

SPECIES RICHNESS AND INDICES OF ABUNDANCE OF MEDIUM-SIZED MAMMALS IN ANDEAN FOREST AND REFORESTATIONS WITH ANDEAN ALDER: A PRELIMINARY ANALYSIS

Riqueza de especies e índices de abundancia de los mamíferos medianos en bosque andino y en reforestaciones con aliso: un análisis preliminar

FRANCISCO SÁNCHEZ

Universidad Nacional de Colombia, Bogotá. fasbos@gmail.com

PEDRO SÁNCHEZ-PALOMINO

Departamento de Biología. Universidad Nacional de Colombia. psanchez@ciencias.unal.edu.co

ALBERTO CADENA

Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá D. C., Colombia. acadena38@yahoo.es

ABSTRACT

We studied the species richness and two indices of abundance of medium-sized mammals in areas with Andean forest and Andean alder (*Alnus acuminata*) reforestations in a reserve at the Central Andes of Colombia. Since reforested areas have a less complex habitat structure and lower plant diversity than native forests, we predicted that they have lower richness of mammals than areas with Andean forest. We obtained the indices of abundance from direct contacts in transects and from the use of track stations. Our results suggest that, indeed, areas with Andean forest had a higher richness of mammals than reforestations, but this pattern may be modified by anthropogenic factors. We found no differences between the indices of abundance of the squirrel, *Sciurus granatensis*, in the two forest types. In contrast, the coatis were recorded more frequently in the reforestations than in areas with Andean forest at the reserve.

Key words. *Alnus acuminata*, Andes, Colombia, plantations.

RESUMEN

Estudiamos la riqueza y dos índices de abundancia de mamíferos medianos en áreas con bosque nativo y con reforestaciones de aliso (*Alnus acuminata*) en una reserva en los Andes centrales de Colombia. Las reforestaciones son menos complejas en estructura de hábitat y tienen menor diversidad vegetal que las áreas con bosque nativo. Por ello esperábamos que las reforestaciones tuvieran una menor riqueza de mamíferos que las áreas con bosque andino. Obtuvimos los índices de abundancia de conteos directos en transectos y del uso de estaciones de huellas. Nuestros resultados sugieren que, en efecto, las áreas de bosque andino tuvieron una mayor riqueza de mamíferos que las reforestaciones, pero este patrón puede ser modificado por efectos

antropicos. No encontramos diferencias entre los índices de abundancia de la ardilla, *Sciurus granatensis*, en los dos tipos de bosque. Sin embargo, los coaties se registraron con mayor frecuencia en las reforestaciones que en las áreas con bosque andino de la reserva.

Palabras clave. *Alnus acuminata*, Andes, Colombia, plantaciones.

INTRODUCTION

Modification of habitats may generate boundaries for species due to the newly created patchiness in the landscape, and this process may alter the structure and dynamics of biological communities (Cadenasso *et al.* 2003). A dramatic example of habitat modification is deforestation, which reduces, or eliminates, the area available for forest-dwelling species and also exposes them to edge-related effects (Murcia 1995). One way to restore the forest cover is the use of reforestations, i.e., the planting of seeds, plants, or parts of plants to establish trees where forests used to be present. The planting of trees often benefits the recovery of degraded sites, because of the tree's ability to use water and nutrients inaccessible to plants with shallow roots (Anonymous 1983, Parrotta *et al.* 1997b). In addition, tree canopies act as protection against the direct impact of raindrops on the soil and therefore reduce erosion. Forested sites also have lower variation in temperature than non-forested ones, allowing re-accumulation of organic matter that restores soil structure and microbiota, and also enhance moisture- and nutrient-holding abilities (Anonymous 1983, Lugo 1997). Hence, forest restoration in mountainous regions, such as the Andes, may be particularly important for reducing land degradation, given that these soils are on steep slopes, which are prone to erosion.

In the Andes of Colombia, large areas have been deforested due to human activities such as construction of settlements, conventional agriculture, and growing of illegal crops (Cavelier & Etter 1995, Kattan & Alvarez-

López 1996). According to Etter (1998), less than 30% of the original forest remains on the Colombian Andes, and plantations of exotic and native species have been used to reforest the Andes of Colombia for economic purposes and restoration (Murcia 1997, Cavelier & Tobler 1998). Thus, several questions arise: do these plantations affect the fauna and flora that inhabit the Andes, and should these plantations be considered for managing and preserving diversity in this region of Colombia?

