MICROHABITAT USE BY A TROPICAL FOREST RODENT, *PROECHIMYS SEMISPINOSUS,* IN CENTRAL PANAMA

Thomas D. Lambert and Gregory H. Adler*

University of Wisconsin–Oshkosh, Department of Biology and Microbiology, Oshkosh, WI 54901

We studied microhabitat use by *Proechimys semispinosus* (Central American spiny rat) by livetrapping along transects in 5 forested sites in central Panama. Microhabitat was quantified by measuring 14 variables at each sampling station. Relative abundance of *P. semispinosus* was 1.86 individuals/100 station-nights, which was typical of abundances of this species and other members of the genus. Spiny rats were distributed throughout sampled microhabitat space defined by factor analysis of 14 variables. We used logistic regression analysis to relate presence–absence at trap stations to microhabitat structure. Variables describing disturbed and younger forest were strong predictors of presence at trap stations. Associations of *P. semispinosus* with younger forest (smaller trees and lianas and lower canopies) and treefall gaps within older forest may have implications for regeneration of local forest patches through the activities of these rodents as seed predators and dispersers of seeds and arbuscular mycorrhizal fungi spores.

Key words: Echimyidae, habitat use, Neotropics, Panama, *Proechimys semispinosus,* spiny rat

Echimyid rodents of the genus *Proechimys* (spiny rats) often are the most abundant and widespread lowland forest rodents throughout much of their range in the Neotropics (Eisenberg 1989). Virtually any forested lowland habitat is likely to harbor at least 1 species of *Proechimys,* and some areas may have up to 4 sympatric species (Patton and Gardner 1972). Recent studies suggested that these rodents play an important role in forest dynamics through their activities as seed predators and dispersers of seeds (Adler and Kestell 1998; Asquith et al. 1997; Forget 1991; Hoch and Adler 1997) and arbuscular mycorrhizal fungi spores (Emmons 1982; Janos et al. 1995; Mangan and Adler, in press). *Proechimys semispinosus* (Central American spiny rat) is the sole member of the genus within its geographical range in Central America and northwestern South America. This species is the best-studied member of the genus and is found in lowland tropical forests ranging

* Correspondent: adler@uwosh.edu

from dry to pluvial and from secondary to primary (Adler 1996).

Despite the ubiquity and abundance of *P. semispinosus,* only 2 previous studies have assessed habitat use, with both showing a generalized habitat use. In a study conducted in a tropical pluvial forest on the Pacific slope of Colombia, this species was found in all forested habitats but was more abundant in secondary forest (Gonzalez-M. and Alberico 1993). In a tropical moist forest in central Panama, microhabitats occupied by *P. semispinosus* did not differ from the overall habitat that was available, although it was again more abundant in secondary forest (Tomblin and Adler 1998). No attempt has been made to quantitatively describe microhabitat characteristics with which this species may be associated. Thus, specific structural features of secondary forest that may promote abundance of spiny rats remain unknown. Such information is essential to understand the role of spiny rats in Neotropical forests, particularly with re-
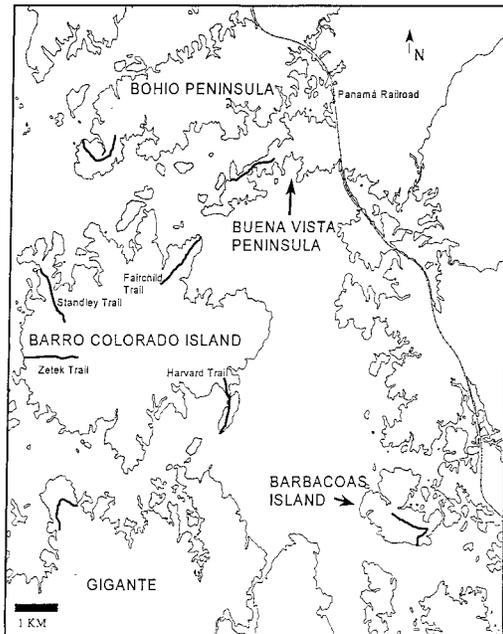
FIG. 1.—Locations of the sampling sites within and adjacent to the Barro Colorado Nature Monument in central Panama.

spect to forest regeneration via interactions with seeds and arbuscular mycorrhizal fungi, upon which many species of plants depend for improved growth (Janos 1980). We present an analysis of microhabitat use by *P. semispinosus* in tropical moist forests in central Panama.

