Small mammal-microhabitat associations in a disturbed landscape in northern Luzon, Philippines

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ABSTRACT

Microhabitats occur as patches of conditions that offer various resources for small mammals. Studies have shown that microhabitat conditions influence local distribution patterns, but the extent to which small mammals in the Philippines are affected by microhabitat characteristics is unknown. This study sought to identify the characteristics of microhabitats and the patterns of microhabitat use by six small nonflying mammals (*Apomys abrae*, *A. musculus*, *Rattus everetti*, *R. exulans*, *R. tanezumi,* and *Suncus murinus*) in a disturbed landscape that consisted of 3 habitats (pine stand, regenerating montane forest, and agricultural area). We live-trapped small mammals and collected 23 habitat variables in 135 trapping stations. Trapping stations with captures exhibited higher soil moisture, higher rock cover, and lower *Ayapana* cover than those in stations without captures. *Apomys abrae* and *R. everetti* preferred areas with high tree cover but differed in their preferred type of forb cover. *Rattus exulans* and *R. tanezumi* were strongly associated with characteristics of open habitats but distinguished from each other by difference in preference for tree cover and ground steepness. *Apomys musculus* and *S. murinus* preferred similar areas, but the former was strongly associated with the high cover of *Ayapana* and the latter with a moderate slope and high soil moisture. Results suggest that the coexisting species may exhibit microhabitat-level selection, and this process may be considered as one factor that influences the spatial distribution of Philippine small nonflying mammals in disturbed landscapes. Future works that will employ a similar methodology can test and expound our findings.

KEYWORDS

disturbance, habitat selection, Muridae, Philippine mammals, Soricidae, wildlife

INRODUCTION

Vegetation structure has been known to influence local small-mammal community structure, affecting species assemblages and spatial distribution patterns (e.g., de Lima et al. 2010; Pardini et al. 2005; Laurance 1994; August 1983). Other studies attempted to explain the coexistence of competing species within a habitat, and they suggest that the existence of multiple niches (Kotler and Brown 1988; Levins 1968; Mac Arthur and Levins 1964) that may vary in degree of heterogeneity and complexity of vegetation structure (Williams et al. 2002; August 1983) or quality (e.g., Delciellos et al. 2016; Rickart et al. 2011a) makes coexistence possible. The Philippines, an area with rich small mammals that occupy various types of habitats (Heaney et al. 2016; Ong and Rickart 2008), is an ideal place to investigate

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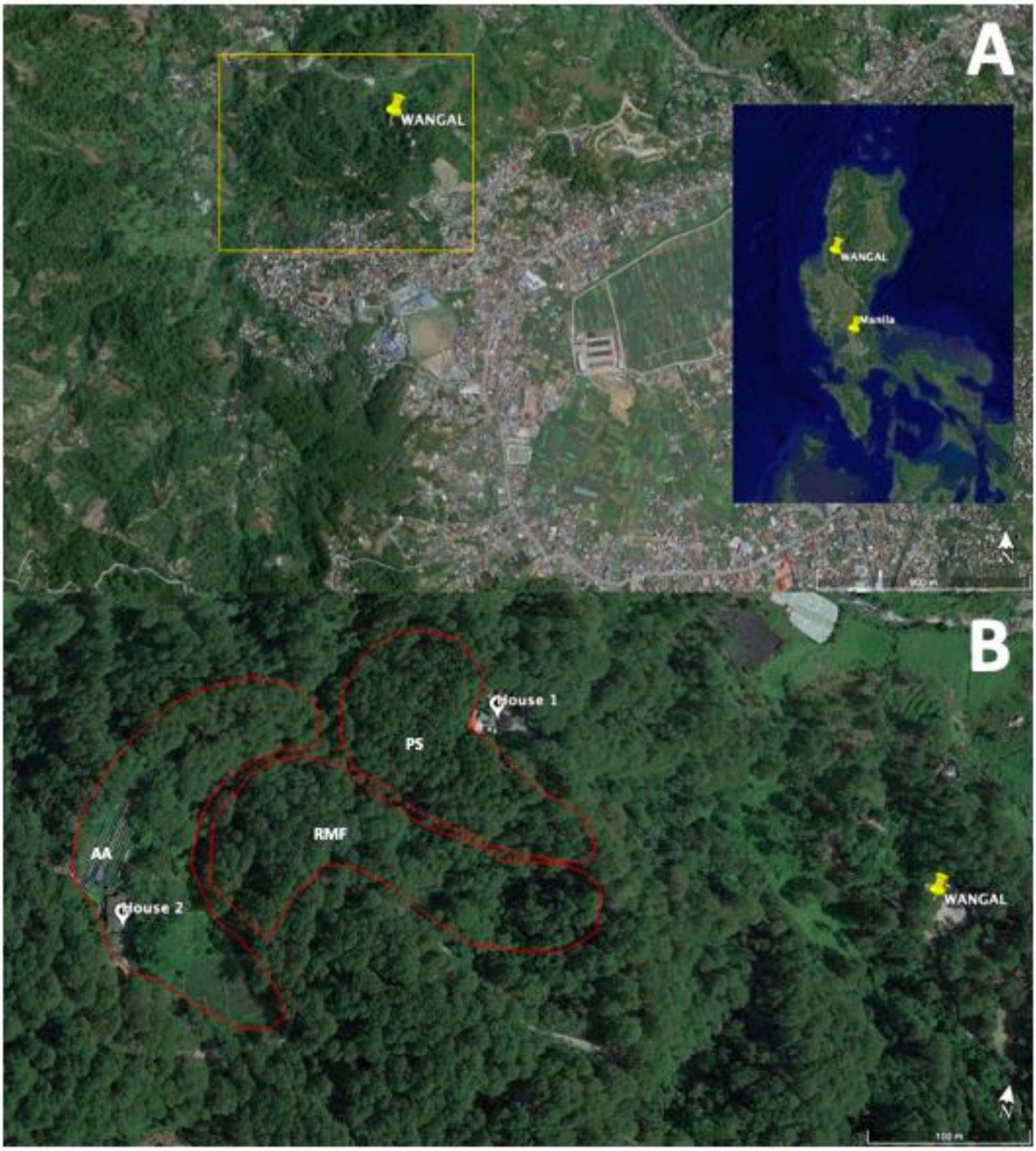


Figure 1: Satellite Image View of the Study Area. (A) The forest fragment in Wangal showing its location in the municipality of La Trinidad. Inset map of the Philippines showing the location of Wangal on Luzon Island. (B) Section of the forest fragment showing the three habitats: pine stand (PS), regenerating montane forest (RMF), and agricultural area (AA) (*Google Satellite Map, 2017; Accessed November 2019*).

the relationship of small-mammal community structure and habitat structure.

Most ecological studies of small mammals in the Philippines have investigated species occurrences across different types of habitats (or macrohabitats) that vary in disturbance levels (e.g., Reginaldo and Ong 2020; Rickart et al. 2011a; Stuart et al. 2007). Information on habitat use by small mammals at the macrohabitat level (e.g., montane forest, agricultural area) has been derived primarily from abundance estimates and general descriptions of habitats. In these studies the degree of disturbance in various habitat types has been inferred from differences in structure of vegetation; thus the habitat preference by different species of small mammals can also be inferred to be influenced by characteristics of the vegetation. The results were straightforward; species distribution patterns were strongly associated with differences in the characteristics of habitats (Rickart et al. 2011a; Miller et al. 2008; Stuart et al. 2008). However, the specific component of disturbance and/or habitat structure remains to be determined. To date, only one study has attempted to determine microhabitat use by small nonflying mammals. Canopy and ground cover were reported to influence the pattern of habitat use by the pest *Rattus tanezumi* and native *R. everetti* (Stuart et al. 2016). This progress clearly suggests that additional studies are needed to understand further the pattern of habitat use by the different species of small nonflying mammals in the Philippines and identify the specific components of habitat that influence distribution, both at the

