

# Structure of small non-flying mammal communities in disturbed habitats in the Central Cordillera, Luzon Island, Philippines

Aris A. Reginaldo\*<sup>1</sup> and Perry S. Ong†<sup>2</sup>

<sup>1</sup>Department of Biology, College of Science, University of the Philippines, Governor Pack Road, Baguio City, Benguet 2600 Philippines

<sup>2</sup>Institute of Biology, College of Science, University of the Philippines, Diliman, Quezon City, 1101 Philippines

The Central Cordillera on Luzon Island, Philippines, is home to a diverse set of small mammals. Unfortunately, substantial anthropogenic perturbation occurred in the past; the effects of habitat disturbance to animal communities are yet to be determined. This study sought to determine species richness, relative abundance, and macrohabitat use patterns of small non-flying mammals in patches of disturbed habitats in La Trinidad, Benguet. Our survey consisted of three trapping periods that utilized live trapping and some snap trapping. Over a total of 3,551 trap nights, seven species were recorded: four native species, namely *Apomys abrae*, *Apomys musculus*, *Chrotomys whiteheadi*, and *Rattus everetti*, and three non-native species, namely *R. exulans*, *R. tanezumi*, and *Suncus murinus*. Overall, the number of species was low, and small mammal abundance was moderate. Across adjacent habitat types, abundance between small mammal groups and most of the species did not vary, whereas habitat use by small mammal groups and by each species varied. Native species, except *A. musculus*, preferred the montane forest patch, and there was an indication that native populations are isolated. *Suncus murinus* preferred the pine stand but showed the ability to use other habitats. *Rattus exulans* and *R. tanezumi* segregated—the former preferred the pine stand and the latter the agricultural area. Our results attest to habitat disturbance's negative effect on

native small-mammal fauna and its support of non-native species persistence. We show that montane forest patches in disturbed landscapes are important because they act as potential sources of native populations that can re-establish as the forest regenerates. Future studies that employ similar methodology will test the generality of our findings.

## KEYWORDS

Community ecology, habitat disturbance, habitat use, Muridae, native mammals, non-native mammals, Soricidae, wildlife biology

## INTRODUCTION

The Philippine mammal fauna is a leading example of mammalian diversification within an ancient oceanic archipelago (Jansa et al. 2006, Steppan et al. 2003). However, this fauna is considered among the most threatened in the world because of habitat loss. Logging and agriculture led to a reduction in the country's old-growth forest cover to only 7% of the total land area in the 20<sup>th</sup> century (Heaney and Regalado 1998). The recent estimate of closed/open forest in the Philippines, based on a 2015 data, is about 6.71 million hectares (Forestry Management Bureau, 2018). Many studies have demonstrated that change in vegetation structure, also often used as a proxy for disturbance (e.g., Rickart et al. 2011b, Pardini et al. 2005, Laurance 1994), has a strong influence on local distribution, species richness, diversity, biomass, and dynamics

\*Corresponding author

Email Address: aareginaldo@up.edu.ph

Date received: August 21, 2019

Date revised: December 20, 2019

Date accepted: July 21, 2020

in a population (See August 1983, Williams et al. 2002, Pardini 2004). Research on Luzon Island has demonstrated that small non-flying mammal communities are greatly affected by forest structural changes caused by human activities (e.g., Rickart et al. 2016, Rickart et al. 2011a, Balete et al. 2009). A study on the patterns and occurrence of small non-flying species on Luzon Island suggested that some native species are tolerant disturbance and resilient to invasion by non-native species (Rickart et al. 2011b).

However, local extinctions of some species were reported in heavily disturbed forest habitats (e.g., Heaney et al. 2006).

Luzon Island, the largest island in the Philippines, has been the subject of several recent studies on small non-flying mammal evolution and ecology. The Central Cordillera, the largest and oldest of the mountain range in northern Luzon, holds the record for the greatest number of local endemics for small non-flying mammals in the Philippines (Heaney et al. 2016). This mountainous region has been reported to have experienced substantial environmental perturbation in the past (Stevenson et al. 2010, Kowal 1966.). This perturbation has resulted in widespread alteration of vegetation cover, specifically the replacement of the original montane forests by pine forest and grassland (Kowal 1966, Whitford 1911.) as well as consequent fragmentation of forest habitats (Heaney et al. 2006, Reginaldo et al. 2013). However, there were also reports that provided evidences of forest regeneration or equivalent plant successional stage (e.g. secondary forest) in the region (e.g. Rickart et al. 2016, Reginaldo et. al 2013, Buot and Okitsu 1998, Kowal 1966). Our observations on the present structure of some forests in the southern section of the Central Cordillera, including isolated patches of montane forest along streams and gullies in pine-dominated forest fragments, also suggest evidence of forest regeneration. Remnants of the original population of organisms in forest fragments or patches are of interest because they represent the survivors of past perturbations. For the small non-flying mammals in forest fragments, what species remain, and how small mammal community structure formed under local processes merit exploration. A preliminary study in Baguio City, an upland urban area that maintains pine forest reserves, reported that three native species coexisted with three non-native species in a disturbed pine forest fragment (Reginaldo et al. 2013). Given this initial result, it is clear that additional work is needed to understand the structure of small non-flying mammal communities in forest fragments in the Central Cordillera.

This study sought to describe small-mammal community in disturbed habitats along the border of a pine-dominated forest fragment in La Trinidad, Benguet Province, Central Cordillera. Specifically, this work aimed to determine the small non-flying mammal diversity in the forest fragment and describe the macrohabitat use patterns by small non-flying mammals therein. The study highlights its use of live trapping procedure in an ecological study in a disturbed landscape; such methodology provided a better picture of how animals use habitat patches. We provided evidence that disturbed landscape can support a moderately diverse community of small non-flying mammals, and montane forest patches within pine-dominated forest fragment had the potential to facilitate re-establishment of native fauna. The generated information contributes to the further understanding of the effect of local conditions and processes, such as the local changes in habitat structure and the presence and degree of local disturbances, on Philippine small non-flying mammal assemblage, abundance, and habitat use in disturbed landscapes.

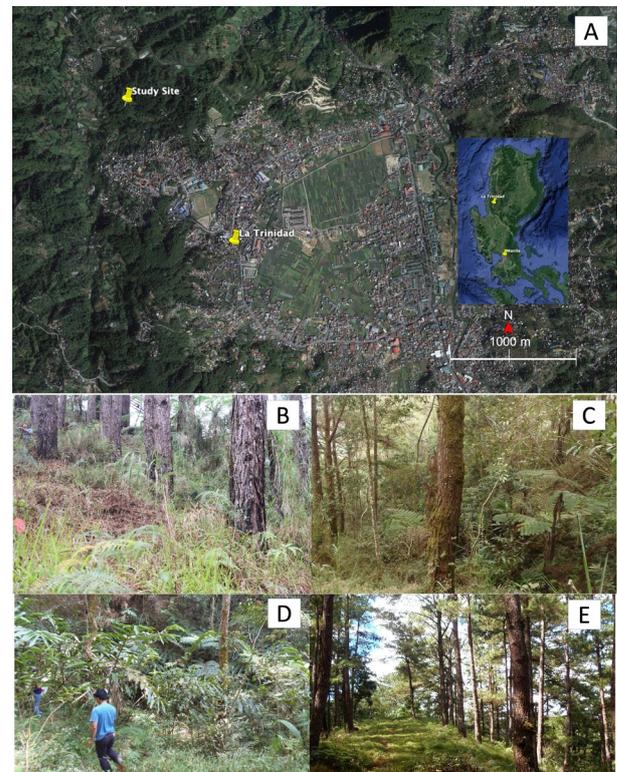
## METHODOLOGY

### Study Area

Our study area is situated in La Trinidad municipality (16° 26' N, 120°35' E, ~1300 m elevation), which is located at the southern end of the Central Cordillera on Luzon Island. It is a municipality adjacent to Baguio City and 206 kilometers northwest of Manila (Figure 1). This section of the Central Cordillera has a Type I Climate with distinct dry (November to April) and wet (May to October) seasons. Throughout the time of the survey, which ran from February to March 2017, the average daily high temperature was 21 °C, and it only rained once in March.

The town of La Trinidad is a highly urbanized municipality with a long history of human occupation. In the Spanish period, 1521 to 1898, La Trinidad became the capital of Benguet, and it was once the trade center between the people of the upland and nearby lowland areas (Bagamaspad and Hamada-Pawid 1985). The municipality remained as a populated area during the American period (1900s to the 1940s) and served as a vegetable producer for the then newly instituted Baguio City (Bagamaspad and Hamada-Pawid 1985). Commercial vegetable farming became highly extensive beginning in the 1950s (Kowal 1966).