The studies addressing the effects of plantations on biological communities in the Andes indicate that plant diversity is lower in plantations of both native (e.g. *Alnus acuminata*) and exotic (e.g. *Pinus* spp., *Cupressus lusitanica*) species than in native forests or even secondary forests (Cavelier 1995, Murcia 1997, Cavelier & Tobler 1998, Cavelier *et al.* 1999). Vertebrate groups such as anurans also have lower species richness and abundance in *Quercus humboldtii* plantations than in native Andean forests (Gutiérrez-Lamus *et al.* 2004). In contrast, understory birds appear to show little differences in their abundance in plantations of the exotic species *Fraxinus chinensis* and secondary forest (Durán & Kattan 2005), and also show little differences in the use of strata in *F. chinensis* plantations and native Andean forests (Lentijo & Kattan 2005). Nevertheless, to the best of our knowledge, there is no information on how reforestation affects the mammals inhabiting the Colombian Andes. In particular, although the Andean alder, *A. acuminata*, has been the preferred species for the restoration of forest cover and the protection of water sources in

the Central Andes of Colombia, there is no information on whether these monocultures affect mammals.

In this study, we compare species richness and indices of abundance of medium-sized mammals, i.e., animals with body mass between ~0.2 and 10 kg, in areas with Andean forest and areas reforested with Andean alder, in a protected reserve near the city of Manizales, Caldas Department. Reforestation is expected to benefit forest-dwelling species by extending their available habitat, due to the low contrast between native and planted forests (Foster *et al.* 2002). However, given that differences in habitat structure and plant diversity may affect the species diversity of animal groups, via the modulation of available niches (MacArthur & MacArthur 1961, August 1983), we expected to find differences in richness between Andean forest and reforested areas. Thus, we predicted that areas with Andean forest have a richer fauna of mammals than reforested ones, owing to the lower habitat complexity and plant diversity of the reforestations (Cavelier 1995, Murcia 1997).

MATERIALS AND METHODS

Study site: We did the study during January and April 1999, in the Río Blanco Reserve, Municipality of Manizales, Department of Caldas. The Reserve is on the Cordillera Central of the Colombian Andes, covers approximately 34 km², its altitude ranges from 2150 to 3750 m, and it protects the watershed for Manizales' aqueduct. The climate of the Reserve can be classified as isomesothermic in the lower parts, i.e., annual average temperatures around 15 °C, and as isomicrothermic in the upper ones, i.e., annual average temperatures around 9 °C (Hernández-Camacho 1992). The annual average precipitation is 2400 mm, and its distribution follows a bimodal, tetra-

seasonal pattern with two pluviosity peaks: March – May, and September – November. However, due to the phenomenon of “La Niña”, January and February 1999 had values of precipitation above the average, between 200 and 280 mm, which are typical of rainy months.

The Reserve is a forest remnant surrounded by pastures, agricultural fields and urban areas. Areas with native forests cover 15.79 km², whereas reforestations with *A. acuminata* and areas in regeneration dominated by grasses cover 7.26 km² and 5.26 km², respectively (Fig. 1). Areas in regeneration dominated by secondary forest and reforestations with exotic species cover about 5.70 km². Between 2150–2350 m of altitude, the native vegetation corresponds to sub-Andean forest, and above 2350 m it is represented by Andean forest (Cuatrecasas 1958).

We sampled areas with Andean forest and reforestations of *A. acuminata*, between 2600 and 3200 m of altitude. Areas with Andean forest are characterized by the presence of at least two strata of trees (5–15 m and 20–25 m), and the understory is up to 5 m (Anonymous 1987). Trees have umbrella-shaped canopies, with branches and trunks abundant in vascular and non-vascular epiphytes due to the influence of frequent mist (Hernández-Camacho & Sánchez 1992). In general, areas with Andean forest in the Reserve are associated with water streams, and the height of the trees tends to decrease with altitude. In this kind of forest the families Asteraceae, Melastomataceae, Solanaceae, and Ericaceae are well represented in terms of genera and species; in particular, the species *Weinmannia pubescens*, *Freziera canescens*, and *Saurauia brachybotris* are abundant (Alvear 2000). The tree ferns of the genus *Cyathea* and the palm *Ceroxylon quindiuense* are also characteristic of the areas with Andean forest.