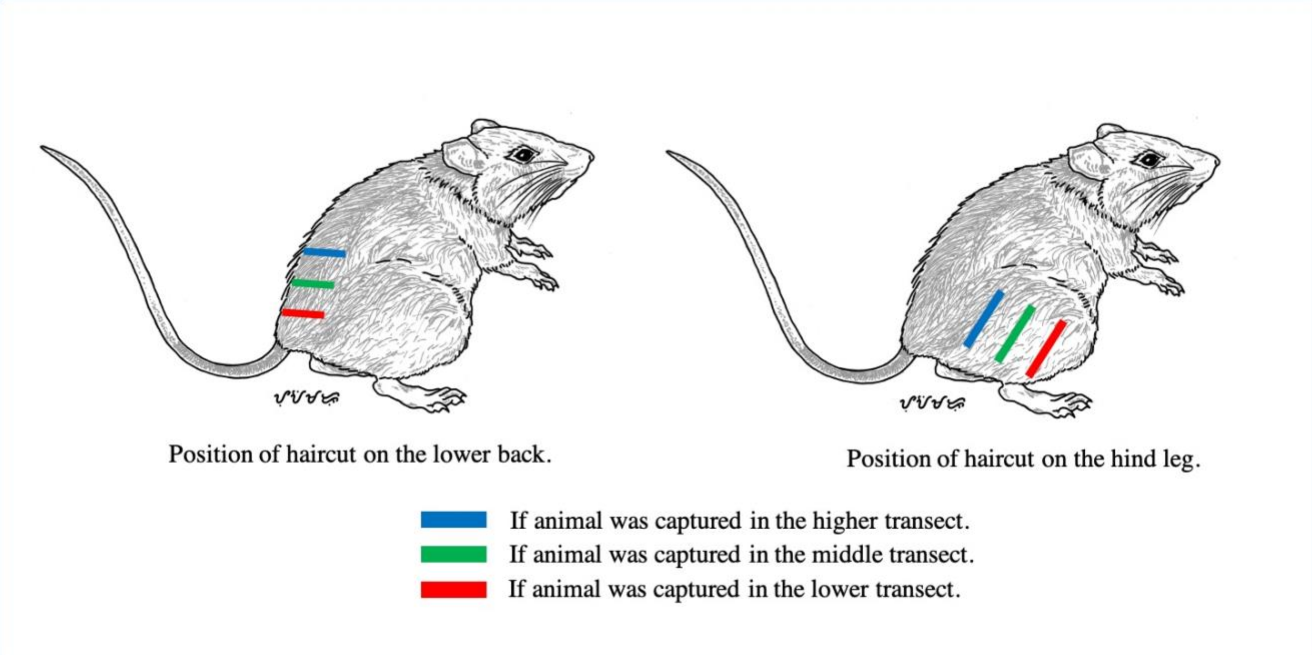


Figure 2: Illustration of the codes used to mark individual animals. The animals were marked on a specific body region that matched a specific capture site: left leg—pine stand, right leg—agricultural areas, and lower back—regenerating montane forest. The relative position of each hair-cut per body region corresponded to the transects (lower, middle, and higher) in a grid.

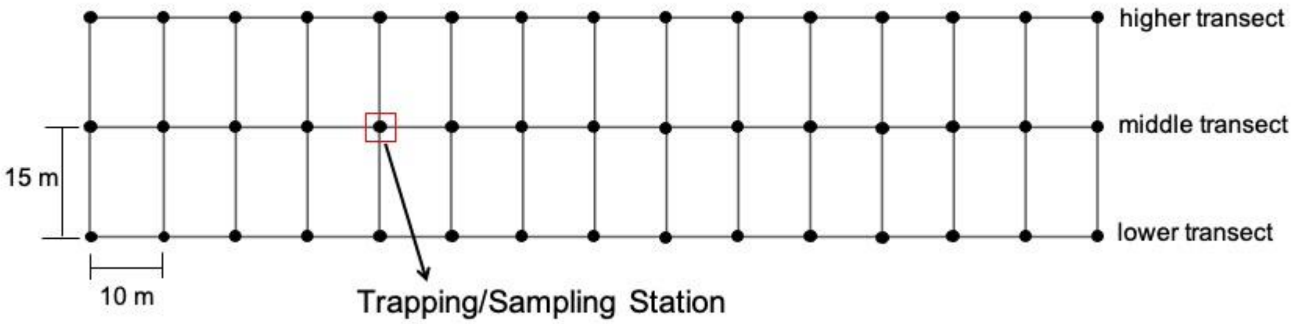


Figure 3: Illustration of the trapping grid that we set in each of the three habitat types (regenerating montane forest, pine stand, and agricultural area) we sampled. The illustration also shows the sampling and trapping stations, where we recorded small-mammal capture frequencies and habitat variables, respectively.

macrohabitat and microhabitat levels. While macrohabitat analysis provides a general picture of habitat selection, microhabitat-level analysis can provide clues to understand within-habitat distribution or the process that allows species coexistence.

The small mammals in Central Cordillera in northern Luzon have been the subject of several recent studies on Philippine mammals (e.g., Rickart et al. 2016, 2011b). These studies report that many species occur in mature forests, but several others occur in disturbed habitats adjacent to forest habitats along with nonnative species (e.g., Reginaldo and de Guia 2014; Rickart et al. 2011a; Miller et al. 2008). While these works generally show which species are associated with a particular habitat and briefly mention information on microhabitat–small mammal associations, detailed accounts of microhabitat characteristics that may reflect varying disturbance levels remain lacking. Another particular interest is the conditions that allow the coexistence of supposedly competing native and nonnative species in disturbed habitats. Data on specific microhabitat–small mammal association may well also help identify specific conditions that support the existence of native species in disturbed landscapes.

Our study investigated the patterns of microhabitat use of small nonflying mammals in a disturbed landscape. Specifically, we sought to determine if a microhabitat-level selection was evident in the small-mammal community and identify the characteristics of microhabitats associated with each small-mammal species. We conducted our study in patches of disturbed habitats in La Trinidad, Benguet Province, Philippines. The study provides evidence of microhabitat selection among Philippine small mammals and preliminary information on microhabitat characteristics associated with different native and nonnative mammal species.

MATERIALS AND METHODS

Study area

The study area selected was along the border of a pine-dominated forest fragment in La Trinidad, Benguet Province, Philippines (fig. 1A). Remnant montane forest patches occupied gullies and stream, and in many places shrubby vegetation grew under the pine trees. Pine stands along the border of the forest fragment had lower vegetation cover dominated by grass, which continued as grasslands in the agricultural areas. La Trinidad occupies about 7,000 hectares, and it is an upland urban area (~1200 masl to ~1700 masl) situated on a large valley and surrounding hills. La Trinidad has a distinct dry and wet season. During the time of study (February to April 2017) the morning temperature on average was 18 °C; and the hottest times (25 °C) were between 1300 and 1500 hours on cloudless days. In the forest fragment several secondary lower montane forest patches were surrounded by pine stand and agricultural areas. In the last century two major waves of disturbances occurred in the area: pine tree logging during the American occupation (1900s to 1940s) and large-scale cattle raising dating back to the 1500s (Bagamaspad and Hamada-Pawid 1985). Local informants reported that large-scale cattle raising ended in the 1970s.Within the area selected for the study, two distantly separated (~300 m) households had managed this section of the forest fragment (fig. 1B).