MATERIALS AND METHODS

Study area.—The study was conducted within and adjacent to the Barro Colorado Nature Monument in central Panama (Fig. 1). We selected 5 separate sites for sampling *P. semispinosus,* including Barro Colorado Island (1,560 ha), Barbacoas Island (140 ha), and 3 adjacent mainland peninsulas (Bohio Peninsula, Buena Vista Peninsula, and Gigante Peninsula). These sites were covered with tropical moist forests of varying ages, ranging from young 2nd-growth forest <80 years old (most of Barbacoas Island and sampling sites on Buena Vista, Bohio, and Gigante Peninsulas) to older 2nd-growth forest about 110 years old (northern Barro Colorado Island) and old-growth forest about 300–500 years old (southern Barro Colorado Island). All

study sites were located within an 80-km^2 area and therefore experienced similar climatic patterns.

The climate was highly seasonal with respect to precipitation, with an 8-month rainy season (typically late April to mid-December) followed by a severe dry season of 4 months. Less than 10% of annual precipitation (long-term mean = 2,612 mm/year on Barro Colorado Island; Windsor 1990) typically falls during the dry season. During the year in which our study was conducted, a strong El Niño event resulted in the lowest precipitation total (1,702 mm) recorded on Barro Colorado Island in any calendar year since measurements were initiated in 1925 (Windsor 1990).

Sampling procedures.—We sampled *P. semispinosus* by livetrapping within each study site. For this purpose, we established transects consisting of 50 sampling stations (1 transect on Gigante Peninsula) or 75 stations (all other transects except 1 on Barro Colorado that had 74 stations). A single transect was established on each of the mainland peninsulas and on Barbacoas Island. The transect on Gigante Peninsula followed Robin Foster and Lago trails and the transect on Bohio Peninsula followed the Game Warden Trail. Transects on Barbacoas Island and Buena Vista Peninsula did not follow previously established trails. Four transects were established on Barro Colorado Island that followed Fairchild (2nd-growth forest), Harvard (2nd-growth forest), Standley (old-growth forest), and Zetek (old-growth forest) trails.

Sampling stations within a transect were located about 20 m apart, and each station had 4 live traps; 1 Tomahawk live trap (40.6 by 12.7 by 12.7 cm) and 1 Sherman live trap (22.9 by 8.9 by 7.6 cm) were placed on the ground ≤2 m from each other, and the same types of traps were placed on trees or lianas. Most arboreal traps were set ≤3 m from the forest floor (mean trap height = 1.6 m for both Tomahawks and Shermans), but several traps of both types also were placed in the canopy at heights of ≤24 m. We did not expect to capture *P. semispinosus* in these canopy traps because this species is known to be almost exclusively terrestrial (Tomblin and Adler 1998), but we also were interested in documenting other rodents in the study area. Each trap was baited with a mixture of ripe plantain, peanut butter, and bird seed. Traps along a given transect were set in sections within a 2-week pe-

riod, and each trap was set for 10 consecutive nights and checked each morning. Each transect was sampled once between September 1997 and January 1998 (late rainy season and early dry season, typically the period of greatest trappability of spiny rats in central Panama; Adler and Lambert 1997).

All captured *P. semispinosus* were uniquely toe-clipped for permanent identification, weighed, and placed into sex and age classes. Age was recorded as either juvenile, subadult, or adult according to stage of pelage development (Adler 1994). Individuals were released at their station of capture immediately after data collection.

We measured 14 variables at every trap station to quantify microhabitat structure (Appendix I). Variables 2–7 were estimated in a 15-m^2 circle centered between the 2 traps set on the ground. Variables 9–12 were based on the point-quarter method, whereby the 1st tree ≥10 cm in diameter at breast height encountered in each of the 4 cardinal compass directions was selected for this series of measurements. Canopy height was measured to the highest point of the forest directly above each trap station. Tree density was the number of trees within a 100-m^2 circle centered between the 2 ground-based traps.

Data analysis.—We tallied numbers of captures by trap type (Tomahawk and Sherman) and placement (ground and arboreal) and total number of captures and number of 1st captures of each individual at each of the 574 trap stations.