The Central Cordillera region is believed to have been covered originally by broad-leaf trees (Whitford 1910, Kowal 1966). The vast pine and grassland habitats that now cover a wide area of the Central Cordillera replaced the original vegetation, and the broad-leaf plants have since been prevented to regenerate because of continuous and heightened human activity (Kowal 1966, Stevenson et al. 2010). Historical accounts reported that cattle raising in Benguet was long-practiced during the Hispanic



**Figure 1: Study Areas.** (A) Satellite image of the location of La Trinidad, Benguet, northern Luzon, Philippines. Inset map shows the location of the study area in Luzon (Source map: Google Earth Pro 2018 ). (B) A close-up photograph of a section of the pine stand showing the common species (*Pteridium*, *Imperata*) of the lower vegetation. (C) A regenerating montane forest along a gully (D) Lower section of the pine stand and the adjacent stream (E) A section of the agricultural area that had been flattened and cleared of some pine trees, and was used for grazing.

period, and pine forest was extensively logged during the American period (Bagamaspad and Hamada-Pawid 1985. Kummer (1992) also reported that upland secondary forests were cleared to give way to commercial farming. Similar to other areas in Central Cordillera, the present vegetation cover in La Trinidad is a product of past disturbances, primarily through *kaingin* in the town's earliest histories, and clearing of secondary montane forest habitats, agriculture, and urbanization more recently.

The study area was situated along the border of a pine-dominated forest fragment, with an area of about 40 hectares, within the jurisdiction of Barangay Wangal, La Trinidad (16°27'25.29" N 120°34'02.74" E, 1280-1330 m elevation) (Figure 1). Pine trees (*Pinus kesiya*) were the dominant trees. Broad-leaved vegetation grew with the pine trees in some areas, while it occurred as patches along stream banks and gullies in other places. The fragment was on a hill that rises from an elevation of about 1240 masl to 1370 masl, and separated from other hills by vegetable and flower gardens, residential areas, and streams (Figure 1A). Three related families hold a long claim to a large portion of the fragment and managed the area since it had been heavily exploited for pinewood during the American period. Local informants also reported that, in the past, the entire area was utilized as a pasture for cattle. At present, pasture areas (~2.5 hectares) are still maintained. Historical accounts regarding cattle-raising in Benguet (Bagamaspad and Hamada-Pawid 1986) suggest a possibility that a large section remained deforested for a significant amount of time. The broad-leaf tree vegetation probably was present only as patches in steep areas adjacent to streams and along gullies. In the area selected for the study, the greatest disturbances and habitat modifications were restricted to the location of the three family houses, a patch of vegetable garden, a grazing area for some cattle, and areas planted with citrus and coffee.

An area along the border of the fragment that constituted several disturbed habitats was selected for study. We selected three habitat types that were adjacent to each other, and we classified these as pine stand, regenerating montane forest, and agricultural area. At the intersections of these habitats were small streams (2-3 meters wide) that converged to a single, wider drainage (3-6 meters). The entire sampling area was about 18% (~7 hectares) of the total area of the fragment.

## Habitats

**Pine Stand.** This habitat exhibited typical characteristics of a pine forest (Figure 1B). The tree layer was composed of a single species of pine tree (*Pinus kesiya*). A number of scattered broad-leaf trees (e.g., *Ficus* spp.) were also present. The understory vegetation consisted mostly of the composite *Ayapana triplinervis*, several grass species (e.g., *Miscanthus* and *Imperata*), and ferns (*Pteridium* and *Gleichenia*). The stand occupied an entire west-facing hill slope with an average slope of 33°. Pine trees and broad-leaf trees had average sizes of 33.0 cm and 6.8 cm, respectively. Pine tree cover, based on DBH, was more than twice the broad-leaf tree cover. From the ridge, the slope descended about 120 meters to the stream and narrowed toward one end. The peak was flattened and had been converted to residential and recreational areas. The higher section of the pine stand, which was adjacent to the residential area, was mostly covered by patches of the large creeping fern, *Gleichenia longissima*. The lower slope, adjacent to the stream (Figure 1D), was a less steep area (ave. 24°) and covered mostly by broad-leaf trees (e.g. *Ficus* spp. and *Lithocarpus*), some pine trees, and tree ferns. The lower vegetation in this area consisted mainly of *Ayapana* (in relatively open areas), low lying grass

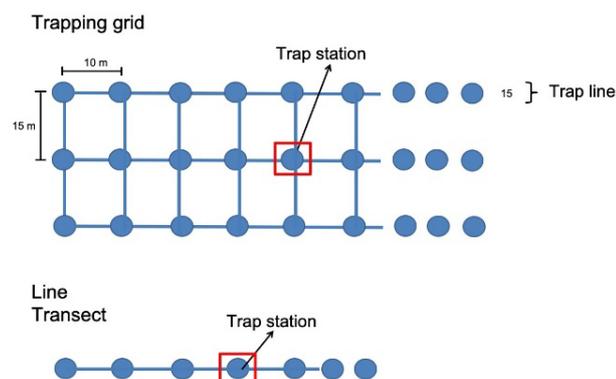
that formed a dense cover on the ground, and scattered communities of *Vanoverberghia* (Zingiberaceae).

**Regenerating Montane Forest.** The regenerating montane forest occurred as large patches on slopes and as smaller patches on stream borders and gullies (Figure 1C). The large patch that was sampled occupied an entire slope of a hill from the stream to the ridge. Common to all patches was a dense cover of broad-leaf trees (3 - 20 cm in DBH; mostly *Ficus* spp. and *Lithocarpus*) with scattered, old pine trees (45 - 60 cm in DBH); pine trees that were overgrown by broad-leaf trees within montane forests is primary evidence of past disturbance and forest regeneration (Kowal 1966). Other evidence of forest regeneration was the advancing community of large and small broad-leaf trees (and understory vegetation consisting of dense forbs and grasses) along the borders of a patch. In the interior of patches, the understory vegetation consisted of species of herbs (e.g., *Alocasia*, *Calanthe*, *Arisaema* sp. and *Vanoverberghia*). In some places, a number of broad-leaf trees reached 100 centimeters DBH, creating a canopy that effectively prevented the establishment of a dense lower vegetation. In addition to the broad-leaf trees, the growth of *Vanoverberghia*, *Schismatoglottis* and low-lying herbs (e.g., Urticaceae) were also evident in some places, especially along stream banks. The matrix surrounding the patches consisted of pine trees and (or only) grasses (e.g., *Paspalum*, *Imperata*), indicating recent and frequent disturbance. There were fewer broad-leaf trees and thicker cover of *Ayapana* and grass on forest edges than in the interior of patches. On the basis of vegetation structure, we classified the flora on streams (and stream banks), and gullies as regenerating montane forests. During the survey period, the streams were almost dry, with water pools only in certain areas. A number of plastic water pipes, 2-3 cm in diameter, to supply farming activities around the forest fragment created some disturbance.

**Agricultural Area.** This habitat occupied a relatively wider area than the other two habitats. A section was used as a residential area, and the surrounding areas were utilized for various purposes: vegetable gardens, fruit tree (coffee and lemon) plantations, and pastures for cattle grazing. A flower garden, which was previously managed was also present beside a house. The grazing area was an open area covered primarily by grass and other species such as *Ayapana*, *Pteridium*, and *Melastoma* (Figure 1E). Along the edges, several pine trees that varied in sizes were scattered. Several shallow (1 to 2 meters deep) and narrow (5 to 10 meters wide) gullies cut through the open and farm areas. All gullies were adjacent to a fruit tree plantation; the rest of their borders were surrounded by open areas. Within the gullies, the fern *Gleichenia*, several individuals of pine trees and tree ferns (*Cyathea*), and several broad-leaf trees (e.g., *Ficus* spp. and species of Family Euphorbiaceae) of variable sizes (2.0 cm to 1000 cm) were the dominant vegetation.

## Trapping Methods

Trapping comprised of three 8-day sessions over a month (February 20 to March 20, 2017). Three consecutive days of pre-baiting period were employed prior to the start of each trapping session to allow animals to adjust to the presence of the traps in the habitats. The entire effort comprised of 3,351 trap nights. The first and second sessions involved trapping using live traps on three rectangular grids established in each habitat type. Each grid measured 30 m x 140 m with three trap lines (upper, middle, and lower) (Figure 2). Each line consisted of 15 trapping stations, effectively making a total of 45 stations for each grid. A single type of bait was used in each session: roasted coconut (coated with peanut butter) during the first, and live earthworms during the second. Total effort across both sessions



**Figure 2: A diagram of the trapping grids and line transects that were used in the survey of small non-flying mammals.**

was 2,160 trap nights.

The third trapping session was meant to extend the effort of capturing additional individuals and other species in our study area. Traps consisted of a mix of cage and snap traps. Snap trap is known to effectively capture various small mammal species (e.g. Rickart et al. 1991, Balete et al. 2009, Rickart et al. 2011b). In addition to the grid in each habitat type, we also set line transects at various locations outside the grids in order to increase the area of sampling. Line transects were set in smaller patches of habitats such as along dry sections of streams, stream banks, vegetable garden edges, and other gullies. Each line transect consisted of 10 trapping stations, which were laid five meters apart (Figure 2). On both grids and transect lines, snap and cage traps were alternately placed on the ground. We used coconut (~60%) and live earthworms (~40%) as baits. A number of snap traps that were baited with coconut were also set on trees and vines. Traps on grids were maintained for five days, while traps on transects and those above the ground were maintained for 3-4 four days. A total of 1,191 trap-nights were set during this session.