We selected three different disturbed habitats (fig. 1B), which we identified as pine stand, regenerating montane forest, and agricultural area. The habitats occurred as a continuous habitat that formed the disturbed landscape (fig. 1B). The three habitats occupied different slopes and were cut by streams. The pine stand (~1.1 ha) consisted mainly of pine tree (*Pinus kesiya*), and the lower vegetation was dominated by grasses (e.g., *Miscanthus sinensis* and *Imperata cylindrica*), ferns (*Pteridium aquilinum* var. *wightianum*), and other species of plants such as *Rubus fraxinifolius*, *Ageratina adenophora*, and *Ayapana triplinervis*. In the 1940s the ridge adjacent to the pine stand was occupied by a sawmill that catered to the logging industry (Heald Corporation) for pine. After logging activities were discontinued, further modifications (establishment of residential and recreation areas) were made along the ridge. The regenerating montane forest was a large patch (~1.40 ha) that occupied a slope and consisted mainly of broad-leaf trees (e.g., *Ficus* spp., *Omalanthus* sp., *Eurya* sp.), tree ferns (*Cyathea* sp., *Angiopteris* sp.), various species of low-lying ferns (from families Dryopteridaceae and Thelypteridaceae), and tall ginger plants (*Vanoverberghia sepulchrei*). Some old pine trees (~450 cm) were scattered throughout, a feature that is inferred as evidence of past disturbances (Kowal 1966). The montane forest patch covered the banks of a stream that separated it from the pine stand. The higher sections of the forest patch were adjacent to a road and an area used for small-scale vegetable and fruit tree (coffee and lemon) farming. In the agricultural area (~1.7 ha) several patches of vegetation covers were present. An open grazing area (~0.30 ha) was mainly covered with low-lying grasses, ferns (*P. aquilinum* var. *wightianum*), and shrubs (*Melastoma malabathricum*) and with sparse naturally growing pine trees. In other sections lemon and coffee stands, an abandoned flower garden, and a wide area (~0.44 ha) used as a vegetable farm were adjacent to a house (fig. 1B; house 2). Gullies, with a thick cover of the fern *Gleichenia longissima*, several small broad-leaf trees (e.g., *Ficus* sp.), and tree fern (*Cyathea* sp.) cut through several sections of the open areas.

Trapping methods

In each habitat type we laid out a rectangular grid (140 m × 30 m) consisting of three parallel transects, labelled as lower, middle, and higher (fig. 2). Each transect consisted of 15 trap stations, 10 meters apart, that produced a total of 45 trap stations per plot. Live trapping of small mammals consisted of two consecutive trapping periods, with each period composed of a three-day prebaiting and an eight-day live-trapping session. Roasted coconut coated with peanut butter and live earthworms (e.g., Rickart et al. 2011b; Rickart et al. 1991) were used as bait for the first and second period, respectively. The variation in baiting was employed in each period to capture all possible species and individuals in our study area.

Cage traps of three different sizes (13 × 18 × 42 cm, 10 × 10 × 25 cm, and 10 × 10 × 42 cm) were used. The top surfaces of the cage traps were covered with plastic to cover the bait and shelter the animal from potential rain and dew. Traps were baited each afternoon and checked early in the morning. All traps without capture were kept open until the time of next baiting. Three cloth bags of different sizes and each narrowed at one end were used to retrieve the animals from the cages. While the animal was on the bag, the weight, hind foot and tail lengths (tail vertebra) were measured, and the sex and age of the animal were recorded. The captured animals were marked by cutting off a narrow hair patch on particular areas of their bodies (lower back or either hindleg) following a code that indicated the habitat and transect visited by the animals (fig. 3). The body marks and the morphometrics of each animal served as bases for identifying an individual. All the animals were released at the capture sites.

Habitat variables

We hypothesize that different microhabitats created by the combined effect of physical condition, soil characteristic, ground cover, and vegetation structure influence the preference of the various species of small mammals. Microhabitat conditions can affect various activities of small mammals, such as foraging and nesting. To cover all possible factors, 23 habitat variables were used to characterize the microhabitats and determine microhabitat–small mammal species association. The criteria (Dueser and Shugart 1978) in selecting the habitat variables were used. Some of the variables that we used were adopted from earlier microhabitat studies (e.g., Horvath 2008; Laurance 1991; Dueser and Shugart 1978), and the rest were selected based on the characteristics of the habitats that we studied. We categorized the variables into four groups, namely, physical and edaphic conditions, ground cover, lower vegetation structure (synonymous with understory vegetation), and tree characteristics.

All 23 variables were recorded from each trapping station (45 trapping stations in a grid; fig. 2) using three independent sampling plots (adopted from Dueser and Shugart 1978). The physical and edaphic variables were recorded within a *1.0 m^2 ring plot* by taking four measurements and taking the average as the final value. The variables were degree of slope (Slope), average midday soil temperature (SoTemp), and soil moisture (SoM). Ground and lower vegetation covers were recorded from two *perpendicular 20 m^2 arm-length transects* by following the *point-intercept method* (with 0.5 m intervals). The ground cover variables were rock cover (RckC) and overall ground cover (OGrdC), which was contributed mostly by plant litter. The variables that described the structure of lower vegetation included general categories of plants and certain plant species that were dominant and/or forming distinct plant habit. We used the term lower vegetation to include all plants that formed the layer of vegetation closest to the ground, with heights that ranged from 0.5 m to 3.0 m. It included understory vegetation and grassland/open habitat vegetation that consisted of graminoids (grass and sedge), forbs, ferns, and shrubs. The lower vegetation directly influences how small mammals use the ground for foraging and nesting. The variables were the tall grass *Miscanthus sinensis* cover (MisC), overall grass cover (OGrsC), Cyperaceae spp. cover (CypC), overall graminoid cover (OGrmC), the fern *Gleichenia longissima* cover (GleC), overall fern cover (OFrnC), the exotic, perennial composite *Ayapana triplinervis* cover (AyaC), Zingiberaceae (*Vanoverberghia sepulchrei*) cover (ZgC), Araceae (*Schismatoglottis* sp.) cover (AraC), overall forb cover (OFrbC), overall herb cover (OHrbC), and viney shrub cover (VSC). The lower vegetation height

(LVegH) was also recorded from the perpendicular plot by measuring the height of lower vegetation at 1.0 m intervals. The tree characteristics category included the cover of pine trees and broad-leaf trees and the distances and size of pine trees. The presence of trees affects the type of vegetation that grows on the ground, amount of litter, and microclimate. Tree covers included pine tree cover (PTC), broad-leaf tree cover (BLTC), and overall tree cover (OTC). We used DBH as proxy for cover; it was recorded by measuring the DBH of all trees within the perpendicular transects. The two other variables were the distance of the nearest pine tree (DiPT) and the size of the nearest pine tree (SiPT). These variables were recorded from a *10 m-radius circular plot*, divided into four sections, by measuring the distance of the nearest pine tree from the center of the and measuring the size (DBH) of that tree.

Average values for each variable were computed for each sampling point. Understory vegetation cover was computed by dividing the number of intercepts with the total intercepts and converting the final value to a percentage. Tree cover was computed by dividing the total DBH (in cm) by the total length of the transect (1000 cm) and converting the quotient to percent. The measurement units for the variables were as follows: slope in degrees, the temperature in °C, soil moisture in scale units of 1 to 8 (as indicated in the soil analyzer; handheld soil pH and moisture analyzer with conical probe), percentage (%) for cover, distances of the nearest tree in centimeters (cm), size of the nearest tree in millimeters (mm), and height of vegetation in meters (m).

Data analysis

Difference between stations with captures and without captures

To have a general idea of how the disturbed landscape was utilized by the community of small mammals, the average values of the 23 variables for stations with and without captures were compared using T-tests. Since the three habitats were adjacent to one another, we assumed that each species was free to use the three habitats in relation to its preferred microhabitat. By comparing the stations with and without captures we could identify the characteristics of microhabitats that were generally preferred by the entire small-mammal community. All values in percentage were first converted to decimal values. Most of the variables were not normally distributed, and 13 failed to meet the assumption of equal variances. Transformations did not improve the normality and homogeneity of variances; hence actual raw values were used in the analyses. Variables that met the assumption of equal variances were tested using Student's T-test, whereas those that did not were tested with Welch's T-test.

Characteristics of microhabitats

We also sought further to describe the characteristics of the trapping stations with capture (n = 36). We used Principal Component Analysis (PCA; Paleontological Statistics or PAST 3) to describe the variation among the trapping stations with capture and identify the *key habitat variables* that explained the variation using the 23 habitat variables. The first few principal components explained the greatest variation, with 8 of them having an eigenvalue greater than 1. However, the key habitat variables that explained the highest variation among the trapping stations with captures were identified only from the first five principal components. The key habitat variables were the variables that were most strongly correlated with each component. We treated the composite characteristics made by the key habitat variables from each of the principal components as the smaller patches of habitat or microhabitat in the disturbed landscape. PCA biplots (ordination) were also used to evaluate visually the relative differences between the trapping stations with captures and show the key habitat variables that were associated with the trapping stations. In PCA ordination, trapping stations that are close together on the plot are more similar in terms of the habitat variables.

