mostly on butterflies,[17-19] ants,[20,21] spiders,[22] frogs,[21] and birds.[23,24] Only a few studies looked at the effects of fragmentation on small mammals in Borneo.[8,10,11,25-27] Moreover, most studies on small mammals in Borneo have concentrated on the effects of logging in dipterocarp forests.[25,28-36] Some have found that logging has negative consequences on species richness and abundance. For example, species richness and abundance were lower in logged forests compared with primary forests.[29,31] Others have noted the opposite results, with increased species richness and abundance in logged forests compared with unlogged forests.[34,35] The disparity in their results might be because of small sampling areas and unequal number of samples,[34] but clearly more knowledge is needed on the impact of forest disturbance including fragmentation on small mammal communities including kerangas forests.

Kerangas or heath forest is characterized by its low uniform canopy (10m height compared to dipterocarp forest which is usually 40-60m in height) with no emergent trees and dense stands of small pole-sized trees that develop on acidic sandy soils that are nutrient deficient.[37] Kerangas forests are rare and occupy only 1.46 percent (6 558 ha) of Brunei Darussalam's land mass.[38] Kerangas forests are found mainly in the coastal area where most of the residential and infrastructure development occurs; as such, many are now fragmented patches. Only 23 percent of pristine kerangas forests remain.[38] Furthermore, kerangas forests are continuing to decline because of increased development as well as recurring disturbances such as fire and invasion by exotic tree species (*Acacia* spp.).[39] Kerangas forests generally have less biodiverse faunal communities compared with dipterocarp forests on Borneo (e.g., birds[40]).

Small mammals play an important ecological role. They are important prey items for a number of predators such as barn owls, *Tyto alba javanica*[41] and leopard cats, *Prionailurus bengalensis bornensis.*[42] In addition, they are important seed predators and dispersers of many tree species contributing to forest regeneration and the maintenance of diversity of tropical forests.[43-46] Loss or defaunation of small mammals in forest ecosystems can impact the important small mammal-dependent ecological processes which can have a major effect on the stability and/or resilience of forests. For example, reductions in rodent functional diversity have caused a decline in the abundance of small-seeded plant species.[49] Therefore, faunal studies in this type of forest is of considerable ecological interest.

In this study, the impacts of forest disturbance, including forest fragmentation on the species richness and faunal composition of small mammals in kerangas forest in Brunei, were examined. Specifically, the aims of the study were to answer the following questions: (1) what small mammals are found in the fragmented, disturbed and undisturbed kerangas forests? Is there any difference in the small mammal species composition between the different forest types? (2) Does the species richness, abundance and biomass of small mammals differ in fragmented, disturbed and undisturbed kerangas forests? (3) Do the species richness, abundance and biomass of small mammals differ in different sized forest?

2. Experimental.

2.1 Study site

The study was conducted in twelve study sites in Brunei Darussalam: four in fragmented forests, four in disturbed forests and four in undisturbed forests (see **Figure 1**). All study sites were between 0.28 and 48.77 km (mean 26.13 ± 22.8) apart. The four fragmented forest study sites were located in the Brunei-Muara district, specifically in Kampong Rimba (N 4°.4", E 114°54'29.6"). The conversion of continuous kerangas forest into isolated forest patches occurs mainly in this area due to housing developments. They were isolated and separated from each other by drains, roads, houses, and the matrix. The fragmented forests were F1 (2.07 ha), F2 (17.6 ha), F3 (4.47 ha) and F4 (17.13 ha).