We used three sizes of cage traps, 13 cm x 18 cm x 42 cm, 10 cm x 10 cm x 25 cm, 10 cm x 10 cm x 42 cm, and one type of metal snap trap with a dimension of 9 cm x 16 cm. All traps had been baited in the afternoon and checked the following morning. Traps that did not catch any mammal were left open and checked again during the baiting time. Eighty-three percent were cage traps, and the remainder were snap traps. Ninety-eight percent of traps were set on the ground, and the rest (2 %) were arboreal.

To identify each species, we measured tail length (tail vertebrae), hindfoot length, and weight, and recorded the sex and age of each individual. For small and nonaggressive individuals, we also measured ear length and total body length. To record the patterns of intra- and inter-habitat use, live animals were marked by cutting the hair of the left leg, of the right leg, and the lower back, respectively. In each body part, we systematically put the mark at a certain level relative to the length of the body part; a mark in each individual corresponded to a specific trapline at which an individual was captured. Cutting the hair was a non-intrusive technique of marking animals that we developed for this study. We observed that it is an efficient technique for short-duration surveys because the marks were easily made, and they remained visible for the duration of the entire survey. To verify individual identity, we combined the hair marking with the morphological measurements. Animals were released at the site of captures. Animals that were captured with snap traps were preserved as voucher specimens.

### Data Analyses

Community structure, as defined by Magurran (2004), refers to a collection of species occurring at a specified place (whether

natural or arbitrarily assigned) and time. In our study, we sought to describe the community structure of the small-nonflying mammals that inhabit disturbed landscapes. We measured species richness to identify community composition, computed relative abundance to describe the relative number of the different species, and described habitat use to identify patterns of distribution. The data generated were used for two levels of describing small non-flying mammal structure – one for the whole study area and across the three disturbed habitat types.

### Species Richness

The overall species richness for the whole study area was determined by combining all species lists from grids and line transects from all the three trapping sessions. The adequacy of sampling was evaluated with a sample-based rarefaction curve (Mao's tau, with standard deviation, PAST3). We also presented a typical species accumulation curve based on daily capture to show the trend at which species were recorded.

### Abundance

The actual number of unique individuals (only first captures) was used as the estimate of abundance. An overall comparison of *relative abundance*, using the estimate of abundance, among the different species and between native and non-native species groups was reported for the whole study area.

Patterns of abundance across the three habitat types were assessed by comparing the abundance of each species and each small mammal group using the data from the grids. All first captures, including recaptures from another habitat, were counted as unique individuals for a particular habitat category. The assumption that the abundance of small non-flying mammals was even across the three habitats was first tested; the *Fisher's Exact* test (IBM SPSS Statistic Trial) was used due to relatively low capture rates. Significance of *P-value*, was evaluated at  $\alpha = 0.05$  level of appraisal. We then conducted a post-hoc test using the *Exact Binomial Test of goodness-of-fit* to detect significant differences between observed and expected abundance across the three habitat types for each species and each small mammal group. Because we compared among three categories (habitat types) a *Bonferroni correction* was employed in the post-hoc tests; the significance level that we used was  $\alpha = 0.017$ .

### Patterns of Habitat Use

Habitat use was inferred from the patterns of occurrences and capture frequencies (first captures plus recaptures) across the three habitats. In each habitat category, we pooled all data of captures from the grids and excluded the captures from transects outside the grids. A sample-based rarefaction curve (Mao's tau, with standard deviation, PAST3) was used to determine the adequacy of effort in determining the possible number of species for each habitat. We also illustrated the trend in the addition of species in each habitat type using a species accumulation curve. In the analysis of capture frequencies, we first evaluated the overall heterogeneity in spatial distribution of the different species using *Fisher's Exact Test* (IBM SPSS Statistic Trial); we used  $\alpha = 0.05$  as the significance level. A post-hoc test using the *Exact Binomial Test of goodness-of-fit*, was used to test proportional capture frequencies for each species and for the groups of native and non-native species across the three habitat types. In the post-hoc tests, we applied the *Bonferroni correction* for significance level; the  $\alpha$  was 0.017. It was assumed that the distribution of species or group of species among the three habitats was random. To support the patterns revealed by the capture frequencies, field observations of capture locations, habitat conditions, and records of captures from line transects outside the grids were also presented.

## RESULTS

### Species Richness of Small Non-Flying Mammals

Seven species of small non-flying mammals were recorded in 3,551 trap nights, of which four were native (*Apomys abrae*, *Apomys musculus*, *Chrotomys whiteheadi*, and *Rattus everetti*) and three were non-native (introduced) species (*Rattus exulans*, *Rattus tanezumi*, and *Suncus murinus*). At least four species were recorded from both the regenerating montane forest patches and pine stand and five from the agricultural area. Notably, all four native species were detected in the agricultural area.

The species accumulation curve for the entire area showed a very steep increase in the number of species on the first four days, with six species of the species were already recorded. An additional species, *Chrotomys whiteheadi*, was added at the end of the second trapping session, i.e., only after 13 days (Figure 3A). More than 500 trap nights were set in the large gully adjacent to the pasture area, where the single individual was

captured, but no additional individuals of *C. whiteheadi* were captured. Also, there was no additional species in the third trapping session. The sample-based rarefaction curve estimated that there were seven species, but it did not show a very defined plateau, suggesting that further trapping might still yield additional one or two species, which are possibly present within the whole sampling area (Figure 3B).

### Abundance of Small Non-flying Mammals

#### Overall Relative Abundance of the Different Species

Pooling all first captures from all grids and transects, there were a total of 55 small non-flying mammal individuals; native species contributed nearly 60%. *A. abrae* and *S. murinus* were the most abundant (Figure 4). *A. musculus*, *R. everetti*, and *R. tanezumi* closely followed. The relative abundance of *R. exulans* was also low, only 7% of the total number of individuals. The overall abundance per 100 trap nights was 1.94 (Table 2).

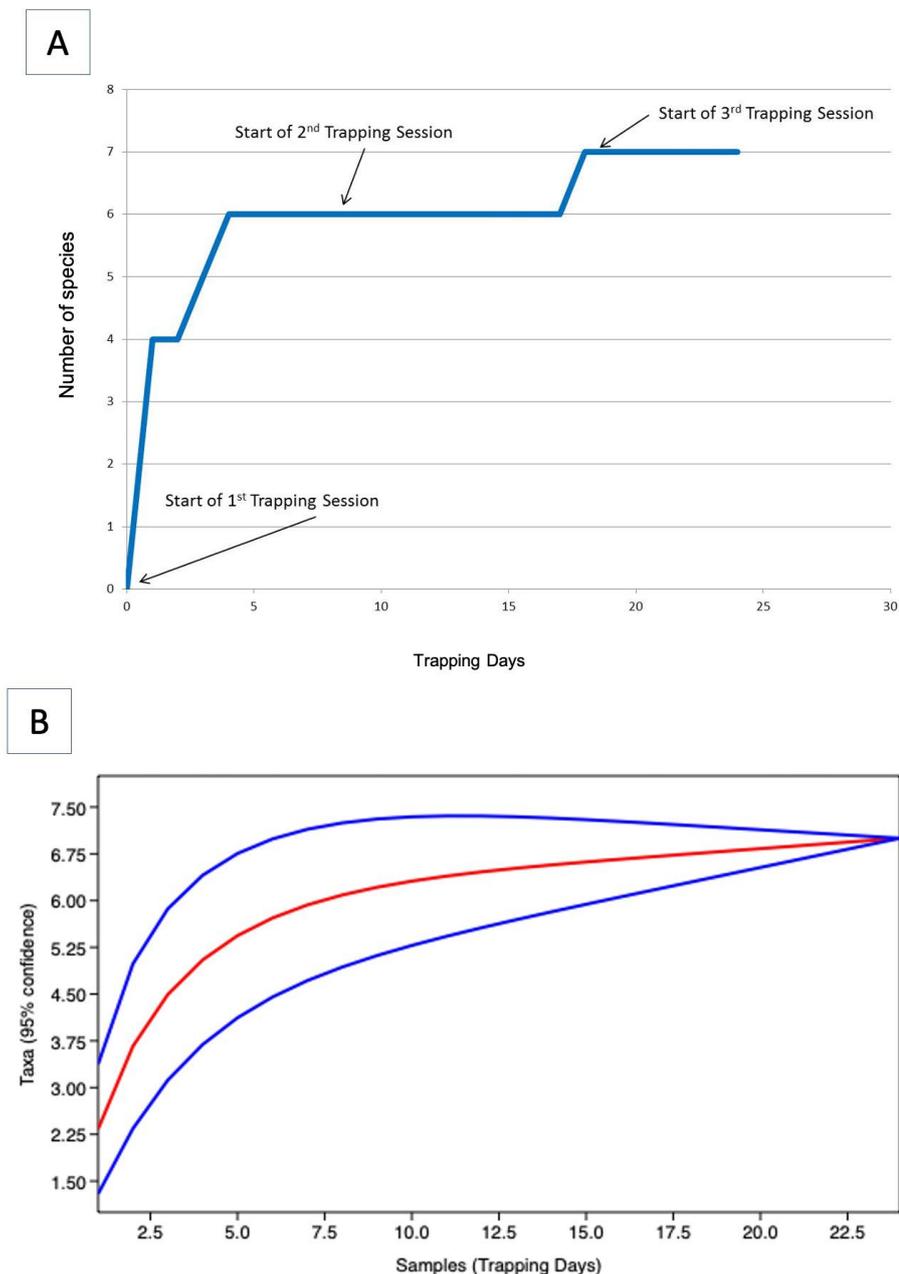


Figure 3: Species accumulation curves for the entire survey. (A) Species accumulation curve based on daily captures. (B) Sample-based rarefaction curve (red line) with 95% confidence limits (blue lines).