Microhabitat–small mammal associations

To infer microhabitat use in the disturbed landscape, we evaluated the relationships between small-mammal captures and habitat variables. We used the Canonical Correspondence Analysis (CCA; IBM SPSS Statistics) to evaluate specific associations between species of small mammals and particular sets of habitat conditions for the disturbed landscape. This ordination technique maximizes the correlations between the frequency of capture and the habitat variables among 36 trapping stations with captures. Transformations of habitat variables did not improve linearity; thus raw values were used in the analyses. The capture frequencies (or total captures that included recaptures) for each species were pooled from the two trapping sessions. Microhabitat preference by each species was inferred from CCA scores of each of the first five CCA Axes. We selected key habitat variables by selecting those that had higher CCA scores (absolute value), with 0.20 as the minimum. The different set of variables associated with each species was interpreted as the defining microhabitat characteristics preferred by each small mammal species. We also used the patterns in CCA biplots of small-mammal capture frequencies and microhabitat variables to illustrate the associations.

To provide a relative comparison of the conditions associated with each species, the actual average values of the associated habitat variables for each species from the CCA analysis were compared. To facilitate a qualitative comparison, we used the following ranking system: lower vegetation cover (very low, 10% and below; low, 11% to 40%; moderately high, 41% to 60%; high, 61% to 89%; very high, 90% and above), tree cover (very low, 0.5% and below; low, 0.6% to 1.0%; moderately high, 1.1% to 1.7%; high, 1.8% to 2.4%; very high, 2.5% and above), amount of soil moisture (very low, 1.9 and below; 2 to 3.9; moderately high, 4 to 5.9; high, 6 to 7.9; very high, 8 and above), distance of the nearest tree (very near, 100 cm and below; near, 110 cm to 400 cm; moderately distant, 410 cm to 600 cm; far, 610 cm to 890 cm; very far, 900 cm to 1000 cm), size of the nearest tree (very small, 100 mm and below; small, 110 mm to 400 mm; moderately large, 410 mm to 600 mm, large, 610 mm to 890 mm; very large, 900 mm to 1000 mm), and height of lower vegetation (short, <50 cm,; tall, 50 cm to 100 cm; >100 cm very tall).

RESULTS

The small mammals

A total of 59 captures (36 individuals) were accumulated from the two trapping sessions, which comprised a total of 2,160 trap nights (table 3). A total of six small mammal species, five rodents and a shrew (table 3), were recorded. Among the species captured, *Apomys abrae*, *A. musculus,* and *Rattus everetti* are native to the Philippines, whereas *R. exulans*, *R. tanezumi*, and *Suncus murinus* are nonnative species. The highest capture, 24 (41%), was recorded for *A. abrae*. All the other species had six to nine captures. Seventy-nine percent of the trapping stations with capture were in the pine stand and regenerating montane forest. Only *A. abrae* was captured from all three habitat types, whereas *R. tanezumi* was captured only in the agricultural area. The rest of the species were captured in two habitat types: *A. musculus* in the pine area and agricultural area, *R. everetti* in the regenerating montane forest and agricultural area, and *S. murinus* and *R. exulans* in the regenerating montane forest and pine stand.

Table 1: Comparison of the means of 23 habitat variables between stations with and without captures.

HABITAT VARIABLES	VARIABLE ACRONYM	TRAPPING STATIONS		*t-value*	P
		With Captures (n = 36)	Without Captures (n = 99)		
Physical and Edaphic Conditions					
Degree of slope	Slope	28.56±1.84	31.59±1.03	-1.48	0.14
Soil temperature	SoTemp	20.12±0.25	20.51±0.16	-1.3	0.196
Soil moisture	SOM	**6.34±0.45**	5.16±0.16	2.075	0.04
Ground Cover					
Rock cover	RckC	**0.011±0.005**	0.004±0.001	2.064	0.041
Overall ground cover	OGrdC	0.989±0.009	0.989±0.009	-0.384	0.701
Tree Characteristics					
Distance of the nearest pine tree	DiPT	468.22±46.46	450.15±26.12	0.35	0.727
Size of the nearest pine tree	SiPT	363.33±33.86	341.01±18.61	0.603	0.547
Pine tree cover	PTC	0.014±0.004	0.015±0.002	-0.378	0.706
Broad-leaf tree cover	BLTC	0.017±0.003	0.015±0.002	0.276	0.79
Overall tree cover	OTC	0.030±0.005	0.034±0.004	-0.83	0.409
Lower Vegetation Structure					
Lower vegetation height	LVegH	97.62±15.26	92.96±9.46	0.256	0.798
Miscanthus cover	MisC	0.278±0.012	0.031±0.003	-0.234	0.816
Overall grass cover	OGrsC	0.293±.041	0.346±0.023	-1.817	0.237
Cyperaceae cover	CypC	0.014±0.005	0.012±0.004	0.306	0.76
Overall graminoid cover	OGrmC	0.031±0.043	0.342±0.023	-0.815	0.417
Gleichenia cover	GleC	0.0553±0.018	0.068±0.015	-0.532	0.596
Overall fern cover	OFrnC	0.257±0.041	0.203±0.188	1.278	0.171
Ayapana cover	AyaC	0.478±0.063	**0.615±0.031**	-2.24	0.027
Zingiberaceae cover	ZgC	0.037±0.015	0.024±0.006	0.809	0.423
Araceae cover	AraC	0.010±0.003	0.024±0.031	0.581	0.563
Overall forb cover	OFrbC	0.784±0.030	0.75±0.04	-0.118	0.906
Overall herb cover	OHrbC	0.836±0.033	0.892±0.014	-1.589	0.118
Viney shrub cover	VSC	0.070±0.011	0.066±0.007	0.385	0.721

Value (mean) of habitat variable in bold was significantly higher for those stations than in the other stations.

Variation in habitat characteristics of the trapping stations with captures

Stations with captures versus stations without captures

Thirty-six (~27%) of the 135 trapping stations set for our entire study area had at least one small mammal capture. In each of the trapping grid that consisted of 45 trapping stations, 16 (36%), 14 (31%), and 6 (13%) of the trap stations had at least one capture in the regenerating montane forest, pine stand, and agricultural area, respectively. Notably, in each trapping grid, species were always captured in stations that were adjacent to each other. A comparison of the means of the 23 habitat variables between the stations with captures and stations without captures revealed significant differences in three variables: higher average soil moisture (6.34±0.45; P=0.04, t=2.075; table 1) and rock cover (1.10%; P=0.04, t=2.064; table 1) in the stations with captures than in those without captures and a higher average cover of *Ayapana* (61.50%; P=0.27, t=-2.24; table 1) in the stations without captures than in those with captures.

Microhabitats of the stations with captures

Principal component analysis of the habitat variables from the 36 trapping stations with captures showed eight principal components with eigenvalues greater than 1.0; these components explained 79% of the variance. Only the variables that showed the highest correlation with the first five components were presented. Together these five components explained 61% of the total variation (table 2).

Principal Component 1, which explained 27% of the variation, suggested a negative relationship of broad-leaf tree cover and soil moisture with soil temperature and three vegetation covers, namely, overall grass (OGrsC), overall herb, and *Ayapana* (AyaC) (table 2; fig. 4). A repeated contribution by tree characteristics was revealed in PC2, PC3, and PC4 (table 2). In PC2 the distance (DiPT) and size (SiPT) of the nearest pine tree, together with soil moisture (SOM) and overall graminoid cover (OGrmC), were negatively correlated with fern covers (*Gleichenia* and overall fern cover) and degree of slope (Slope) (table 2). For PC3, distinct habitat conditions were contributed by the negative relationship of overall ground cover (OGrdC), size and distance of pine trees (SiPT and DiPT), and overall tree

Table 2: Principal component loadings of the 23 habitat variables recorded from small-mammal capture stations.