Our goal in the habitat analysis was to quantify gradients in forest microhabitats by explaining as much variation in structure using the fewest variables (Seamon and Adler 1996). For this purpose, we used factor analysis following the factoring protocols of Cureton and D'Agostino (1983). We conducted an initial principal-axes factoring to determine communalities, and those communalities were inserted into the matrix as the diagonals. After this initial factoring, we conducted a final factoring and performed a promax rotation of axes. Number of axes to be retained for further analysis was determined by examining a scree plot and calculating the critical minimum eigenvalue as $N^{0.6}/15$, where N was the number of variables (14) in the analysis (Cureton and D'Agostino 1983). Thus, the critical minimum eigenvalue for factor retention was 0.32. Factors thus retained represented gradients in microhabitat structure (Seamon and

Adler 1996) and were interpreted by examining correlations between those factors and original (raw) variables.

We plotted all trap stations in multivariate habitat space defined by the 1st 2 axes derived from the factor analysis. That plot showed the distribution of the total sampled microhabitat, as defined by those 1st 2 axes, that was available to *P. semispinosus.* We then plotted all trap stations at which *P. semispinosus* was captured in this same multivariate space, which revealed the distribution of spiny rats within this available microhabitat space. However, specific microhabitat features with which *P. semispinosus* was associated were not identified in that plot.

To identify such microhabitat variables, we used multiple logistic regression. We included only the 1st capture of an individual to avoid problems of statistical dependence of multiple captures of the same individual. The dichotomous dependent variable was presence or absence of spiny rats at each trap station, and independent variables were factors retained from the factor analysis. We constructed a full logistic regression model that included all retained factors to avoid problems associated with stepwise analysis. In this analysis, factors served as explanatory variables to predict presence or absence of *P. semispinosus* at a trap station. We also examined relationships between *P. semispinosus* presence–absence at trap stations and raw microhabitat variables by calculating the significance level of each variable separately entering into a logistic regression model.

RESULTS

We recorded 150 captures of 107 individual *P. semispinosus* in 22,960 trap nights (Table 1). We also captured 11 *Didelphis marsupialis* (common opossum; 3 on Barro Colorado, 1 on Bohio, 4 on Buena Vista, and 3 on Gigante), 8 *Marmosa robinsoni* (Robinson's mouse opossum; 5 on Barro Colorado and 3 on Gigante), and 1 *Heteromys desmarestianus* (spiny forest pocket rat) and 1 *Oecomys bicolor* (bicolored arboreal rice rat) on Barro Colorado Island. Of the total *P. semispinosus* captures, 147 were in traps set on the ground (134 in Tomahawks and 13 in Shermans). The 3 arboreal captures (in 1 Sherman and 2 Tom-

TABLE 1.—Sampling dates, effort, and numbers of individuals and captures of *Proechimys semispinosus*. Sampling effort was divided equally between Tomahawk and Sherman traps and between traps set on the ground and in trees and lianas.

Site	Dates	Trap nights	Individuals	Captures
Barro Colorado Island				
Fairchild	16–28 October 1997	3,000	4	4
Harvard	14–25 November 1997	3,000	41	64
Standley	13–23 December 1997	2,960	22	34
Zetek	12–27 September 1997	3,000	7	7
Barbacoas Island	26 September–7 October 1997	3,000	5	5
Gigante Peninsula	7–18 January 1998	2,000	7	13
Bohio Peninsula	6–17 October 1997	3,000	9	9
Buena Vista Peninsula	31 October–12 November 1997	3,000	12	14
Total		22,960	107	150

ahawks) were of a subadult female captured on a 0.7-cm-diameter liana 1.2 m aboveground, a juvenile male captured on a 6.3-cm-diameter log 1.1 m aboveground, and a juvenile female captured on a 5.8-cm-diameter tree 1.3 m aboveground. Of the 14 captures in Sherman traps, 6 were of juveniles, 3 were of subadults, and 2 were of small adults (≤370 g). Overall capture success of *P. semispinosus* in Tomahawks set on the ground (the only traps that effectively captured this species) was 2.33% (134 captures, including recaptures, in 5,740 trap nights). Number of individuals per 100 station-nights, an index of relative abundance that accounted for multiple traps at a single station (Malcolm 1990), was 1.86 (107 individuals at 574 trap stations, each station of which was set for 10 consecutive nights).