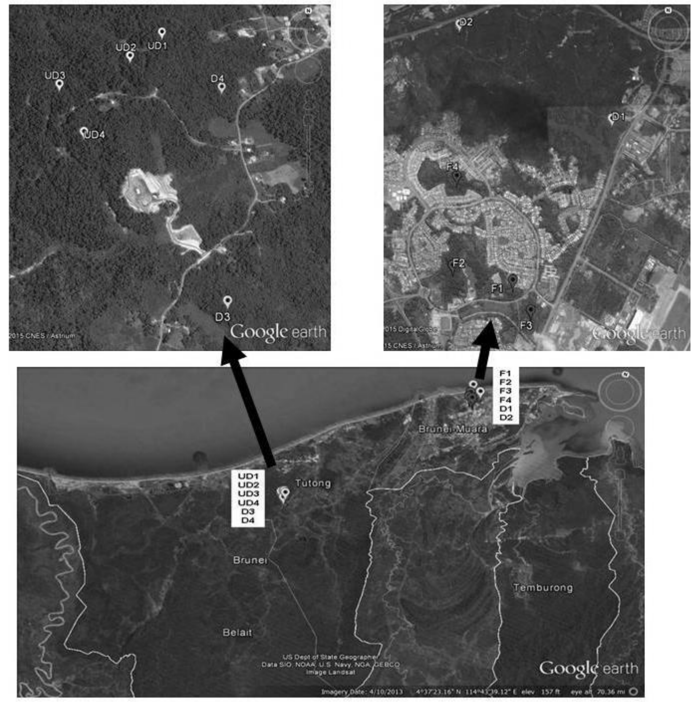

Figure 1. The study area in Brunei Darussalam and locations of the twelve study sites.

Disturbed forests refer to areas that have had anthropogenic disturbance such as fire or logging that have led to noticeable changes in terms of forest composition and structure. Two disturbed forest study sites were located in Brunei-Muara district (N 4°58'58.8", E 114°54'34.1"). D1 and D2 (both 443.55 ha) were located in disturbed kerangas forest that had been subjected to repeated forest fires and were extensively covered by the invasive species, *Acacia mangium* and *A. auriculiformis*. D1 and D2 were located 2.24 km apart and were separated by a trail (3 m in width) that was established for an underground gas pipeline. D2 was affected by forest fires in February 2013, during the field study period and thus, D1 and D2 were not structurally similar. D2 had disrupted canopy, pronounced gaps (canopy cover of 43.16 ± 21.37 %) and thick undergrowth covered with *Imperata cylindrica* (lalang grasses) and *Dicranopteris* spp. D1, in contrast, had canopy cover (85.44 ± 5.81 %) and less thick undergrowth. The other two disturbed forest study sites (D3 – 483.79 ha and D4 >500 ha) were located in the Tutong district (N 4°38'55.6", E 114°37'36.7"). D3 and D4 were old secondary kerangas forests which were clear felled 40–50 yrs prior to this study. D3 and D4 had understory that was typically covered by dense vegetation of abundant plant species, such as ginger (Zingiberaceae) and rattan *Calamus* spp., and *Hevea brasiliensis* (rubber tree). Undisturbed forests refer to primary forest areas that are relatively undisturbed by anthropogenic influences that could cause changes in forest structure. However, poaching and hunting do occur in these forests so there is some degree of anthropogenic disturbance. The four undisturbed forest study sites were located in a continuous pristine forest of the Andulau Forest Reserve (N 4°39'38.4", E 114°37'24.1") in Bang Nalud in the

Tutong district. All these undisturbed forest study sites comprised more than 500 hectares. UD1 was dominated by the endemic and endangered conifer *Agathis borneensis* (tulong).

2.2 Trapping protocol

Small mammals were captured with collapsible cage traps (30 cm long x 14 cm wide x 14 cm high)[9] between May 2012 and March 2014. The targeted small mammals were non-volant mammals (thus excluding bats) including tree shrews (Tupaiidae), rats (Muridae) and squirrels (Sciuridae). An index lines technique was employed at each study site where a 200-m line transect was established with 63 cage traps in total set along the transect at 10-m intervals.[48] At each trapping point, one above-ground trap between 18 and 176 cm above ground height (mean 82.52 ± 33.31) and two traps on the ground were set with the location of traps remaining constant throughout the sampling period. We conducted 36 trapping sessions, alternating between the twelve study sites with a mean interval of 20 ± 16 d between sessions along the same transect line, giving a total of three sampling units per site. Trapping was carried out for 7 consecutive days and nights during each trapping session. The traps were baited with aromatic banana (pisang rasthali) which has been shown to be the most effective bait for attracting small mammals.[8,10] Because bananas were the only baits used for this study, the targeted species were limited to omnivores and frugivores. Baits were replaced every evening (only once per day) throughout the trapping session. The traps were checked for animals every morning and evening. Animals that were trapped both in the morning and evening of the same day account for the previous trap night. The trapping effort was 441 trap nights (traps active for 24 h) per session, giving a total of 15 876 trap nights. Captured animals were marked with non-toxic dyes (Artline, Shachihata), sexed and then released at the point of capture. The dyes were reapplied during capture, which lasted throughout the trapping sessions. Species identification was based on Phillipps and Phillipps.[49] All animal handlings were approved by the University Research Ethics Committee (UREC), Universiti Brunei Darussalam, and followed the guidelines given by the American Society of Mammalogists.[50]