**Table 1: A comparison of abundance of small mammal non-flying mammals in the three habitat types along the border of a pine-dominated forest fragment in La, Trinidad, Benguet, Philippines.**

SPECIES NAME	COMMON NAME	HABITATS			TOTAL
		Regenerating Montane Forest	Pine Stand	Agricultural Area	
<b>Native Species</b>					
<i>Apomys abrae</i>	Cordillera pine forest mouse	8 (0.85)	5 (0.53)	1 (0.11)	14
<i>Apomys musculus</i>	Least Philippine forest mouse	0	6 (0.63)	4 (0.42)	10
<i>Rattus everetti</i>	Common Philippine forest rat	3 (0.32)	0	3 (0.32)	6
Abundance for Native Species		11 (1.16)	11 (1.16)	8 (0.85)	30
<b>Non-native Species</b>					
<i>Rattus exulans</i>	Polynesian rat	1 (0.11)	3 (0.32)	0	4
<i>Rattus tanezumi</i>	Oriental house rat	0	0	<b>8 (0.85)</b>	8
<i>Suncus murinus</i>	Asian house shrew	3 (0.32)	<b>10 (1.06)</b>	<b>0</b>	13
Abundance for Non-natives		4 (0.42)	13 (1.38)	8 (0.85)	25
Overall Abundance		15 (1.59)	24 (2.54)	16 (1.69)	55 (1.94)
No. of trap nights		945	945	945	2835

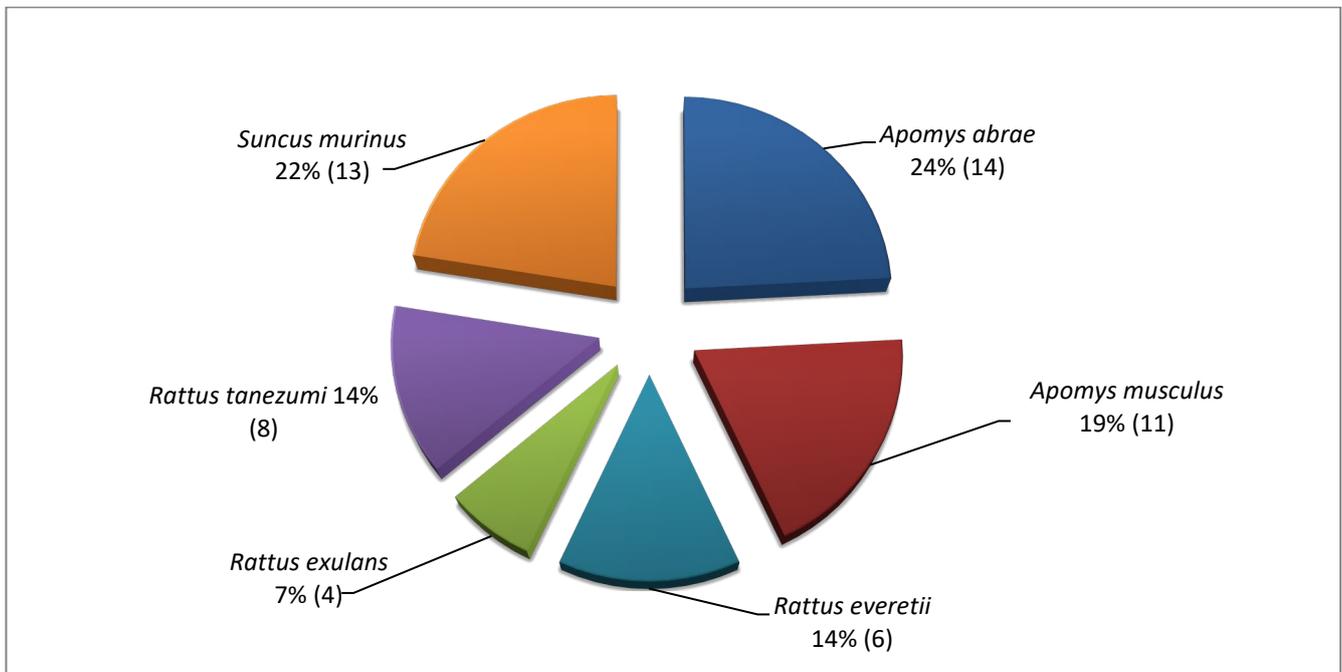
In parentheses are the abundance values per 100 trap nights.

Values in bold fonts are abundance values that are higher or lower than expected, based on Exact binomial test of goodness-of-fit with post-hoc test.

**Table 2: Capture frequencies (first captures and recaptures) of the different species of small non-flying mammals in the three disturbed habitat types along the border of a pine-dominated forest fragment.**

SPECIES NAME	HABITATS			TOTAL CAPTURES
	Regenerating Montane Forest	Pine Stand	Agricultural Area	
<b>Native Species</b>				
<i>Apomys abrae</i>	<b>21</b>	5	<b>1</b>	27
<i>Apomys musculus</i>	0	7	4	11
<i>Rattus everetti</i>	3	0	3	6
Total for Natives	<b>24</b>	12	8	44
<b>Non-native Species</b>				
<i>Rattus exulans</i>	1	<b>7</b>	0	8
<i>Rattus tanezumi</i>	0	0	<b>8</b>	8
<i>Suncus murinus</i>	3	<b>11</b>	<b>0</b>	14
Total for Non-natives	<b>4</b>	<b>18</b>	8	30
Overall Captures	28	30	16	74
No. of trap nights	945	945	945	
Trap success per 100 trap nights	2.96	3.17	1.69	
No. of native species	2	2	3	
No of non-native species	2	2	1	

Values in bold fonts are the number of captures higher or lower than expected based on Exact binomial test of goodness-of-fit with post-hoc test.



**Figure 4: Comparison of the overall relative abundances of small non-flying mammals. The data was derived from first captures from all grids. In parentheses are the number of individuals.**

#### **Abundance of Species across the Habitat Types**

The difference in the abundance of species across the three habitat types resulted in significant heterogeneity in local small-mammal abundance (Fisher's Exact Test,  $P < 0.001$ , Table 1). However, post-hoc tests resulted in only two species abundances (*R. exulans* and *S. murinus*) that deviated from expected across the three habitat types (Table 1). The overall, between groups of native and non-native species, and all other species abundances did not vary significantly, suggesting that the abundances across the three habitat types were equal. In addition, there was an almost equal abundance between native and non-native species in the pine stand and agricultural areas, whereas regenerating montane forest consisted mostly of native species.

The abundance of *R. tanezumi* was significantly higher than expected in the agricultural area (Exact Binomial Test of goodness-of-fit,  $P = 0.001$ ). For *S. murinus*, the abundances in the pine stand (10) and agricultural area (0) were significantly higher (Exact Binomial Test of goodness-of-fit,  $P = 0.002$ ) and lower (Exact Binomial Test of goodness-of-fit,  $P = 0.007$ ) than expected, respectively.

#### **Patterns of Occurrence and Capture Frequencies among the Three Habitat Types**

In all habitat types, all, but one, species in our entire study area were recorded in the grids. There were four species in each habitat type but the assemblages varied (Table 2). There were three native species, *A. abrae*, *A. musculus*, and *R. everetti* and one non-native, *R. tanezumi*, in the agricultural area. In the montane forest patch, *A. abrae* and *R. everetti*, *R. exulans* and *S. murinus* were recorded. In the pine stand, we captured *A. abrae*, *A. musculus*, *R. exulans* and *S. murinus*. In the regenerating montane forest and the pine stand, the species accumulation curves (Figure 5A) suggested that all possible species that were present were recorded, but the sample-based rarefaction curves suggested that this may only be true for the pine stand (Figure 5B and 5C). In the agricultural area, both species accumulation and rarefaction curves suggest that all possible species in the area may have not been sampled yet (Figure 5A and 5D).

A test for heterogeneity on the local spatial distribution and capture frequencies was significant (Fisher's Exact Test,  $P < 0.001$ , Table 2). Overall capture frequencies across the three habitat types did not deviate significantly. However, the capture frequency of natives species group was significantly higher than expected in the regenerating montane forest (Exact Binomial Test of goodness-of-fit,  $P = 0.002$ ). In contrast, the capture frequencies of non-native species group was significantly higher than expected (Exact Binomial Test of goodness-of-fit,  $P = 0.003$ ) in the pine stand. Moreover, the lower capture frequency of non-native species group in the regenerating montane forest was nearly significant than expected (Exact Binomial Test of goodness-of-fit,  $P = 0.019$ ). Notably, the capture frequencies of native species group in the regenerating montane forest was almost exclusively contributed by one species (*A. abrae*).