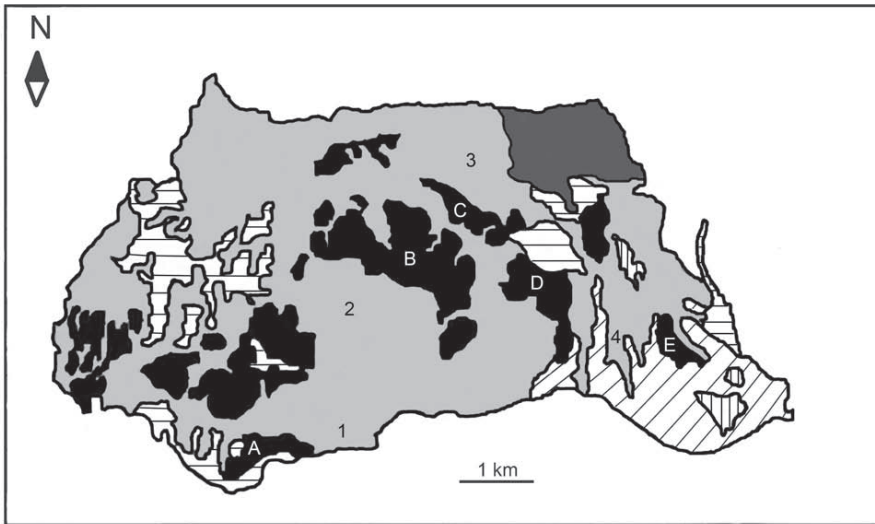


Figure 1. Vegetation types in the Río Blanco Reserve (Manizales, Caldas): Native forest (Light grey), secondary forest (dark gray), areas reforested with Andean alder, *Alnus acuminata* (Black), pastures (Horizontal lines pattern), areas in regeneration where grasses are dominant (Diagonal lines pattern), and areas reforested with exotic tree species (Vertical lines pattern). Sampling sites in native Andean forest areas: 1) La Coca, 2) La Guerra, 3) Río Blanco, 4) Hoyo Grande. Sampling sites in areas reforested with Andean alder: A) El Zancudo, B) Betania, C) Río Blanco, D) Pinares, E) El Laurel. Altitude, in general, increases from West to East from ~2150 to 3750 m.

Reforestations of *A. acuminata* in the Reserve are characterized by a uniform canopy. In plantations older than 20 years there are one or two strata of trees. Usually, reforestations with 40 years or more of growth have trees of 35 to 40 m, but in some of the plots trees do not exceed 30 m. The understory is usually dominated by *Bocconia frutescens*, and other heliophilous plants also accompany this species. Young plantations are abundant in grasses, but the older the reforestation, the lower the cover of grasses and the higher the cover of other herbs and shrubs. Moreover, the older the plantation, the higher the abundance of organic matter accumulated in the soil. Water streams are not as often in the reforestations, as they are in the Andean forest areas. Additional information on the vegetation of the reforestations in the Cordillera Central of Colombia can be found in Cavellier (1995) and Murcia (1997).

Direct counts: We walked the available trails in four areas with Andean forest, and five areas reforested with *A. acuminata* (Table 1). These reforestations were between 16 and 42 years old in 1999 (Table 1). We did 36 censuses in Andean forest areas and 43 censuses in reforestations, between 05:00 h and 07:00 h. The walking speed in Andean forest was 0.7-1.0 km/h, and 1.5-2.0 km/h in the reforestations. Due to the low number of contacts, we did not estimate absolute abundance or density of mammals. Instead, we calculated an index of abundance for each species that was expressed relative to the total distance walked in each area, i.e., individuals/km (Tellería 1986). Groups of animals sighted were considered as single contacts.

Table 1. Distances traveled in search for mammals in areas with Andean forest and areas reforested with Andean alder, *Alnus acuminata*. Age = age of the reforestations in 1999.