We obtained 5 retainable factors from the factor analysis that we interpreted as representing gradients in forest stature (negative correlation with gap and positive correlation with canopy height), large logs (positive correlation with large logs and negative correlation with log distance), lianas (positive correlations with number and size of lianas), small logs (positive correlations with small and medium logs), and tree-stem density (positive correlation with tree density). The first 2 factors explained 84.2% of total variance in the raw variables. Sampling stations were not evenly distributed throughout microhabitat space (Fig. 2).

Most sampling stations were clustered into 2 groups along the gradient in forest stature, representing stations that were within either tree-fall gaps or intact forest. Variation among sampling stations along this gradient also was due to differences in canopy height. One extreme outlier along the gradient in large logs (which greatly expanded the space of sampled microhabitat; Fig. 2) represented a sampling station within a tree-fall gap that contained 8 large logs.

Excluding microhabitat space accounted for by the single outlier, *P. semispinosus* was distributed throughout available microhabitat space (Fig. 2). However, presence of *P. semispinosus* at a trap station was related negatively to the factor interpreted as forest stature and positively to the factors interpreted as small logs and tree-stem density (Table 2). Presence of *P. semispinosus* at trap stations was related positively to 3 raw microhabitat variables (gap and small and medium logs; Table 3) and negatively to 3 such variables (tree size, liana size, and canopy height).

DISCUSSION

Proechimys semispinosus was by far the most abundant small mammal in the study area, comprising 84% of all captured mammals. Relative abundance of 1.86 individuals/100 station-nights was fairly similar to previous abundance estimates of *Proechimys* on mainland areas. In a previous study
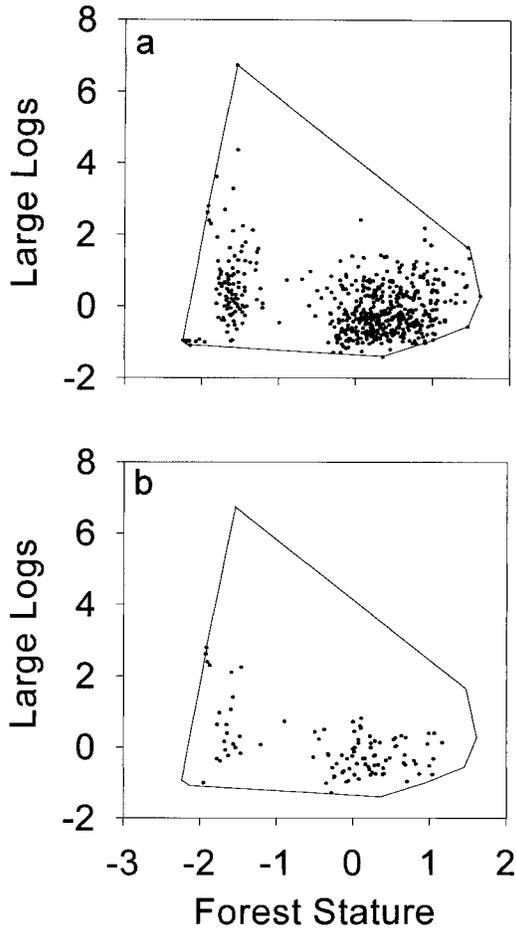
FIG. 2.—Distributions of a) all sampling stations and b) those sampling stations recording ≥ 1 capture of *Proechimys semispinosus* within multivariate microhabitat space defined by the first 2 factors from a factor analysis; polygons delineate limits of microhabitat sampled in this study.

TABLE 2.—Logistic regression analysis between presence–absence of *Proechimys semispinosus* at a trap station and composite habitat variables derived from factor analysis. Variable names are based on factor structure.

Variable	Slope	χ^2	P
Intercept	−1.86	211.86	0.0001
Forest stature	−0.30	4.55	0.0329
Large logs	−0.26	1.22	0.2699
Lianas	−0.21	1.31	0.2525
Small logs	0.48	4.58	0.0324
Tree-stem density	0.43	4.30	0.0381

Cashu, Peru, had combined relative abundances of 2.28 individuals/100 station-nights (Malcolm 1990; Voss and Emmons 1996).