HABITAT VARIABLES	ABBRE-VIATION	PRINCIPAL COMPONENTS				
		PC 1 27%	PC 2 24%	PC 3 20%	PC 4 18%	PC 5 8%
Physical and Edaphic Conditions						
Degree of slope	Slope	0.063	-0.350	0.122	0.193	0.043
Soil temperature	SoTemp	0.266	-0.040	0.073	0.187	-0.194
Soil moisture	SOM	-0.219	0.317	-0.026	0.018	-0.009
Ground Cover						
Rock cover	RckC	-0.195	0.143	-0.109	0.123	0.013
Overall ground cover	OGrdC	0.134	-0.154	0.354	0.259	0.279
Tree Characteristics						
Distance of the nearest pine tree	DiPT	-0.098	0.252	0.326	0.343	0.079
Size of the nearest pine tree	SiPT	0.011	0.228	0.430	0.275	-0.056
Pine tree cover	PTC	0.199	-0.207	0.224	-0.347	-0.124
Broad-leaf tree cover	BLTC	-0.281	-0.119	0.187	-0.244	0.165
Overall tree cover	OTC	-0.046	-0.234	0.317	-0.439	-0.013
Lower Vegetation Structure						
Lower vegetation height	LVegH	0.024	0.151	-0.337	-0.006	0.056
Miscanthus cover	MisC	0.208	-0.115	0.009	-0.161	-0.197
Overall grass cover	OGrsC	0.349	0.215	0.092	-0.150	0.063
Cyperaceae cover	Cyc	-0.011	0.228	-0.121	-0.123	0.392
Overall graminoid cover	OGrmC	0.343	0.243	0.073	-0.157	0.108
Gleichenia cover	GleC	-0.115	-0.295	-0.131	-0.080	0.325
Overall fern cover	OFrnC	-0.167	-0.363	-0.132	0.297	0.098
Ayapana cover	AyaC	0.375	0.077	0.051	-0.055	0.023
Zingiberaceae cover	ZgC	-0.093	0.160	-0.190	-0.092	-0.316
Araceae cover	AraC	-0.211	0.071	0.117	0.102	-0.218
Overall forb cover	OFrbC	0.256	-0.197	-0.242	0.157	-0.010
Overall herb cover	OHrbC	0.310	-0.065	-0.276	0.221	-0.040
Viney shrub cover	VSC	0.101	0.111	-0.048	-0.030	0.595

Table 3: Summary of small-mammal captures and recaptures accumulated from the two trapping sessions.

SPECIES	TRAPPING PERIOD		TOTAL
	I	II	
Native			
Apomys abrae	21 (7)	3 (1)	24 (8)
Apomys musculus	6 (4)	0	6 (4)
Rattus everetii	2 (2)	4 (4)	6 (6)
Nonnative			
Rattus exulans	8 (4)	0	8 (4)
Rattus tanezumi	6 (6)	0	6 (6)
Suncus murinus	6 (5)	3 (3)	9 (8)
Total	49 (28)	10 (8)	59 (36)

In parentheses are numbers of individuals for each species based on first capture.

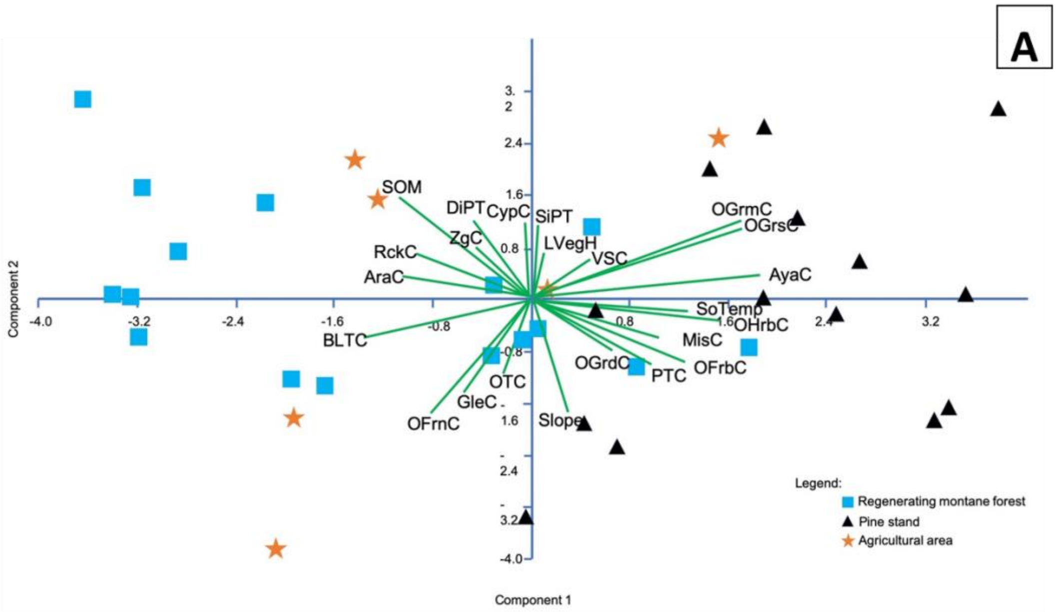
cover (OTC) with lower vegetation height (LVegH), overall herbaceous (OHrbC), and forb (OFrbC) covers (table 2). Principal Component 4 showed negative relationships of the size (SiPT) and distance (DiPT) of pine tree with overall tree cover (OTC), pine tree cover (PTC), and broad-leaf tree cover (BLTC; table 2). Lastly PC5 revealed a negative relationship of Zingiberaceae (ZgC) and Araceae (AraC) cover and understory vegetation cover (Cyperaceae, overall fern, and viney shrub cover) with overall ground cover (OGrdC) (table 2). Photographs of some of these microhabitats are shown in figure 5.

The combination of microhabitat characteristics and the inverse relationships between variables generally separated most of the trapping stations in the regenerating montane forest from those in the pine stand, as shown in the PCA biplots (fig. 4). High soil moisture (SOM) and high broad-leaf tree cover (BLTC) were associated with the regenerating montane forest. In contrast, high soil temperature (SoTemp), grass cover (OGrmC/OGrsC), and herbaceous/forb covers (primarily contributed by *Ayapana* cover) were associated with the pine stand. A number of trap stations also occupied the center of the plot; this pattern implies intermediate characteristics (fig. 4). Meanwhile, stations in the agricultural area did not form a distinct cluster but joined the stations from the broad-leaf forest and pine stand, with more stations joining those from the former (fig. 4).

Small mammal–microhabitat association

The result of Canonical Correspondence Analysis (CCA) of the frequency of captures and the 23 habitat variables from the 36 trapping stations showed that distinct microhabitat conditions were associated with the different species of small mammals (table 4; fig. 6).

Axis 1 shows that *R. everetti* and *R. tanezumi* were associated with microhabitats distinct from those associated with the other three species (table 4; fig. 6A). The two *Rattus* species correlated more strongly with four variables: positively with *Gleichenia* cover (GleC) and negatively with overall grass/graminoid cover (OGrsC/OGrmC) and overall forb cover OFrbC (table 4; fig. 6A). Axis 2 shows that the native species *A. abrae* and *R. everetti* (less strongly) were more positively correlated with soil moisture (SOM) and covers of Araceae (AraC) and broad-leaf trees (BLTC; table 4; fig. 6B). In contrast, the other four species, including the native species *A. musculus*, were more strongly associated with soil temperature (SoTemp) and covers of *Ayapana* (AyaC), *Miscanthus* (MisC), grasses/graminoids (OGrsC/OGrmC), forbs/herbs, and pine trees (table 4; fig. 6B).