Andean forest			Reforestations			
Site	Altitude (m.a.s.l.)	Distance (km)	Site	Altitude (m.a.s.l.)	Age (years)	Distance (km)
La Coca	2600	9.72	Betania	2800	40	46.32
La Guerra	2750	28.56	El Zancudo	2500	20-43	5.76
Río Blanco	2600	10.8	Pinares	2800	20	7.56
Hoyo Grande	3200	9.75	Río Blanco	2850	43	2.58
			El Laurel	3100	16	5.88

Track stations: We prepared circle-shaped track stations (diameter ~1 m) by removing vegetation and rocks, and plowing the soil. After plowing, the surface of the station was smoothed. In areas near water streams, we prepared stations with sand or humid mud. Each station had banana, potato pieces, maize, and/or sausage as attractants. Roofs made of branches and leaves were placed at 1.5 m above stations in places of open canopy, to protect them from the rain. The stations were located along transects and separated by 20 to 120 m. The distance between stations depended on the accessibility of the area. We used track stations in three areas with Andean forest and three areas with reforestations (Table 2). We made transects in areas with Andean forest following both already existing and new trails. In reforestations, we set transects perpendicular to available trails and separated them by 300 to 500 m. We identified tracks using the figures from Aranda (1981) and Emmons (1997), and with the help of a former hunter. We checked stations for presence of tracks between 07:00 h and 10:00 h. We calculated an index of abundance expressed as the number of stations with tracks of a species divided by the total number of stations used in each area. Tracks found in consecutive stations or from the same station in consecutive days, and with similar shape, length and

width, were considered to be from the same individual. The tracks of the coatis, *Nasua nasua* and *Nasuella olivacea*, were pooled due to their similarity in shape. For the same reason, we also pooled the tracks of the foxes, *Urocyon cinereoargenteus* and *Cerdocyon thous*.

Species richness: We compared species richness between the sampled areas with individual-based rarefaction curves (Colwell *et al.* 2004), using only the data from the track stations. To estimate total species richness, we used the non-parametric estimators of Chao 1, incidence-based coverage (ICE), abundance-based coverage (ACE), and first Jackknife (reviewed by Colwell & Coddington 1994). We used EstimateS 7.5 (Colwell 2006) to obtain the rarefaction curves and species richness estimators, after randomizing the samples 100 times.

Statistical analyses: We used Mann-Whitney test (Zar 1999) to compare the indices of abundance of the squirrel *Sciurus granatensis*, Squirrels/km, between Andean forest and reforested areas. We also applied this test to analyze the results from the track stations for the coatis. $P < 0.05$ was chosen as the minimum level of statistical significance.

Table 2. Number of nights and total number of track stations for mammals used in areas with Andean forest and areas reforested with Andean alder, *Alnus acuminata*. The ages of the reforestations are the same as presented in Table 1.

Andean forest				Reforestations			
Site	Altitude (m.a.s.l.)	Nights	Stations	Site	Altitude (m.a.s.l.)	Nights	Stations
La Coca	2600	8	132	Betania	2800	12	194
Río Blanco	2600	15	279	Pinares	2800	9	110
Hoyo Grande	3200	7	129	El Laurel	3100	9	178
Total		30	540	Total		30	482

RESULTS

Direct counts: We sighted ten individuals of four mammal species after walking a total of 58.83 km in areas with Andean forest; after walking 68.1 km in reforested areas we sighted 16 individuals belonging to three species. In areas with Andean forest, we sighted the following three species only once: *Sciurus pucheranii* at La Coca (0.1 individuals/km), *Nasua olivacea* at La Guerra (0.035 individuals/km), and *Mustela frenata* at La Guerra (0.035 individuals/km). In reforested areas, we recorded only once *Nasua nasua* at El Zancudo (0.17 individuals/km) and *Didelphis albiventris* at Betania (0.02 individuals/km). The squirrel *S. granatensis* was the only species sighted in all sampled areas, and was also the most sighted mammal in areas with Andean forest, 0.158 ± 0.118 (Mean \pm SD) individuals/km, and reforestations, 0.402 ± 0.307 individuals/km. Nevertheless, we found no significant difference between the indices of abundance of this squirrel in both forest types (Mann-Whitney $U = 4$, χ^2 approximation = 1.33, df = 1, $P = 0.248$).