Spiny rats were sampled most effectively by Tomahawk traps set on the ground. Only young and small adults were captured in Sherman traps, and only young were captured in either Tomahawk or Sherman traps above ground level. Large adults simply were too large to enter Sherman traps and apparently were not adept at climbing to even 1 m aboveground. This terrestrial tendency was consistent with previous studies conducted in central Panama, relative abundance of *P. semispinosus* over an 18-month period was 0.60 individuals/100 station-nights (Tomblin and Adler 1998). Malcolm (1990) reported a combined relative abundance of sympatric *P. cuvieri* and *P. cayennensis* ranging from 0.60 to 2.36 individuals/100 station-nights north of Manaus, Brazil. Four species of sympatric *Proechimys* (*P. brevicauda, P. simonsi, P. steerei,* and *Proechimys* species novae) at Cocha

TABLE 3.—Relationships between presence–absence of *Proechimys semispinosus* at a trap station and 14 raw habitat variables, determined as initial entry criteria in a logistic regression analysis.

Variable	Sign of relationship	χ^2 to enter	P
Gap	+	3.87	0.0492
Rock cover	+	1.89	0.1687
Woody cover	+	2.73	0.0984
Herbaceous cover	+	1.11	0.2920
Small logs	+	4.09	0.0432
Medium logs	+	6.56	0.0104
Large logs	+	0.34	0.5577
Log distance	−	0.01	0.9037
Tree distance	−	2.12	0.1451
Tree size	−	7.56	0.0060
Number of lianas	−	0.38	0.5355
Liana size	−	6.07	0.0137
Canopy height	−	5.56	0.0184
Tree-stem density	+	2.20	0.1376

on *Proechimys* (Malcolm 1990; Tomblin and Adler 1998).

Spiny rats were distributed throughout available microhabitat that we sampled. That distribution was consistent with previous observations that this species is a generalist with respect to use of forested habitats (Adler 1996; Tomblin and Adler 1998). However, presence of spiny rats was best predicted by variables that characterized younger or more disturbed forest, in accordance with previous studies (Gonzalez-M. and Alberico 1993; Tomblin and Adler 1998). In particular, spiny rats were associated with forest gaps and areas with shorter canopies and higher densities of smaller trees, logs, and lianas. Indeed, the transect along Harvard Trail, which recorded by far the most individuals and captures of any transect (Table 1), passed through 2nd-growth forest frequently devastated by rainy-season storms that swept across the study area from the southeast. That forest was characterized by dense understory vegetation, a short canopy, many gaps and fallen trees, and dense tangles of lianas. Emmons (1982) found that *P. hendeei* and *P. longicaudatus* in southeastern Peru also were associated with tree-falls and masses of lianas that had fallen from the canopy.

Because habitat use is likely to change temporally (both across seasons and years) and in response to changes in density, it would not be surprising to find changes in the strengths of associations of *P. semispinosus* with the measured microhabitat variables. Depending upon season, year, and density, some variables may assume greater or lesser importance as explanatory variables for *P. semispinosus* presence and absence. Temporal changes in microhabitat use may be pronounced, particularly during major climatic disturbances such as El Niño events. Thus, trap stations that did not record a capture in the present study may be likely to record captures after sufficient sampling. However, we suggest that our results are robust with respect to use by *P. semispinosus* of younger or more disturbed forests and gaps within older forest because of the congruence with previous studies of this species.

Younger forests and tree-fall gaps within older forest represent areas of rapid plant recruitment and growth due to increased light availability. Effects of spiny rats on seed survival via predation and dispersal and on arbuscular mycorrhizal fungal infection via spore dispersal may be particularly pronounced in such areas. For instance, individuals preferentially eat larger seeds (Adler 1995), and such activities may influence germination success of large-seeded plant species within gaps with which *P. semispinosus* are associated. If individuals cache seeds in dense undergrowth of gaps (Adler and Kestell 1998; Forget 1991), such seeds may have increased survival and germination success. Similarly, if spiny rats import spores of mycorrhizal fungi into gaps, seedlings and saplings dependent upon such fungi for improved growth may have increased opportunity for infection by means other than by root-to-root contact (Janos et al. 1995; Mangan and Adler, in press). This potentially important role of spiny rats in affecting forest regeneration warrants further study.

LITERATURE CITED

ADLER, G. H. 1994. Tropical forest fragmentation and isolation promote asynchrony among populations of a frugivorous rodent. The Journal of Animal Ecology 63:903–911.

ADLER, G. H. 1995. Fruit and seed exploitation by Central American spiny rats, *Proechimys semispinosus*. Studies on Neotropical Fauna and Environment 30:237–244.