2.3 Data analysis

The relative abundance of small mammals at each study site was calculated as the number of individuals trapped per 100 station nights. This index provides a more accurate indicator of relative abundance than trap nights.[51] Relative biomass was calculated as the total weight of all individuals trapped per 100 station nights.[51,52] Species richness was calculated as the total number of species captured during the trapping session. Non-parametric estimators (Chao2 and Jackknife1) were also used to estimate the true number of species expected to be present in each study site.[53] Three Chao and Jackknife replications were used. Chao and Jackknife estimators are effective and provide accurate predictions of species richness from small samples.[54,55] The Species Diversity and Richness 2.65 program[56] was used to estimate species richness. The non-parametric Kruskal-Wallis (K-W) test was used to compare species richness between study sites and forest types. The total number of species, relative abundance and relative biomass were correlated with forest size using Pearson correlation test. The total number of species were log 10 transformed for achieving normality. Statistical analyses were performed with SPSS 20.0.[57] Means are given as $\overline{X} \pm 1$ *SD*. Cluster analysis was performed using the PC-ORD version 6 program.[58] Sorensen distance measures was used based on group average to define small mammal community correlations among sites and produce a dendrogram.

3. Results and Discussion.

A total of 353 individuals were captured (2849 times trapped) from 13 species, representing eight genera from four families (see ***Table 1***). In the fragmented forests (F1-F4), only three species but more individuals (183 individuals) were recorded compared with disturbed and undisturbed forests. In the disturbed forests D1 and D2 in Brunei-Muara, there were fewer species but more individuals (4 species, 60 individuals) recorded than in the disturbed forests

D3 and D4 in Tutong (9 species, 27 individuals). In the undisturbed forests, more species but fewer individuals (8 species, 83 individuals) were recorded. The disturbed forest D4 had the highest number of species captured (eight species) but contained the lowest number of individuals (nine individuals) among all study sites.

Callosciurus notatus (plantain squirrel) was the only species captured in all 12 study sites (see ***Table 1***). *Sundamys muelleri* (Müller's rat) was captured in all fragmented forests and the two disturbed forests D1 and D2 in Brunei-Muara, but not in the disturbed forests in Tutong (D3 and D4) or in any undisturbed forests (see ***Table 1***). *Sundamys muelleri* was the dominant species (*i.e.* with highest number of individuals captured compared with other species) present in all fragmented forests and two disturbed forests D1 and D2 in Brunei-Muara (see ***Table 1***). *Tupaia minor* (lesser tree shrew) was another species that was commonly found in disturbed habitats.[8,10] It was captured in all fragmented forests and disturbed forest D2, but not in disturbed forests D1, D3 and D4 or in undisturbed forests (see ***Table 1***).

Table 1. Mean number of individuals (averaged over three replicated capture sessions) for all species trapped in the study sites. The total times trapped for all study sites are in parenthesis.