Only four of the six common species had capture frequencies that deviated from expected. Among the native species, only *A. abrae* was captured from all three habitat types; the capture frequencies were higher than expected in the regenerating montane forest (Exact Binomial Test of goodness-of-fit,  $P < 0.001$ ) and lower than expected in the agricultural area (Exact Binomial Test of goodness-of-fit,  $P < 0.001$ ) (Table 2). The other native species, *R. everetti*, was recorded in the regenerating montane forest and agricultural area; but, none of the capture frequencies significantly deviated from expected frequencies (Table 2). Meanwhile, *A. musculus* was recorded in the pine stand and agricultural area; the higher and lower capture frequencies in the pine stand and regenerating montane forest, respectively, nearly deviated significantly than expected (Exact Binomial Test of goodness-of-fit,  $P = 0.050$  and  $P = 0.020$ , respectively) (Table 2).

Among the non-native species, *R. exulans* and *S. murinus* were captured in the pine stand and regenerating montane forest but not in the agricultural area. The higher capture frequencies of *R. exulans* in the pine stand was higher than expected (Exact Binomial Test of goodness of fit,  $P = 0.003$ ). For *S. murinus*, the higher and lower (zero) capture frequencies in the pine stand and agricultural area, respectively, significantly deviated from expected frequencies (Exact Binomial Test of goodness-of-fit,  $P$

<0.001 and  $P < 0.007$ , respectively; Table 2). Meanwhile, *R. tanezumi* was only captured from the agricultural area and the capture frequency in this habitat was significantly higher than expected (Exact Binomial Test of goodness-of-fit,  $P < 0.001$ ) in this habitat.

### Records of Recaptures and Site of Captures

To provide additional information for the analysis of the habitat use by the different species, we present our notes on recaptures and the records on the number and location of capture stations. Five individuals of *A. abrae* in the regenerating montane forest were recaptured one to five times, contributing to a total of 13 recaptures. These recaptures of *A. abrae* were captured in 16

adjacent trap stations that were set in the interior of the regenerating montane forest patch; the stations covered an area of 1200 m<sup>2</sup> or ~30% of the total area of the grid. In that similar area, two individuals were recaptured from all three grid traplines, whereas the rest were captured from one to two traplines. In the pine stand, all five individuals of *A. abrae* were recaptured in the adjacent regenerating montane forest patch. The single capture in the agricultural area was recorded along the edge of a grazing area adjacent to another regenerating montane forest patch. For *A. musculus*, there was a single recapture in the agricultural area; it was captured from two trap stations along a single grid trapline that passed through an area with pine trees. In the pine stand, all captures of *A. musculus*, including one recapture, were recorded from seven different trap

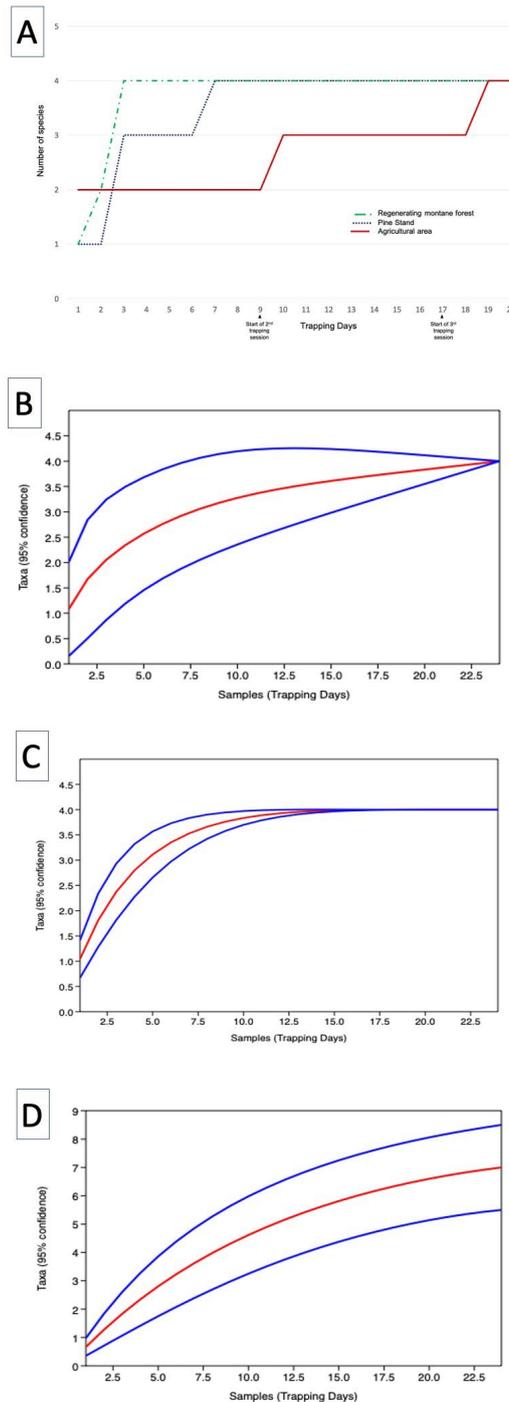


Figure 5: Species accumulation curves for each habitat type. (A) Species accumulation curve based on trapping days. (B) Sample based rarefaction curve for the regenerating montane forest. (C) Sample-based rarefaction curve for the pine stand. (D) Sample-based rarefaction curve for the agricultural area. For each rarefaction curve, the sample-based rarefaction curve is in red color and the 95% confidence limits are in blue color.

stations; all three grid traplines contributed at least one capture. Meanwhile, there was one recapture of *R. everetti*; it had been captured in the regenerating montane forest then recaptured by a transect outside the grid, which was set along a dry stream. The distance between the two trap stations that captured that individual was ~80 meters. In the agricultural area, all three *R. everetti* were unique individuals that were captured from a single grid trapline; two of the individuals were captured in two separate gullies, whereas the other individual was captured in a nearby trap station that was set under a shrub (*Malvaviscus*).

There were no recaptures of either *R. exulans* or *R. tanezumi*. The single *R. exulans* in the montane forest was captured by a trap station adjacent to an open area beside a small vegetable garden. However, the transect lines that were set in that open area (dominated by grass) did not capture any other individual of *R. exulans*. On the other hand, all eight *R. tanezumi* individuals were captured from trap stations adjacent to a house. For *S. murinus*, there was no recapture in the pine stand. In the regenerating montane forest, three *S. murinus* individuals were recorded. Notably, one of the individuals was a recapture from the pine stand. The distance between the trap stations in the pine stand and regenerating montane forest that captured that individual was about 150 meters. Meanwhile, all 11 *S. murinus* captures in the pine stand were from the grid; seven of these individuals were captured came from the grid trapline adjacent to a stream bank.

#### Captures from Line Transects

A total of 17 captures were recorded from the line transects outside the grids. We captured four individuals in other sections of the agricultural area: two *A. abrae* and one *A. musculus*, which were captured in an open area adjacent to a gully; and one *C. whiteheadi*, captured along the edge of the grazing area that was adjacent to a regenerating montane forest patch. Along streams and gullies, eight individuals were captured: three *A. abrae*, one *A. musculus*, one *R. everetti*, and three *S. murinus*. In the other montane forest patches, we captured one *A. abrae* and three *R. everetti*.

## DISCUSSION

### Species Assemblage in Disturbed Landscape

Despite a long history of severe habitat disturbance within our study area, four native species were recorded and coexisted with three non-native species. However, the seven species in our study is lower than records (9 to 17 species) in other studies conducted in areas where disturbance gradients included more intact forest habitats, and at higher elevations in the Central Cordillera where there are generally more native species (Heaney et al. 2016, Rickart et al. 2011a, Rickart et al. 2016, Thomas 1898 and Sanborn 1952, as cited by Rickart et al. 2016, Reginaldo and de Guia 2014). Compared with records in other disturbed landscapes that include villages within an almost similar elevational range as in our study, our record was less also than the 13 total species in Mt Amuyao (1500 to 1800 m elevation) (Rickart et al. 2016) and the eight total species in Ifugao (900 masl to 1200 masl) (Miller et al. 2008, Stuart et al. 2007, Joshi et al. 2004). Our study and these earlier reports highlight the negative effect of disturbance to small-mammal community composition, an impact that was similarly reported in other countries (see Pardini 2004, Bolger et al. 1997, Laurance 1994). Our finding that more species (also mostly native) were in the agricultural area than in the other habitats is not surprising because native species occasionally use agricultural habitats that are adjacent to forests (Reginaldo and

de Guia 2014, Rickart et al. 2011b, Stuart et al. 2007, Joshi et al. 2004). In our study, the presence of some native species in agricultural areas may have been a result of the movement of some individuals from the montane forest patches to adjacent habitats with favorable microhabitats that were tolerated by native species. In other areas, native species were reported to move into agricultural areas and feed on resources (e.g., sweet potatoes, exotic invertebrates) present in such habitats (Stuart et al. 2007, Joshi et al. 2004).