ADLER, G. H. 1996. The island syndrome in isolated populations of a tropical forest rodent. Oecologia 108:694–700.

ADLER, G. H., AND D. W. KESTELL. 1998. Fates of Neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). Biotropica 30:677–681.

ADLER, G. H., AND T. D. LAMBERT. 1997. Ecological correlates of trap response of a Neotropical forest rodent, *Proechimys semispinosus*. Journal of Tropical Ecology 13:59–68

ASQUITH, N. M., S. J. WRIGHT, AND M. J. CLAUSS. 1997. Does mammal community composition control seedling recruitment in Neotropical forests? Evidence from Panamá. Ecology 78:941–946.

CURETON, E. E., AND R. B. D'AGOSTINO. 1983. Factor analysis: an applied approach. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

EISENBERG, J. H. 1989. Mammals of the Neotropics: the northern Neotropics. The University of Chicago Press, Chicago, Illinois.

EMMONS, L. H. 1982. Ecology of *Proechimys* (Rodentia, Echimyidae) in southeastern Peru. Tropical Ecology 23:280–290.

FORGET, P. M. 1991. Scatterhoarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: comparison with *Myoprocta exilis*. Tropical Ecology 32:155–167.

GONZÁLEZ-M., A., AND M. ALBERICO. 1993. Seleccion de habitat en una comunidad de mamiferos pequeños en la costa Pacifica de Colombia. Caldasia 17:313–324.

HOCH, G. A., AND G. H. ADLER. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). Journal of Tropical Ecology 13:51–58.

JANOS, D. P. 1980. Vesicular–arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61:151–162.

JANOS, D. P., C. T. SAHLEY, AND L. H. EMMONS. 1995. Rodent dispersal of vesicular–arbuscular mycorrhizal fungi in Amazonian Peru. Ecology 76:1852–1858.

MALCOLM, J. R. 1990. Estimation of mammalian densities in continuous forest north of Manaus. Pp. 339–357 in Four Neotropical forests (A. H. Gentry, ed.). Yale University Press, New Haven, Connecticut.

MANGAN, S. A., AND G. H. ADLER. In press. Consumption of arbuscular mycorrhizal fungi by spiny rats (*Proechimys semispinosus*) in eight isolated populations. Journal of Tropical Ecology.

PATTON, J. L., AND A. L. GARDNER. 1972. Notes on the systematics of *Proechimys* (Rodentia: Echimyidae), with emphasis on Peruvian forms. Occasional Papers of the Museum of Zoology of Louisiana State University 44:1–30.

SEAMON, J. O., AND G. H. ADLER. 1996. Population performance of generalist and specialist rodents along habitat gradients. Canadian Journal of Zoology 74:1130–1139.

TOMBLIN, D. C., AND G. H. ADLER. 1998. Differences in habitat use between two morphologically similar tropical forest rodents. Journal of Mammalogy 79:953–961.

VOSS, R. S., AND L. H. EMMONS. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bulletin of the American Museum of Natural History 230:1–115.

WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panamá. Smithsonian Contributions to the Earth Sciences 29:1–145.

APPENDIX I

Descriptions of the 14 microhabitat variables measured in this study

Name	Description
1. Gap	Presence or absence of a tree-fall gap at the trap station
2. Rock cover	Amount of rock cover, ranging from 0 to 4 (0 = no cover, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100% cover)
3. Woody cover	Amount of ground cover by woody vegetation, ranging from 0 to 4 (values similar to those for rock cover)
4. Herbaceous cover	Amount of ground cover by herbaceous vegetation, ranging from 0 to 4 (values similar to those for rock cover)
5. Small logs	Number of logs 5–10 cm in diameter
6. Medium logs	Number of logs 11–20 cm in diameter
7. Large logs	Number of logs >20 cm in diameter
8. Log distance	Distance to the nearest log >20 cm in diameter
9. Tree distance	Mean distance of the nearest tree in each of the 4 cardinal compass directions
10. Tree size	Mean diameter of the nearest tree in each of the 4 cardinal compass directions
11. Number of lianas	Mean number of lianas supported by the 4 trees described above
12. Liana size	Mean diameter of the largest liana on each of the 4 trees described above
13. Canopy height	Height of the canopy
14. Tree-stem density	Number of trees within a 100-m^2 circle centered on the trap station