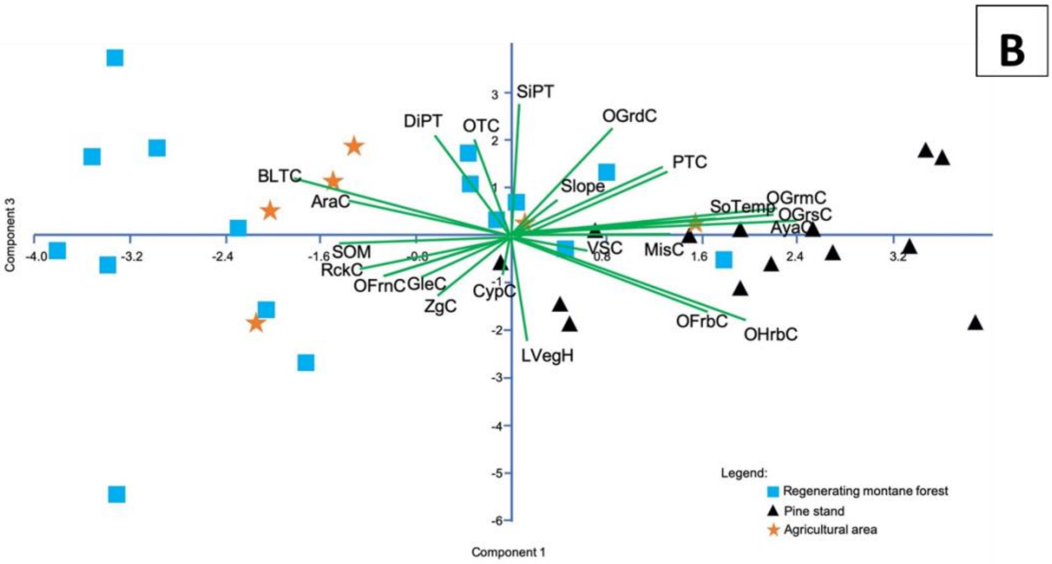


Figure 4: PCA biplot for the 36 trapping stations with captures and the associated habitat variables. (A) Between PC1 and PC2. (B) Between PC1 and PC3.

In Axis 3, *R. everetti* was contrasted with *A. abrae* and *R. tanezumi* for being more associated with steep slope (Slope), Araceae cover (AraC), and ferns (OFrnC), especially the species of *Gleichenia* (table 4). In contrast, *R. tanezumi* was more associated with the distance and size of pine trees (DiPT, SiPT), and with cover of grasses/graminoids (OGrsC/OGrmC), unlike *A. abrae* or *R. tanezumi* (table 4). Axis 4 distinguished the conditions for *S. murinus* from those for *A. musculus* and *R. exulans*; *Suncus murinus* was more associated with soil moisture (SOM) and cover of graminoids (OGrmC) and viney shrubs (VSC; table 4). In Axis 5, *A. musculus* and *R. exulans* were contrasted; the former was more strongly associated with *Miscanthus* cover (MisC) and the latter with the height of vegetation (LVegH) and with covers of Cyperaceae (CypC) and viney shrubs (VSC; table 4).

The comparative description of the specific microhabitat conditions associated with each species is presented in table 5. The characteristics of the lower vegetation, in particular, cover and height of the vegetation, the characteristics of trees, one physical (slope), and one edaphic condition (soil moisture), appeared to play various roles. *Apomys abrae, R. everetti*, and *S. murinus* were associated with areas with high soil moisture, but the latter was set apart by its strong association with dense understory vegetation cover. The native species *A. musculus* differed from the other native species by its weak association with broad-leaf tree cover but strong association with *Ayapana* and grass cover. In contrast, the nonnative *R. exulans* was distinguished from the nonnative *R. tanezumi* by its association with steep areas, low moisture, and high cover of pine trees, *Ayapana,* and grass.

Figure 5: Examples of microhabitats in the study area. (A) *Cyathea* and thick growth of *Gleichenia* (background) in one of the gullies in the agricultural area. (B) Thick growth of the weed *Ayapana* in the pine stand. (C) A community of Araceae (*Schismatoglottis*) in the regenerating montane forest. (D) Dense growth of young broad-leaf trees in the regenerating montane forest.

DISCUSSION

Microhabitats in patches of disturbed habitats

The much fewer number of trapping stations with captures than those without captures suggests that the small mammals utilized only a small area of each disturbed habitats or the entire disturbed landscape. This disproportionate use of available habitats is often interpreted as habitat selection (Garshelis 2000; Wiens 1976). In general, results suggest that the small mammals in the forest fragment selected environments with higher soil moisture and exposed rocks, but they avoided habitats with high understory vegetation cover, particularly cover by the exotic species *Ayapana*. PCA results show that trapping stations with high soil moisture were associated with high broad-leaf tree cover; this set of conditions resembles the characteristics of forests such as montane forest in the Philippines (Heaney et al. 2016; Fernando et al. 2008; Merrill and Merritt 1910). In contrast, the conditions characterized by a dense growth of *Ayapana* and grass, and high cover of pine trees, among others, are features of many open areas, such as pine stands, vegetation bordering vegetable gardens, and along edges of montane forests (Jacobs 1972; Kowal 1966; Merrill and Merritt 1910). These associations of small mammal trapping stations (or sites of capture) and microhabitat characteristics generally suggest that in disturbed landscapes with patches of disturbed habitats, such as in our study area, small mammals more often utilize areas that exhibited characteristics similar to those of montane forests than open habitats.

Understory vegetation, physical and edaphic conditions, and tree characteristics appear as essential factors that define small-mammal microhabitats. The same habitat categories were found strongly associated with small-mammal use of habitat (e.g., Horvath et al. 2008; Laurance 1994; Dueser and Shugart 1978). Despite the different assemblages of small mammals in our study, our results generally corroborate observations of positive relationship of habitat structure and small mammals in many areas, including the temperate region (e.g., Horvath et al. 2008; Yahner 1982), tropics (e.g., Stuart et al. 2016; de Lima et al. 2010; Puttker 2008), and temperate, tropical forest (e.g., Songer et al. 1997). Our findings further support the role of local environmental conditions in influencing the patterns of habitat use among small mammals. Microhabitat selection by small mammals is related to their differences in preference for variable sources of food, characteristics of foraging areas, or quality of cover, which helps defend against predation (Laurance 1994). In our study, these features may have been created by different environmental patches. These patches often reflect various stages of community succession (Wiens 1976) and spatial and temporal differences in plant resources (Foster and Gaines 1991) and may have created various habitats for invertebrates (e.g., earthworms and insects) that serve as food for the different species. Food items are variables that we have not tested in our study, and this is a good topic for future research.

Microhabitat use by small nonflying mammals

The degree of broad-leaf tree cover and the density of lower vegetation cover by various plant species were the primary variables that appeared to influence microhabitat selection among the small mammals in the disturbed landscape. The various set of conditions appeared to have acted at two levels, namely, macrohabitat and microhabitat. The effect at the macrohabitat scale was evident in the two small-mammal groups, namely, native (excluding the native *A. musculus*) and nonnative species, whereas the effect of microhabitat scale was toward each individual species.