Our study reports the occurrence of *C. whiteheadi* and *A. abrae* at ~1300 masl elevation. Rickart et al. (2016) reported a lower elevation record for *C. whiteheadi* in the Central Cordillera at 1500 masl. However, a study in Ifugao Province reported the presence of this species within 900 masl to 1100 masl (Joshi et al. 2004); thus, *C. whiteheadi* may have a broader elevational distribution than previously thought. For *A. abrae*, earlier surveys in Benguet Province reported the presence of this species in Baguio City and the town of Sablan (as reported by Heaney et al. 2011), areas which are at 1500 and ~800 masl elevation, respectively.

Interestingly, *Bullimus luzonicus*, a commonly recorded species in the Central Cordillera (e.g. Rickart et al. 2011b, Heaney et al. 2006), including in nearby places (see Reginaldo and de Guia 2014, Reginaldo et al. 2013), appeared to be absent in our study area. It is possible that this species has been extirpated in our study area similar to the fate of other native species in another forest fragment in the Central Cordillera (see Heaney et al. 2006). Alternatively, it was not captured due to low number; this is likely because there is an evidence that this species may tolerate disturbed pine forest fragments in urban areas (Reginaldo et al. 2013). *Crocidura grayi* and *Apomys microdon* were also expected to be present as these species occur within a broad elevational range (Heaney et al. 2016). *Apomys datae*, a high elevation species (Heaney et al. 2011), and *C. mindorensis* were also reported to occur along an elevational range from 900 masl to 1100 masl (Stuart et al. 2007, Joshi et al. 2004, See also Miller et al. 2008); these species might have also been missed by our trapping. Alternatively, these species might be present in the other montane forest patches within the pine-dominated forest fragment that were not sampled.

### Patterns of Abundance of Small Non-flying Mammals

The community of native and non-native species of small non-flying mammals, are comparably less abundant than report from similarly disturbed landscapes at higher elevation (Reginaldo and de Guia 2014) and even from pine forest fragments in an urban area (Reginaldo et al. 2013). This may be explained by the inherent differences in level of disturbances or quality of habitats among different disturbed landscapes. Small non-flying mammals of the Philippines are known to respond to varying levels of habitat disturbances (Rickart et al. 2011b, Ong and Rickart 2008).

In general, there is a significant heterogeneity in abundances of the small mammals across the three habitat types in our study. This characteristic resembles observations in a number of systems, including along forest edges, disturbed forest, complex agricultural landscapes, and fragmented landscapes in the Philippines (e.g., Reginaldo et al. 2013, Rickart et al. 2011b, Balete et al. 2009, Miller et al. 2008, Stuart et al. 2007) and in moderately disturbed forests and forest fragments in other tropical regions (e.g., Laurance 2004, Pardini 2004, Malcolm 1997). However, many of the patterns of abundances among different species and between groups of small mammals in our study were different from those reported elsewhere (e.g., Rickart et al. 2016, Reginaldo and de Guia 2014, Stuart et al. 2007). In

our study, the lack of significant differences in the overall and between small mammal group abundances across the three habitat types suggest that small mammals are equally common across the three habitat types. Other studies reported a reverse trend in the abundance of native and non-native species group across habitat disturbance, in which the former group is most abundant in the least disturbed habitats than in the most disturbed habitats (e.g., Reginaldo and de Guia 2014; Rickart et al. 2011a, 2007; Miller et al. 2008; Stuart et al. 2007). This general trend was not detected in our study. Our different observations may have been caused by the relative proximity of and the presence of similar characteristics among the three habitat types, which different species may randomly select to thrive. It was inferred that some native species have tolerance to moderate disturbances and non-native species have the potential to invade less disturbed habitats (Heaney et al. 2016, Rickart et al. 2007, 2011a); this may imply that in our study area, any of the three habitats are suitable for all species.

The considerably higher number of *A. abrae* in the regenerating montane forests than in the other two habitats and the presence of several individuals of *R. everetti* in the regenerating montane forest and gullies in the agricultural area are consistent with the observations that these species are common in moderately disturbed habitats such as secondary or regenerating forests (Rickart et al. 2011b), and supports the prediction that most native mammals of the Philippines require forest habitats to persist (Rickart et al. 2011b). This dependence of native species on forest habitats in disturbed landscapes was also reported in fragmented forests (Laurance 2004). In contrast, the absence of *A. musculus* in the regenerating montane forest and its more abundant population in open habitats (pine and agricultural area), suggests that this native species has different response to varying levels of disturbances. However, its absence in the forest habitat may only be a result of non-detection because of the insufficient arboreal trapping in our study. Studies across habitat disturbance gradients reported that this arboreal species is abundant in primary and secondary montane forests, and mossy forest, and sometimes in mixed shrubby and grassy habitats (Balete et al. 2009, Heaney et al. 1999, Rickart et al. 1991). In the case of *C. whiteheadi*, the single capture limits the discussion on any pattern of abundance for this species. Many studies report, however, that this species tends to be abundant in regenerating forest and may also be common in agricultural areas (e.g., Rickart et al. 2011b, Rickart et al. 2007, Stuart et al. 2007). Our observation indicates that *C. whiteheadi* inhabits other sections of the forest fragment and the population was low. Alternatively, as this species is to a great degree fossorial, and is a specialized predator of earthworms (Heaney et al. 2016), it may spend more time foraging underground, particularly during dry periods when fewer earthworms are present on the surface; thus, the low detection.

The observation that there is a higher proportion of non-natives in the pine stand than in the agricultural area is contrary to what other studies reported (e.g., Rickart et al. 2016, Reginaldo and de Guia 2014, Rickart et al. 2011b). However, the lack of significant difference in the number of non-natives among the habitat types suggests in general that they may be common in all habitat types or just transiently using other habitat types (discussed below). Deviating from the general patterns of abundance for non-native species group were *R. tanezumi* and *S. murinus*. Results suggest that *S. murinus* is more common and uncommon in the pine stand and agricultural area, respectively. Reports about the ecology *S. murinus* in the Central Cordillera is very limited; but one study also reported that this species is common in pine forest fragments (Reginaldo et al. 2013), suggesting that this species thrive well in pine stands. For *R. tanezumi*, results strongly suggest that it is common the agricultural area. However, this is not surprising because this is

a common species in disturbed habitats (Heaney et al. 2016, 1998). Notably, the patterns of abundance among the three non-native species in disturbed landscapes that included montane forest habitats is not consistent with other observations in the Central Cordillera. For example, *R. exulans* was often more common than *R. tanezumi*, whereas *S. murinus* tend to be uncommon or absent (See Rickart et al. 2016, 2011a; Reginaldo and de Guia 2014). Different patterns were also observed in highly urbanized areas (See Ong and et al. 1999) and in forest fragments in urban areas (See Reginaldo et al. 2013). These suggest that unknown or specific factors, such as disturbance history and/or the specific type and level of disturbances, may be responsible for the variable responses of these non-native species.

### Habitat Use of Small Non-flying Mammals across Adjacent Habitats

Our trapping procedure that employed the mark-and-recapture method provides direct information on habitat use by different species of small non-flying mammals because animals were allowed to continue with their usual use of a given habitat and the confounding effects of the removal of individuals were avoided.

In general, the different species use all types of habitats, but there was an apparent preference of the native species group for regenerating montane forest and non-native species group for agricultural areas and pine forest. These observations are consistent with the reports for other disturbed landscapes in the Central Cordillera (e.g. Reginaldo and de Guia 2014, Rickart et al. 2011b, Stuart et al. 2007).

All observations on *A. abrae* suggest that it primarily utilizes montane forest habitats and may occasionally use forest edges, and other habitat types (with broad-leaf trees) adjacent to the montane forests (e.g., pine forest and agricultural habitats). This preference that was also observed in other areas (Reginaldo and de Guia 2014, Rickart et al. 2011b.). Miller et al. (2008) also reported the selective use by a closely similar species of *Apomys (A. datae)* of secondary forest despite the presence of other disturbed habitats in an upland agroforest ecosystem. This suggests that these species have a stronger preference for forest habitats than open habitats. The stream crossing of *A. abrae* from the montane forest to the adjacent habitat in our study also appears as a regular habit of this species. Balete and Heaney (1997) noted about the ability of native species in a montane forest to move across intervening streams. Meanwhile, results also suggest that *R. everetti* primarily utilize patches of montane forest habitats, including gullies and dry streams, but it may have also occasionally reach sections of the agricultural area that are adjacent to gullies. In terms of mobility, our record of single recapture suggests that *R. everetti* travels over longer distances than *A. abrae*. In other parts of the Philippines, the reported mean distance traveled by *R. everetti* was 73 meters and some individuals may travel over 140 meters (Stuart et al. 2007) or over 200 meters (Balete and Heaney 1997). This observations suggest that *R. everetti* may have a wider home range than *A. abrae*, and it may regularly move between different preferred habitats. Other studies likewise report that *R. everetti* commonly use pine forests and agricultural areas adjacent to montane forests (Rickart et al. 2016, Reginaldo and de Guia 2014, Rickart et al. 2011a); the latter use of agricultural areas was also observed in this study. In upland agroforest ecosystem, *R. everetti* was also reported to be common in forest habitats, and in disturbed habitats, in particular, frequently in cane lands and occasionally in rice fields and village (Miller et al. 2008, Stuart et al. 2007). Our observation and these earlier reports suggest that *R. everetti* frequently use forest habitats and occasionally use nearby disturbed habitats.