	Fragmented forests				Disturbed forests				Undisturbed forests			
Species	F1 (563)	F2 (390)	F3 (321)	F4 (413)	D1 (170)	D2 (270)	D3 (163)	D4 (53)	UD1 (52)	UD2 (165)	UD3 (149)	UD4 (140)
Sundamys muelleri	21	16	11	22	8	14	-	-	-	-	-	-
Maxomys rajah	-	-	-	-	-	-	2	5	3	4	4	2
Maxomys whiteheadi	-	-	-	-	-	-	1	-	-	-	-	-
Leopoldamys sabanus	-	-	-	-	-	-	-	1	1	-	-	-
Niviventer cremoriventer	-	-	-	-	-	-	3	2	-	-	-	-
Callosciurus notatus	19	8	11	6	3	6	1	0.33	1	3	1	6
Sundasciurus hippurus	-	-	-	-	-	-	-	-	-	0.33	-	-
Tupaia minor	12	10	7	3	-	9	-	-	-	-	-	-
Tupaia picta	-	-	-	-	4	2	-	2	3	5	9	3
Tupaia tana	-	-	-	-	-	-	-	2	-	2	3	4
Tupaia longipes	-	-	-	-	-	-	-	1	-	-	-	0.33
Tupaia gracilis	-	-	-	-	-	-	-	0.33	0.33	-	-	-
Echinosorex gymnura	-	-	-	-	-	-	-	-	1	-	-	0.33
Number of species	3	3	3	3	3	4	4	8	6	5	4	6

Tupaia picta (painted tree shrew) was captured in disturbed forests (except D3) and undisturbed forests but not in fragmented forests (see ***Table 1***). *Maxomys rajah* (brown spiny rat) was captured in all study sites in Tutong, including the two disturbed forests (D3 and D4) and undisturbed forests, but not in the study sites in Brunei-Muara (see ***Table 1***). *Sundasciurus hippurus* (horse-tailed squirrel), listed by the IUCN as near threatened,[60] was captured only once in the undisturbed forest plot UD2. This species is rare and increasingly difficult to find because it has a large home range and is nomadic within that home range.[49]

The mean relative abundance and biomass were much higher in fragmented forests than in disturbed and undisturbed forests (K-W, $P < 0.05$, see ***Table 2***). Site F1, the smallest fragmented forest (2.07 ha) had the highest relative abundance and total biomass (see ***Table 2***). Site D3, one of the disturbed sites in Tutong, had the lowest relative abundance and biomass (see ***Table 2***).

The study sites were clustered into two main groups based on the small mammal species composition (see ***Figure 2***). The first group contained all four fragmented forests and two disturbed forests (D1 and D2 in Brunei-Muara).

The second group contained all four undisturbed forests and two disturbed forests (D3 and D4 in Tutong) (see ***Figure 2***). Based on cluster analysis, there were two cluster dominated by different species: (1) *S. muelleri, C. notatus* and *T. minor;* and (2) *M. rajah, M. whiteheadi, L. sabanus, N. cremoriventer, S. hippurus, T. picta, T. tana, T. longipes, T. gracilis* and *E. gymnura*.

Table 2. Mean relative abundance (mean number of individuals trapped per 100 station nights) and mean relative biomass (total weight (g) of all individuals trapped per 100 station nights). Means are given as $\bar{X} \pm 1$ SD.

Study Site	Relative Abundance	Relative Biomass (g)
Fragmented forests	**8.24 ± 2.66**	**1440 ± 402**
F1	11.94 ± 2.5	1898 ± 544
F2	7.71 ± 1.71	1376 ± 240
F3	6.42 ± 0.35	1128 ±125
F4	6.88 ± 1.02	1359 ± 201
Disturbed forests	**3.91 ± 2.20**	**580 ± 316**
D1	3.25 ± 0.47	655 ± 94
D2	7.03 ± 1.18	933 ± 206
D3	1.36 ± 0	161 ± 68
D4	4 ± 0.13	573 ± 188
Undisturbed forests	**3.06 ± 1.22**	**533 ± 201**
UD1	1.96 ± 1.05	443 ± 218
UD2	3.18 ± 1.04	593 ±147
UD3	3.71 ± 1.25	501 ± 196
UD4	3.4 ± 1.38	675 ±259

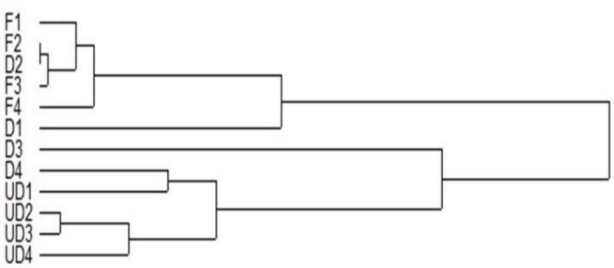

Figure 2. Dendrogram showing the similarity between small mammal species community in all study sites.