With the possible exception of *A. musculus,* results show that the native species were associated strongly with a high density of broad-leaf trees, whereas the nonnative species were associated with open areas that had dense cover of grass and other species of herbs, such as the exotic *Ayapana*. In general, this pattern

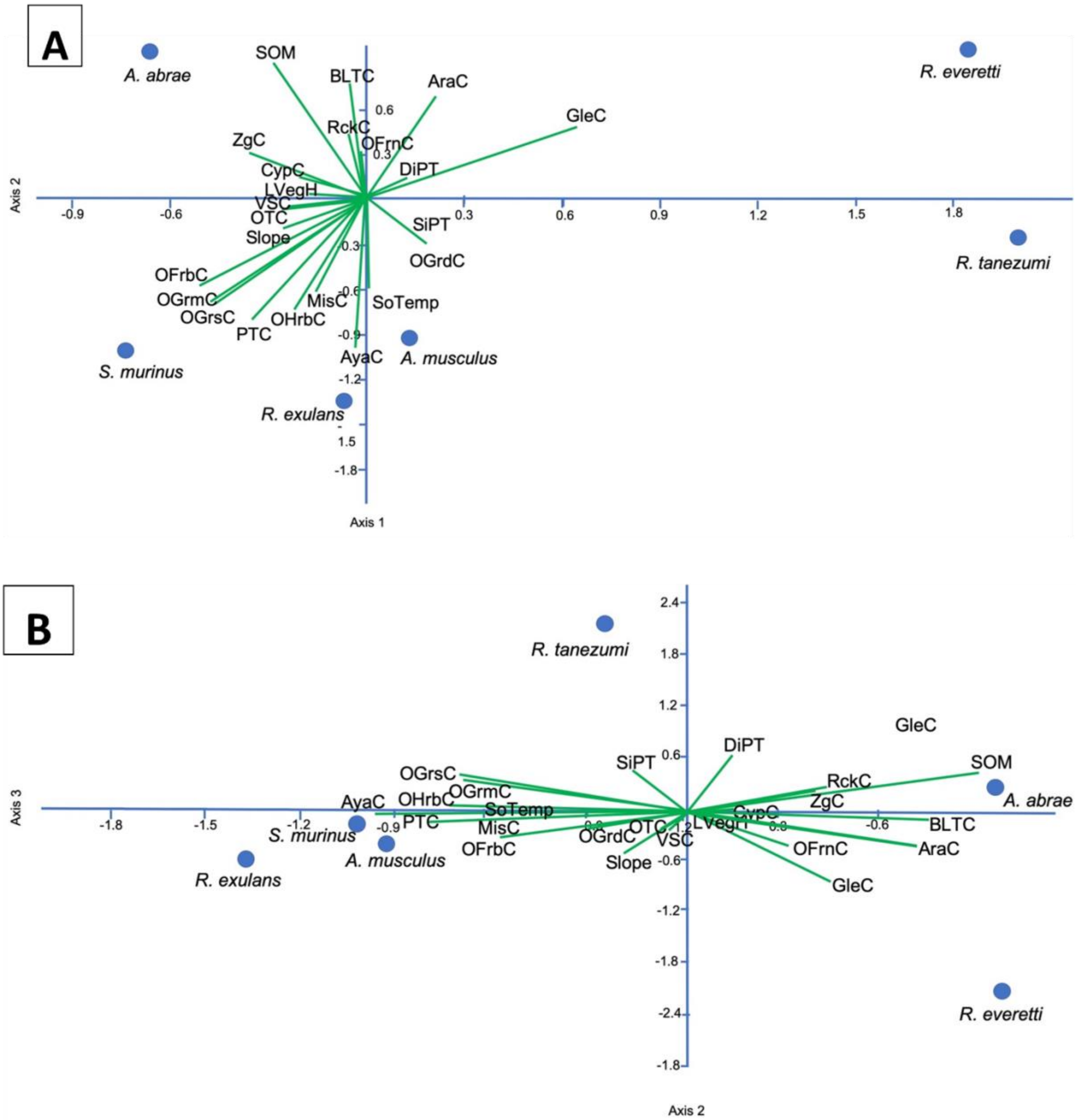


Figure 6: CCA Plot of species captures of small mammals and the different variables that correlated with CCA Axes 1 and 2. The scale of the axes was increased by 1.5. (A) Between Axes 1 and 2. (B) Between Axes 2 and 3.

Table 4: Summary of CCA scores for each small mammal species and microhabitat variables. In parentheses are the percentage variances explained by each axis.

MAMMAL/HABITAT VARIABLES	ABBRE-VIATION	SCORES				
		Axis 1 (29%)	Axis 2 (28%)	Axis 3 (22%)	Axis 4 (14%)	Axis 5 (8%)
Small Mammals						
Apomys abrae	Aa	-0.66	0.96	0.28	-0.23	-0.12
Apomys musculus	Am	0.13	-0.95	-0.35	-1.65	2.29
Rattus everetii	Rev	1.84	0.97	-2.07	0.63	0.00
Rattus exulans	Rex	-0.07	-1.39	-0.53	-1.00	-1.81
Suncus murinus	Sm	-0.74	-1.04	-0.12	1.78	0.44
Rattus tanezumi	Rt	1.99	-0.27	2.21	0.29	-0.12
Habitat Variables						
Physical and Edaphic Conditions						
Degree of slope	Slope	-0.17	-0.14	-0.32	-0.31	-0.04
Soil temperature	SoTemp	0.00	-0.40	-0.01	-0.31	0.06
Soil moisture	SOM	-0.19	0.60	0.29	0.21	0.08
Ground Cover						
Rock cover	RckC	0.13	-0.20	0.12	0.07	0.02
Overall ground cover	OGrdC	-0.03	0.28	0.18	0.08	0.01
Tree Characteristics						
Distance of the nearest pine tree	DiPT	0.09	0.09	0.43	-0.19	-0.01
Size of the nearest pine tree	SiPT	0.08	-0.12	0.31	-0.02	-0.16
Pine tree cover	PTC	-0.23	-0.54	-0.08	0.09	-0.03
Broad-leaf tree cover	BLTC	-0.03	0.50	-0.07	0.07	-0.17
Overall tree cover	OTC	-0.17	-0.05	-0.12	0.03	-0.16
Overall Ground Cover	OGrdC	-0.03	0.28	0.18	-0.08	0.01
Lower Vegetation Structure						
Lower vegetation height	LVegH	-0.11	0.02	-0.03	-0.20	-0.31
Miscanthus cover	MisC	-0.10	-0.41	-0.06	-0.16	0.20
Overall grass cover	OGrsC	-0.31	-0.46	0.28	0.19	0.01
Cyperaceae cover	CypC	-0.14	0.09	0.01	-0.20	-0.25
Overall graminoid cover	OGrmC	-0.31	-0.46	0.25	0.20	-0.01
Gleichenia cover	GleC	0.40	0.29	-0.54	0.17	0.05
Overall fern cover	OFrnC	-0.01	0.21	-0.28	-0.14	-0.05
Ayapana cover	EupC	-0.02	-0.65	-0.02	0.10	0.17
Zingiberaceae cover	ZgC	-0.24	0.21	0.11	-0.05	0.00
Araceae *cover*	AraC	0.15	0.47	-0.26	0.05	-0.01
Overall forb cover	OFrbC	-0.34	-0.39	-0.20	-0.10	0.13
Overall herb cover	OHrbC	-0.15	-0.49	0.05	-0.02	0.12
Viney shrub cover	VSC	-0.16	-0.04	-0.13	0.23	-0.21

revealed by multivariate analysis suggests that native species are associated with forest habitats, nonnative species with open habitats; this finding supports the general macrohabitat-level association of the two groups of Philippine small mammals (e.g., Reginaldo and Ong 2020; Rickart et al. 2011b; Stuart et al. 2008; Balete et al. 2009). In contrast, nonnative species generally treated pine and agricultural areas similarly. Pine and agricultural areas (particularly the open areas covered with exotic herbs) may be recognized as comparable habitats because the lower vegetation structures in these two habitats resemble each other (Kowal 1966). However, the detection of macrohabitat-level selection was expected because the process of selection may occur anywhere along a continuum of spatial scales from microhabitat to macrohabitat levels (Kotler and Brown 1988). Alternatively, the presence of households near the pine stand and agricultural area in our study may have played a role in the general association of nonnative species with open habitats.

In addition to the general association of small mammal groups with macrohabitat-level selection, our findings strongly suggest that microhabitat-level selection was exhibited by each small mammal species. Results reveal that within the regenerating montane forest, *A. abrae* occupied areas with high moisture and areas with tall lower vegetation formed primarily by Zingiberaceae (*Vanoverberghia sepulchrei*) plants (table 5; fig. 5); these conditions may have created a suitable foraging area for the rodent, which is known to depend highly on food items on the ground (Heaney et al. 2009). Several studies report that *A. abrae* primarily used montane forest habitats and occasionally adjacent habitats (Reginaldo and Ong 2020; Reginaldo and de Guia 2014; Rickart et al. 2011a). *Rattus everetti* likewise may have been influenced by the same conditions that affect the foraging of *A. abrae,* but such conditions were created by a different set of plants, particularly creeping fern *Gleichenia* and Araceae (*Schismatoglottis* sp.). These plants allow an unimpeded space on the ground because their leaves were borne at a considerable distance from the ground. These plants also formed dense ground cover. This preference for an environment with dense cover has been inferred as a strategy that allows small mammals to avoid detection by predators (e.g., de Lima et al. 2010). Notably, dense growth of grass and the forb *Ayapana* were negatively associated with these two species. These plants formed a dense cover very close to the ground, and this might have negatively affected the two native species' foraging habits.