We also report briefly about the possible role of matrix habitats in the movement of native species between the montane forest patches. Matrix is regarded as a selective filter for the movements of species across landscapes (Gascon et al. 1999), with different species expected to vary in their ability to pass across different types of matrices (Laurance 1994, 1991). Records of capture frequencies (Table 2) and capture sites, and the absence of any recapture from montane forest patches (including patches along gullies) suggest that *A. abrae* and *R. everetti* exist as isolated populations in different patches of montane forests and do not readily cross open habitats. In the case of *R. everetti*, it might specifically avoid a matrix characterized by early plant successional stage (e.g., low-lying grass and herbs in pine forests and agricultural area in our study). More advanced plant successional stages that are adjacent to forest appear to be tolerated by this species. Open habitats dominated by tall grass (cane land) adjacent to forest habitats was reported to be used by *R. everetti* frequently (Stuart et al. 2007). Our observations may suggest that significant difference in the characteristics of forest patches and surrounding matrix due to excessive disturbance may lead to isolation of native populations. Strips of montane forest habitats or streams, where some individuals of both species were also captured, may have an important role in maintaining the connectivity of different forest patches within a fragment. Understanding the role of the matrix to native species are interesting topics for research in the future. Gascon et al. (1999) highlighted the importance of the matrix in remnants (forest) dynamics and suggested a whole-landscape approach to conservation of fragmented populations.

*Apomys musculus* appeared to use both the pine stand and agricultural area more frequently than montane forest patches. However, the lack of significant difference in the captures across the habitats suggest that this species does not prefer any habitat type. Alternatively, as mentioned in the previous discussion, the lack of any capture from the regenerating montane forest patches may be due to the insufficient arboreal trapping in this habitat. Other studies report that this species arboreal species is common in forest habitats (Balete et al. 2009, Heaney et al. 1999, Rickart et al. 1991). The result in our study and a similar report from an urban pine forest fragment (see Reginaldo et al. 2013) suggest that in disturbed habitats in the Central Cordillera, *A. musculus* may occasionally use non-forest habitats, such as shrubby and grassy habitats adjacent to forest habitats. On the other hand, the lack of any recaptures between the pine and agricultural area suggests that this species does not move between those two habitats, despite the reported ability of some individuals to travel long distances, more than 200 meters in Mt. Isarog, South Luzon (Balete and Heaney 1997). Records of capture locations from the pine stand showed that it moved around but never crossed the stream or moved to the other habitats. Other trapping techniques may help in providing more accurate information about the habitat use by this species.

On the other hand, non-native species group also uses the three habitat types, but, as a group, they demonstrated a strong preference for pine stands and weak preference for montane forest patches. However, this general pattern of habitat use were only reflected by *R. exulans* and *S. murinus*; *R. tanezumi* had a stronger preference for the agricultural area. *Suncus murinus* was the most widely distributed, using both the pine stand and regenerating montane forest. Limited data from an agricultural-forest landscape in Benguet (Reginaldo and de Guia 2014) also suggests that this species often used various types of habitats. Our records of capture sites for *S. murinus* further suggest that it may have a strong preference for areas that are wet or with broad-leaf trees, an observation that was similarly observed in a pine forest fragment in an urban area (Reginaldo et al. 2013). Meanwhile, the other two non-native species appeared to

segregate within the disturbed landscape: *R. exulans* preferred the pine stand, whereas *R. tanezumi* preferred the agricultural area. Studies in the Central Cordillera, however, reported that these two species often coexist within similar habitats (See Rickart et al. 2016, Reginaldo and de Guia 2014, Reginaldo et al. 2013, Stuart et al. 2007, Joshi et al. 2004). Differences in microhabitat preference, a scale of habitat use that was not investigated in earlier studies, may possibly explain these varied results. *R. exulans*, when coexisting with other species, tend to use distinct habitats or microhabitats, in particular low-lying and dense vegetation (Bramley 2014, Harper 2006). Frequently burnt or cleared areas dominated by grass (See Rickart et al. 2016, Reginaldo and de Guia 2014) may well resemble this habitat characteristic preferred by this species. In contrast, the habitat use pattern by *R. tanezumi* may have been affected by the presence of human settlements since this species was only captured in the agricultural area, particularly on the transect nearest to a house, despite the presence of other types of habitats. Various studies report that this species is common in areas near (or in) human habitations (e.g., Stuart et al. 2008, Ong et al. 1999, Heaney et al. 1998). Others, however, report the *R. tanezumi* is occasionally found in disturbed forests and disturbed habitats near human habitations (e.g., Reginaldo and de Guia 2014, Rickart et al. 2011a, Stuart et al. 2007). Interestingly, it seems that fluctuations in available resources preferred by *R. tanezumi*, may be a better predictor of habitat use by this species (See Stuart et al. 2007, also Miller et al. 2008). These previous reports and our result suggest that individuals may use more frequently areas where food is abundant (e.g., near houses or within villages), whereas other individuals wander to adjacent habitats. Shifts in the location of abundant resource may change the habitat use pattern by this species (Stuart et al. 2007).

Local processes are often cited to influence patterns of relative abundance and habitat use in small mammal communities (Southwood 1995, Schluter and Ricklefs 1993), and this may also be true for the small non-flying mammal communities in our study. The response of Philippine small non-flying mammal to disturbance is influenced by differences in habitat structure (e.g., Reginaldo and de Guia 2014, Rickart et al. 2011b, Miller et al. 2008). In our study area, the set of native species, excluding *A. musculus*, represents a group that is tolerant of habitat disturbance and more abundant in moderately disturbed areas than in more pristine habitats (Rickart et al. 2011b). The occurrence of *A. musculus* in the pine stand and agricultural area may also suggest that this species is tolerant to habitat disturbance. Earlier report of the possible absence of other disturbance-tolerant native species in the pine forest fragments in urban areas (Reginaldo et al. 2013), however, provided evidence that heavily disturbed forest fragments may not be tolerated even by the resilient native species. In the case of the non-native species, their presence and their relative abundance in the study area also resembles observation in fragmented landscapes in many areas (e.g., Reginaldo et al. 2013, Pardini 2004, Bolger et al. 1997). The strong preference of non-native species for the conditions in disturbed habitats may also help explain their comparably abundant proportion in the study area. Rickart et al. (2011b) suggested that in the highlands of the Central Cordillera on Luzon Island, the establishment of non-native species adjacent to or in disturbed forests requires substantial disturbance, and their persistence is ensured if a disturbance is sustained.

## SUMMARY AND CONCLUSIONS

We found a low number of species and moderately abundant small mammal population in the disturbed landscape in our study. Overall, non-native species were relatively more

abundant than native species. The overall, native and non-native small mammal groups, and most species abundances across the three habitat types did not vary. Notably, two non-native species, *R. tanezumi* and *S. murinus* were more abundant in certain habitats than in others. The presence and abundance of native species demonstrated a level of tolerance to different types or levels of habitat disturbances. The relatively common occurrences of *A. abrae* and *R. everetti* in patches of regenerating montane forest support observations that some native species may persist when suitable habitats are present. In contrast, *A. musculus* responded, to a certain degree, like the non-native species by occurring in non-forest habitats, but its response may be an artefact of the insufficient arboreal trapping that we used.

The overall pattern of habitat use by the small non-flying mammals in the disturbed habitats showed that all habitat types were equally used. However, native species group preferred the montane forest patch, whereas non-native species group preferred the pine stand. All species, except *A. musculus* and *R. everetti*, preferred certain habitat type over the others. Two native species, *A. abrae* and *R. everetti*, primarily used patches of regenerating montane forests and records of capture locations provided some evidence that populations in the forest patches were isolated. Among the non-native species, *S. murinus* preferred the pine stand and have shown a limited evidence of their ability to use other habitat type. In contrast, the congener *R. exulans* and *R. tanezumi* segregate within the disturbed landscape, with the former being restricted in the pine stand and the latter in the agricultural area.

Our results provide evidence of the ability of disturbed landscape to support a moderately diverse community of small non-flying mammals and the possible role of variation in habitat conditions in forming small non-flying mammal structure. The presence and abundance of native species in the patches of regenerating montane forests highlight the importance of forest patches in disturbed landscapes in the persistence of a potential source of native species. In contrast, the persistence of non-native species is supported by the presence of disturbed habitats.

There are no other reports from the Central Cordillera that directly measured the patterns of abundance and habitat use that employed capture-mark-recapture technique. While there were notable similarities of observations between this study and those conducted along habitat gradients (e.g., Rickart et al. 2011b, Reginaldo and de 2014, Stuart et al. 2007), our study have provided new observations and insights into the role of different habitat types on species assemblage, abundance, and local distribution of small non-flying mammals in disturbed landscape. Other studies in the future that employ similar methodology would help test the generality of the findings presented here.