Track stations: We recorded tracks of eleven to thirteen mammal species in areas with Andean forest, and seven to nine species in reforested areas (Fig. 2). In addition, we found one set of tracks of a domestic cat at

the reforested site of Pinares, which was not included in our analyses. The examination of the indices of abundance suggests that abundances were more evenly distributed among species in Andean forest areas than in reforested ones (Fig. 2). The coatis were the only mammals found in all Andean forest and reforested areas. Furthermore, the values of their indices of abundance in reforestations, 0.042 ± 0.029 (Mean \pm SD) tracks/total stations, were significantly higher than in Andean forest sites, 0.009 ± 0.006 tracks/total stations (Mann-Whitney $U = 0.00$, χ^2 approximation = 3.857, df = 1, $P = 0.049$).

Species richness: We found only one species in the track stations in Hoyo Grande (Fig. 2), and therefore we did not build a rarefaction curve for this site. Species accumulation curves for areas with Andean forest in Río Blanco and La Coca suggest that these areas had a higher number of mammals than the reforested areas examined (Fig. 3). This idea is further supported by most of the estimators of species richness (Table 3). We recorded the species *Caluromys derbianus*, *Cabassous centralis*, *Eira barbara*, *Leopardus tigrinus*, and *Agouti taczanowskii* only in areas with Andean forest (Fig. 2). *Sylvilagus brasiliensis* was the only species recorded exclusively in reforestations. In addition, Río Blanco and La Coca had a similar number of species, but the species found in each of these sites were not the same.