Species richness was significantly different between sites (see ***Figure 3***): observed species richness (K-W, P = 0.004), Chao2 (K-W, P = 0.001) and Jackknife (K-W, P = 0.002).

The number of species trapped was positively correlated with forest size (Spearman's r = 0.730, P < 0.0001, see ***Figure 4A***). In contrast, the relative abundance and biomass were negatively correlated with forest size (Pearson's r = −0.502, P = 0.001 and r = −0.514, P = 0.001 respectively, see ***Figure 4B*** and ***C***).

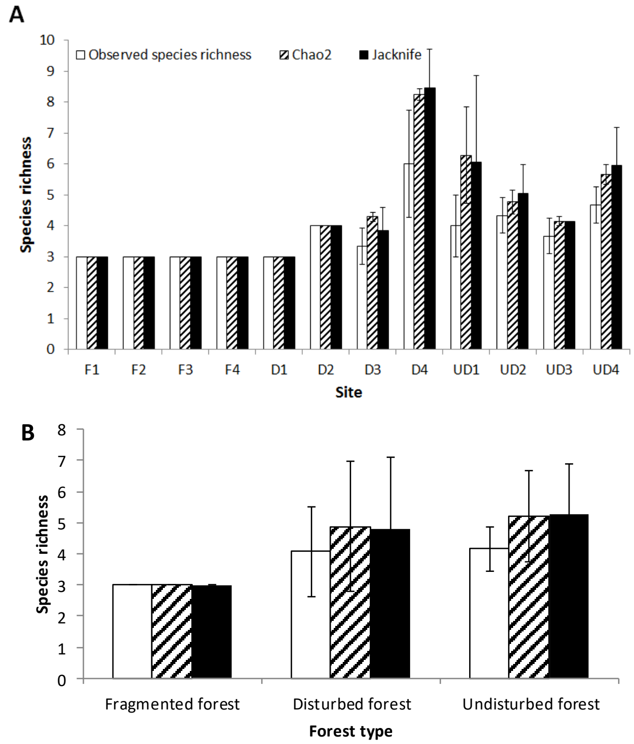

Figure 3. Species richness of small mammals (Mean ± 1 SD) for (**A**) all study sites, and (**B**) all forest types. Clear columns refers to the number of species captured during the trapping sessions, striped columns refers to the estimated number of species based on Chao2 estimates, and black columns refer to Jackknife estimates.

The species richness, abundance and biomass of small mammals in kerangas forests were found to be affected by forest disturbance including fragmentation. Fragmented forests had the lowest species richness compared with disturbed and undisturbed forests. A total of ten species were not recorded in fragmented forests. Only three small mammal species were recorded in all the fragmented forests: Müller's rat, lesser tree shrew, and plantain squirrel. These species are commonly found in disturbed habitats[10] and are of low conservation concern.[60] The presence of these three species in all the fragmented forests suggests that they are tolerant of forest fragmentation. Similar results of low species richness in fragmented forests were obtained in the tropical forests of the Amazon basin.[61] This study also demonstrates a strong correlation between forest size and species richness of small mammals in kerangas forest. Species richness increased with forest size as predicted by the island biogeography theory.[12] However, forest size is not independent of the different forest types and hence, it's difficult to distinguish between the effects of forest size and forest types as a possible driver of gradients in species richness, abundance and biomass.