#### ACKNOWLEDGMENT

We thank Narciso Arugay Jr. and Mark Gerald Mislant, who served as field assistants. M. Mislant also assisted in data recording and encoding. We thank Lawrence Heaney and two anonymous reviewers for their valuable comments, suggestions, and editorial work on the manuscript. Romeo Dizon and Rizavel Addawe helped us with some of the statistical analyses. The permission to conduct the study in the forest fragment was approved by Ms. Sudy Hidalgo and the officials of Barangay Wangal. The permit for fieldwork was issued by the Director of the Department of Environment and Natural Resources–CAR.

#### CONFLICT OF INTEREST

No conflict of interest.

#### CONTRIBUTION OF INDIVIDUAL AUTHORS

Both authors conceptualized the research. AA Reginaldo conducted the fieldwork and wrote the manuscript. Some comments, suggestions, and editorial work of PS Ong improved the manuscript.

#### REFERENCES

- August PV. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 1983; 64(6):1495-1507.
- Bagamaspad A, Hamada-Pawid Z. A people's history of Benguet Province. Baguio City: Baguio Printing and Publishing Company, 1985.
- Balete DS, Heaney LR. Density, biomass, and movement estimates for murid rodents in mossy forest on Mount Isarog, Southern Luzon, Philippines. *Ecotropica* 1997; 3:91-100.
- Balete DS, Heaney, Veluz MJ, Rickart EA. Diversity patterns of small mammals in the Zambales Mts., Luzon, Philippines. *Mamm Biol* 2009; 74:456-466.
- Bolger DT, Alberts AC, Sauvajot RM, Potenza CM, Tran D, Mazzoni S, Soule ME. Response of rodents to habitat fragmentation in Coastal Southern California. *Ecol Appl* 1997; 7(2):552-563.
- Bramley GN. Habitat use by kiore (*Rattus exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island, New Zealand. *NZ Wildl Res* 2014; 33:539-548.
- Buot IE, Okitsu S. Vertical distribution and structure of the tree vegetation in the montane forest of Mt. Pulag, Cordillera mountain range, the highest mountain in Luzon Is., Philippines. *Vegetation Sci* 1998; 15:19-32.
- Forestry Management Bureau. Philippine Forestry Statistics: 2018. Department of Environment and Natural Resources, 2018. <https://forestry.denr.gov.ph/index.php/statistics/philippines-forestry-statistics>.
- Harper GA, Dickinson KJM. Habitat use by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand. *NZ Wildl Res* 2006; 29(2):251-260.
- Heaney LR, Balete DS, Dolar ML, Alcalá AC, Dans ATL, Gonzales PC, Ingle NR, Lepiten MV, Oliver WLR, Ong PS, Rickart EA, Tabaranza Jr, BR, Uzzurum RCB. A Synopsis of the Mammalian Fauna of the Philippine Islands. *Fieldiana Zool*; 1998 8:1-61.
- Heaney LR, Regalado JC. Vanishing treasures of the Philippine rain forest. Chicago: The Field Museum, 1998.
- Heaney LR, Balete DS, Rickart EA, Uzzurum RCB, Gonzales PC. Mammalian diversity on Mount Isarog, a threatened center of endemism on southern Luzon Island, Philippines. *Fieldiana Zool* 1999; 95:1-62.

- Heaney LR, Balete DS, Sarmiento J, Alviola PA. Losing diversity and courting disasters: the mammals of Mt. Data National Park. *Haring Ibon* 2006; 25:15-23.
- Heaney LR, Balete DS, Rickart EA, Alviola PA, Duya MR, Duya MV, Veluz MJ, VandeVrede L, Steppan SJ. Seven new species and a new subgenus of forest mice (Rodentia: Muridae: *Apomys*) from Luzon Island. *Fieldiana* 2011; 2:1-60.
- Heaney LR, Balete DS, Rickart EA. The mammals of Luzon Island: biogeography and natural history of a Philippine fauna. USA: Johns Hopkins University Press, 2016.
- Jansa SA, Barker FK, Heaney LR. Molecular phylogenetics and divergence time estimates for the endemic rodents of the Philippine Islands: evidence from mitochondrial and nuclear gene sequences. *Syst Biol* 2006; 55: 73-88.
- Joshi RC, Gergon EB, Aplin KP, Singleton GR, Martin AR, Cabigat JC, Cayong A, Desamero MV, Sebastian LS. Rodents and other small mammals in Banaue and Hungduan rice terraces, Philippines. *International Rice Research Notes*, 2004; 29: 44-46.
- Kowal NE. Shifting cultivation, fire, and pine forest in the Cordillera Central, Luzon, Philippines. *Ecol Monograph* 1966; 36:389-419.
- Laurance WF. Rainforest fragmentation and the structure of small-mammal communities in tropical Queensland. *Biol Cons* 1994; 69:23-32.
- Laurance WF. Forest-climate interactions in fragmented tropical landscapes. *Philos Trans R Soc London B* 2004; 359:345-352.
- Laurance WF. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conserv Biol* 1991; 5:79-89.
- Magurran AE. *Measuring Biological Diversity*. United Kingdom: Blackwell Science Ltd, 2004.
- Malcolm, JR. Biomass and diversity of small mammals in Amazonian forest fragments. In: Laurance WF, Bierregaard RO, eds, *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. Chicago: University of Chicago Press, 1997: 207-221.
- Miller RW, Stuart AM, Joshi RC, Banks PB, Singleton GR. Biology and management of rodent communities in complex agroecosystems – rice terraces. In: Singleton GR, Joshi RC, Sebastian LS, eds. *Philippine Rats: Ecology and Management*. Philippine Rice Research Institute, 2008: 25-36.
- Ong PS, Pedregosa M, de Guia MD. Wildlife inventory of the University of the Philippines (UP) and the Ateneo de Manila University Campus, Diliman, Quezon City, Luzon, Philippines. *Sci Diliman* 1999; 11:6-20.
- Pardini R. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. *Biodiv Cons* 2004; 13:2567-2586.
- Pardini R, de Souza SM, Braga-Neto R, Metzger JP. The role of forest structure, fragment size and corridor in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biol Cons* 2005; 124: 253-266.
- Reginaldo AA, Ballesteros VF, Gonzales PV, Austria CM. Small non-volant mammals of forest patches in Baguio City, Luzon Island. *Asia Life Sci* 2013; 22:131-139.
- Reginaldo AA, de Guia APO. Species richness and patterns of occurrence of small non-flying mammals of Mt. Sto. Tomas, Luzon Island, Philippines. *Philipp Sci Lett* 2014; 7(1):34-44.
- Rickart EA, Heaney LR, Uzzurum RCB. Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines. *J Mamm* 1991; 72:458-469.
- Rickart EA, Balete DS, Heaney LR. Habitat disturbance and the ecology of small mammals in the Philippines. *J Environ Sci Manag* 2007; 10: 34-41.
- Rickart EA, Heaney LR, Balete DS, Tabaranza BR Jr. Small mammal diversity along an elevational gradient in northern Luzon, Philippines. *Mamm Biol* 2011a; 76:12-21.
- Rickart EA, Balete DS, Rowe RJ, Heaney LR. Mammals of the northern Philippines: tolerance for habitat disturbance and resistance to invasive species in an endemic fauna. *Divers Distrib* 2011b; 17:530-541.
- Rickart EA, Balete DS, Alviola PA, Veluz MJ, Heaney LR. The mammals of Mt. Amuyao: a richly endemic fauna in the Central Cordillera of Northern Luzon. *Mammalia* 2016; 80(6):572-592
- Ricklefs RE. Community diversity: relative roles of local and regional processes. *Science* 1987; 235:167-171.
- Schluter D, Ricklefs RE. Species diversity: an introduction to the problem. In Ricklefs RE, Schluter D, eds. *Species diversity in ecological communities: historical and geographical perspectives* 1993; 1-10.
- Southwood TRE. Natural communities: structure and dynamics. *Philos T R Soc B* 1995; 351(1344):1113-1129.
- Steppan SJ, Zawadzki C, Heaney LR. Molecular phylogeny of the endemic Philippine rodent *Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. *Biol J Linn Soc* 2003; 88:699-715.
- Stevenson J, Siringan F, Finn J, Madulid D, Heijnis H. Paoay Lake, northern Luzon, the Philippines: a record of Holocene environmental change. *Global Change Biol* 2010; 16:1672-1688.
- Stuart AM, Prescott CV, Singleton GR, Joshi RC, Sebastian LS. The rodent species of the Ifugao Rice Terraces, Philippines, target or non-target species for management? *IJ Pest Manag* 2007; 53(2):139-146.
- Stuart AM, Prescott, CV, Singleton, GR. Biology and management of rodent communities in complex agroecosystems – lowlands Philippines. In: Singleton GR, Joshi RC, Sebastian LS, eds. *Philippine Rats: Ecology and Management*. Philippine Rice Research Institute 2008: 37-55.
- Stuart AM, Prescott CV, Singleton GR. Can a native rodent species limit the invasive potential of a non-native rodent species in tropical agroforest habitats? *Pest Manag Sci* 2016; 72(6):1168-1177.

Whitford HN. The forests of the Philippines. Part I: forest types and products. Manila: Philippine Bureau of Forestry Bulletin, 1911.

Williams SE, Marsh H, Winter J. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* 2002; 8(5):1317-1329.