In contrast, *A. musculus*, a known forest species (Rickart et al. 2016; Balete and Heaney 1997; Rickart et al. 1991), exhibited a pattern that resembles those of nonnative species. The variables associated with *A. musculus* also suggest that it utilized open habitats. In such areas the species used sections that had a high

Table 5: Summary of microhabitat characteristics associated with each small mammal species. This summary was based on the key habitat variables identified in the CCA analysis and the actual average values of those variables. See methodology for the qualitative ranks that were used in the comparisons.

SMALL MAMMALS	MICROHABITAT CHARACTERISTICS		
	Lower Vegetation	Tree Characteristics	Physical and Edaphic Conditions
Apomys abrae	High cover of forbs (Zingiberaceae); low cover of fern, grass/graminoid, and *Ayapana*; very tall (126 cm) lower vegetation (mainly by Zingiberaceae plants)	Very high cover of broad-leaf trees; very low cover of pine tree	Moderate degree of slope; high soil moisture
Rattus everetii	Low (but highest) covers of *Gleichenia* (in the agricultural area) and Araceae (in the regenerating montane forest); high cover of herbs and forbs; low *Ayapana* cover; very low graminoid and grass covers	High cover of broad-leaf trees; very low cover of pine tree	Moderate degree of slope; high soil moisture
Apomys musculus	High cover of *Ayapana*; very high cover of herbs and forbs; low cover of fern and grasses/graminoid	Low cover of broad-leaf trees; moderate cover of pine tree but high overall tree cover	Steep slope; low soil moisture
Rattus exulans	Very high cover of herbs and forbs; moderately high *Ayapana* cover; low grass/graminoid and fern cover	Very high pine tree and overall tree cover; low cover of broad-leaf tree	Steep slope; low soil moisture
Suncus murinus	Very high cover of herbs; high cover of forbs; Low grass cover but moderately high graminoid cover; high cover of *Ayapana*; very low cover for fern	High overall tree cover, high cover of pine tree and low cover of broad-leaf tree	Moderate degree of slope and high soil moisture (in the pine stand)
Rattus tanezumi	Moderate cover of grass (highest) cover; high herbaceous cover, moderate forb cover	Low tree covers and none for pine tree cover; sparsely distributed and moderately large pine trees	Low degree of slope; high soil moisture (agricultural area)

forbs cover, especially *Ayapana*, more often than areas covered with grass or fern. Other studies reported that the rodent species was found in pine stand areas covered with grass and exotic herbs (Reginaldo et al. 2013) and occasionally in shrubby and grassy habitats (Heaney et al. 1999; Rickart et al. 1991); these observations suggest that *A. musculus* commonly utilizes habitats associated with open areas, in addition to forest habitats (Heaney et al. 2016; Rickart et al. 2016). Data are insufficient to speculate on the causes of the species' microhabitat use; our lack of arboreal trapping probably affected the results.

The open habitats (pine stand and agricultural area) where the three nonnative species were captured exhibit a general characteristic of a dense cover of herbs and shrubs, and this is consistent with other reports from nearby areas (Reginaldo et al. 2013). The three nonnative species, *R. exulans*, *R. tanezumi*, and *S. murinus*, are common species in disturbed habitats (Heaney et al. 2016, 1998) but were shown to segregate between different habitats (Reginaldo and Ong 2020; Reginaldo and de Guia 2014). In our study the possible difference in the specific microhabitat use of the three nonnative species in open habitats seems to be affected by the degree of slope, degree of tree cover, and soil moisture level. *Rattus exulans* appears more commonly to use areas with steep and high cover of grass (primarily *Miscanthus*) and pine trees (table 5). The association of *R. exulans* with areas dominated by *Miscanthus* and trees may be related to its arboreal nature, that is, the species utilizes both ground and available arboreal habitats. Other studies report that this species used recently cleared or burnt areas (Heaney et al. 2016). Meanwhile, the observed preference of *R. tanezumi* for areas with low tree cover was also reported in lowland agroforest habitats (Stuart et al. 2016). Low tree cover was reported to indicate severe disturbance (Stuart et al. 2016), a characteristic often associated with *R. tanezumi* and the other nonnative species (Heaney et al. 2016). Alternatively, the low tree cover may be incidental, and the microhabitat selection by this species was caused by other factors, such as distance to human settlement (Reginaldo and Ong 2020), a variable not measured in the present study. This explanation is likely, considering that this species has a strong association with humans (Stuart et al. 2007; Heaney at al. 1998).

The observations on *S. murinus* also corroborate reports about the possible preference of this species for upland areas such as the Central Cordillera. This species was reported to occur in areas with mixed growth of trees and several species of herbs and shrubs in pine stands (Reginaldo et al. 2013) and along forest edges (Reginaldo and de Guia 2014). Such characteristic was also found to be generally preferred by species of shrews (Dickman and Doncaster 1987). Moreover, we highlight the association of some *S. murinus* individuals with areas with high soil moisture; this preference distinguishes this shrew from the other two nonnative species.

SUMMARY AND CONCLUSIONS

We investigated the presence and characteristics of microhabitats and described the patterns of microhabitat use by small nonflying mammals in adjacent patches of disturbed habitats in La Trinidad, Benguet, northern Luzon. T-test analyses of variables differentiated the characteristics of trapping stations with captures from those without captures primarily in terms of soil moisture level, rock cover extent, and *Ayapana* cover density. Principal component analysis of the same variables from the trapping stations with captures revealed identifiable key habitat conditions representing microhabitats. We used Canonical Correspondence Analysis to infer microhabitat use by small mammals. Results revealed that native species, except *A. musculus*, preferred areas with dense cover of broad-leaf trees, resembling forest habitats, whereas nonnative species preferred areas with dense cover of low-lying grass and forbs, resembling those of open habitats. In those two general habitat types, each species selected distinct microhabitats. These suggest that macrohabitat-level and microhabitat-level selections were both exhibited by the small mammal communities in the disturbed landscape that we investigated.

The microhabitat use by *A. abrae* and *R. everetti* in the forest was distinguished by their preference for areas with forb cover, specifically with high Zingiberaceae (*V. sepulchrei*) cover for the former species and high *Gleichenia* and Araceae (*Schismatoglottis* sp.) covers for the latter. The three nonnative species selected microhabitats in open habitats based on ground steepness, soil moisture level, and trees density. In contrast with *R. tanezumi*, *R. exulans* was more associated with areas that are steep and with higher tree cover. *Suncus murinus* was associated with areas with moderate slope and areas with high soil moisture. *A. musculus* had a preference similar to the nonnatives, but this observation needs to be further investigated.

Our study showed that the patches of disturbed habitat in the forest fragment consisted of various microhabitats, and the local distribution of small nonflying mammals may have been influenced by these microhabitat conditions. The study provided specific microhabitat–small mammal associations drawn from direct measurements of microhabitat variables and frequency of small-mammal captures in disturbed habitats. Some of these associations corroborate observations from other areas, whereas other associations were first reported here. Information on specific microhabitat conditions preferred by each species helps identify specific conditions that may be used to conserve native species and control pest species effectively. Specific preferences may likely differ if the assemblages of small nonflying mammals or the conditions of habitats vary. Future works that employ similar techniques and analyses will test the findings of this study.

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CONFLICT OF INTEREST

There is no conflict of interest.

CONTRIBUTION OF INDIVIDUAL AUTHORS

AA Reginaldo formulated the study with the supervision and guidance of PS Ong. AA Reginaldo performed the fieldwork. AA Reginaldo wrote the manuscript, and PS Ong had valuable comments and suggestions.

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