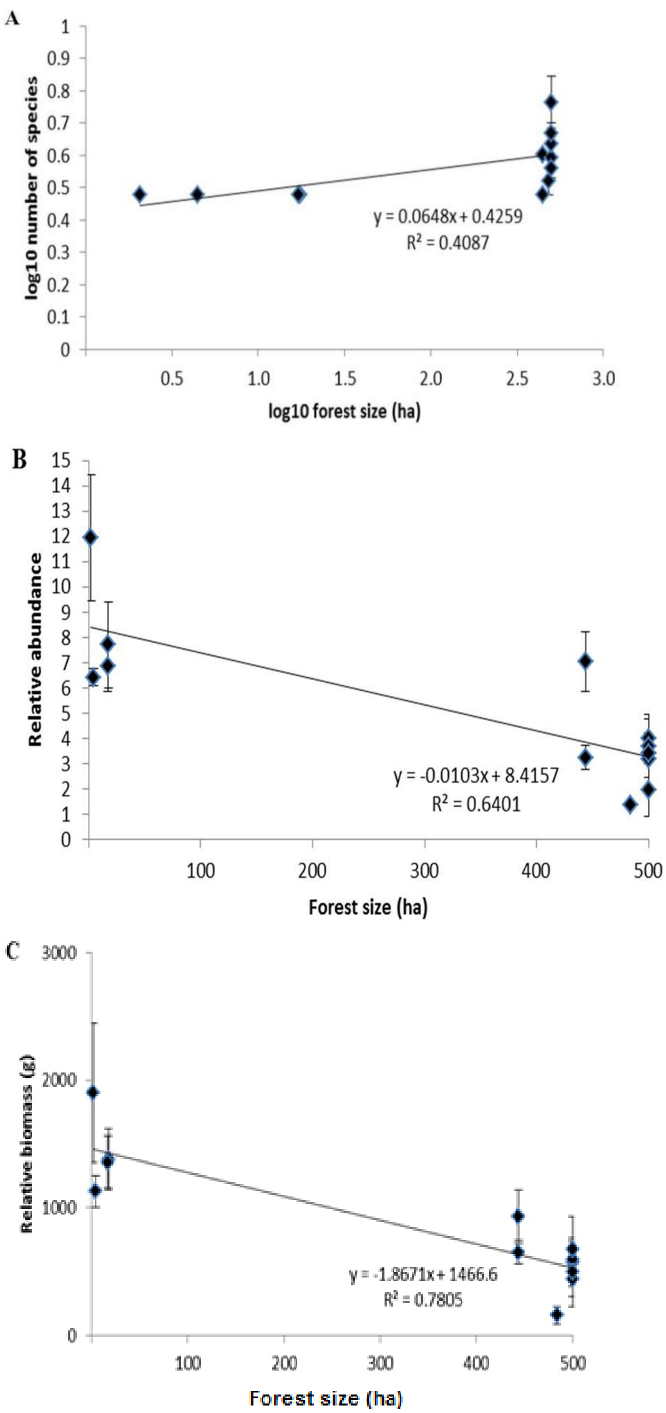

Figure 4. Correlations between species richness, abundance and biomass of small mammals and forest size. Mean ± 1 SD for (**A**) log10 number of species trapped, (**B**) relative abundance (mean number of individuals trapped per 100 station nights), and (**C**) relative biomass (total weight 9g) of all individuals trapped per 100 station nights).

In addition, displacement and loss of native forest species from fragmented forests due to the invasion of generalist species caused the decline in species richness in Brunei.[10] Extinction of native forest species in fragmented forests also occurred in Brazil[7,9,13] and Thailand.[62] These patterns were consistent with this study where loss of rare species and native forest species was observed in fragmented forests.

Reduced forest area in fragmented forests may contribute to the decreased species richness. Larger areas are able to accommodate more individuals because more physical space and resources are available.[72] Thus, larger areas allow the coexistence of ecologically similar species.[72] For example, the co-occurrence of *T. picta*, *T. tana*, *T. longipes* and *T. gracilis*, in this study were only recorded in all undisturbed forests and disturbed forest D4 but did not occur in fragmented forests. Some species, especially those with specific requirements are more vulnerable to the effects of fragmentation and forest disturbance.[73,74] For example, the comparatively large-bodies *Leopoldamys sabanus* (long-tailed giant rat) which requires large home ranges to survive[10] was absent in fragmented forests in this study. A similar pattern was seen in Thailand.[16]

Distance effects may also help explain the low species richness in fragmented forests in comparison with disturbed and undisturbed forests. Increased distance from source areas acts as a barrier to dispersal which prevents the immigration of new individuals.[12] In this study, fragmented forests were located further from continuous, pristine forests and were isolated by roads and a matrix of open savannah consisting of shrubs, scattered trees, and lalang grasses that appears unable to regenerate into kerangas forest. Roads and large clearings were found to pose barriers to dispersal of the *Maxomys rajah*,[63] and other species.[64,65] The geographical distance separating these areas may explain why the study sites in Brunei-Muara have lower species richness compared with those in Tutong.

Another interesting point we found is that there were differences in species composition between the disturbed forests in Brunei-Muara (D1 and D2) and Tutong (D3 and D4). The time since disturbance may explain the differences between the disturbed sites. The disturbed forests in Brunei-Muara were recently subjected to repeated forest fires whereas the disturbed forests in Tutong were clear felled 40–50 yrs prior to this study.

Jones & Schmitz[66] found that the average recovery time for animal community after disturbance (logging) is over 40 yr. Thus, the small mammal communities in Tutong may have recovered from disturbance. This may also explain why the species compositions in D3 and D4 were similar to the undisturbed forests. Fragmented forests had the highest pooled abundance and biomass of small mammals compared with disturbed and undisturbed forests. This has been reported for small mammal communities in the fragmented and continuous forests of Amazonia.[67,68] In addition, the current study found a negative correlation of forest size on relative abundance and biomass of small mammals in kerangas forest. Previous studies have reported an increase in small mammal abundance and biomass with decreasing size of fragmented forests in Amazonia,[68] Brazil,[7] Brunei,[10] and Venezuela.[51] They highlighted that edge-induced habitat changes and an increase in individuals from the secondary habitats surrounding the forest fragments were the reasons for the increase in abundance and biomass.

One possible factor contributing to the high abundance and biomass of small mammals in fragmented forests is release from top-down control from predators.[45] Predators limit population growth. Fragmented forests, however, typically have depauperate predator communities.[75] For example, six species of predators including *Prionailurus bengalensis* (leopard cat) and *Viverra tangalunga* (Malay civet) were recorded in the undisturbed forests but were absent in fragmented forests in Brunei as determined by cage and camera trapping.[10] Thus, the removal or absence of predators would lead to increased densities of their prey—in this case, increased small mammal abundance. In Brazil, densities of the opossum *Didelphis marsupialis* increased due to fewer predators in small fragmented forests.[68]

Forest fragmentation could also enhance favourable conditions for certain small mammals and thus increase their abundance and biomass.[69] Edge-induced habitats such as habitats with decreased canopy cover and increased number of lianas lead to invasion by generalists that are better adapted to the fragmented forest environment.[70] In addition, there are greater opportunities and diversity of habitat in fragmented forests. For example, higher arthropod diversity and abundance and increased quantities of fallen timber due to edge effects have resulted in increased small mammal populations in fragmented Amazonian forests.[68] Here, the dominance of the three species (*S. muelleri, T. minor* and *C. notatus*) was observed in fragmented forests. Dominance of certain species over other co-occurring species was also observed in other fragmented forests.[10,16,51]

We found kerangas forests were rather species poor with a maximum of six species in a single undisturbed forest. Similar results were obtained by Charles and Ang[10] with eight species. Studies in primary dipterocarp forests have recorded 18 and 19 species in Brunei[71] and Sabah[29], respectively. This may reflect the actual low species numbers in kerangas forests. Similar patterns were observed in bird communities on Borneo.[40] However, the methods used could affect this result. Species caught were limited to omnivores and frugivores; other species with different diets, such as the bark-eating pygmy squirrel were not included. Future research could apply other methods to effectively capture different species to see if the same results are found especially species which are more relevant in regard to conservation issues. Another limitation of the study is that it was not possible to distinguish the effects of fragmentation and forest disturbance on small mammals because of the nested study design. It would be ideal to partition the different drivers of species occurrence and subsequent changes in animal assemblages as part of the experimental design. Other aspects of the landscape context of the forest, such as presence or absence of corridors, shape of fragments, may also be of interest in future work.

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