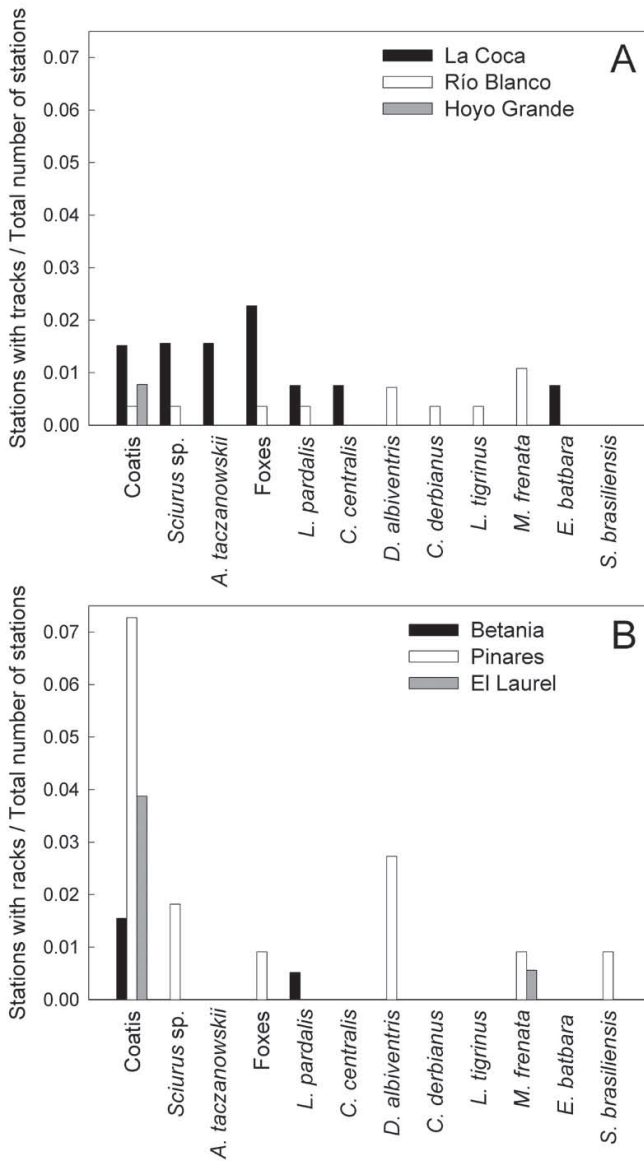


Figure 2. Indices of abundance, based on track stations data, of mammals in areas with Andean forest (A) and areas reforested with Andean alder, *Alnus acuminata* (B). The indices were expressed as the number of stations with tracks of a species divided by the total number of stations used in a particular area. The coatis were significantly more abundant in reforested areas than in areas with Andean forest (Mann-Whitney test, $P < 0.05$). Coatis = *Nasua nasua* and *Nasuella olivacea*; *A. taczanowskii* = *Agouti taczanowski*; Foxes = *Cerdocyon thous* and *Urocyon cinereoargenteus*; *L. pardalis* = *Leopardus pardalis*; *D. albiventris* = *Didelphis albiventris*; *C. derbianus* = *Caluromys derbianus*; *L. tigrinus* = *Leopardus tigrinus*; *M. frenata* = *Mustela frenata*; *E. batbara* = *Eira batbara*; *S. brasiliensis* = *Sylvilagus brasiliensis*.

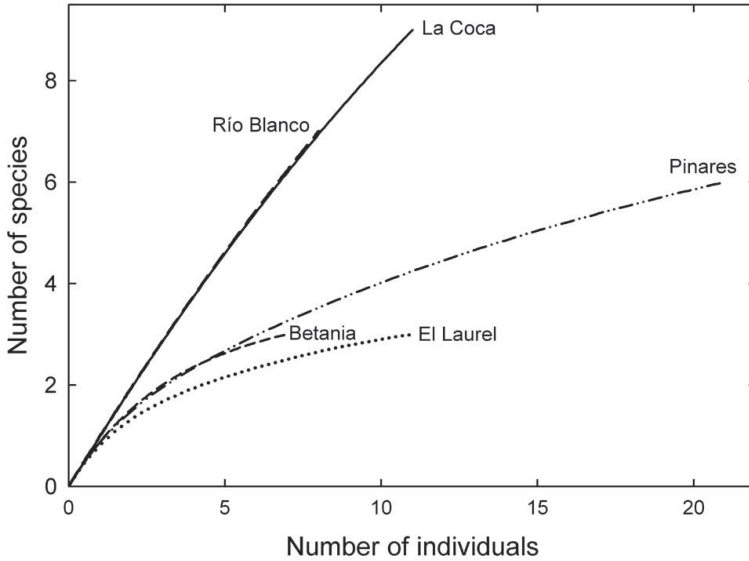


Figure 3. Rarefaction curves for mammals estimated from the track stations data, in areas with Andean forest (long-dashed line, Río Blanco; solid line, La Coca) and areas reforested with Andean alder, *Alnus acuminata* (dash-dotted line, Pinares; short-dashed line, Betania; dotted line, El Laurel).

Table 3. Total species richness of mammals for areas with Andean forest and areas reforested with Andean alder, *Alnus acuminata*, estimated with the non-parametric estimators of abundance-based coverage (ACE), incidence-based coverage (ICE), Jackknife 1 (Jack 1), and Chao 1. CI 95% = Confidence interval 95%

	ACE Mean ± SD	ICE Mean ± SD	Jack 1 Mean ± SD	Chao 1, CI 95%
<i>Andean forest</i>				
Río Blanco	27.93 ± 0.7	27.93 ± 0.7	12.96 ± 2.42	8.47 - 44.84
La Coca	24.76 ± 2.25	24.77 ± 2.29	15.88 ± 2.56	10.47 - 41.42
<i>Reforestations</i>				
Betania	3.69 ± 0.01	3.69 ± 0.01	3.99 ± 0.99	3 - 4.44
Pinares	9.48 ± 0.74	9.13 ± 0.7	8.83 ± 1.68	6.07 - 19.95
El Laurel	4.09 ± 0.21	4.09 ± 0.21	3.99 ± 0.99	3.03 - 11.44

DISCUSSION

Our prediction that species richness would be higher in areas with Andean forest than in reforestations was partially supported by the results. Indeed, the data from the track stations suggested that the Andean forest areas of La Coca and Río Blanco had more species

of mammals than the reforestations studied. Nonetheless, the Andean forest of Hoyo Grande appeared to have the lowest richness of mammals in the Reserve. The Hoyo Grande area was the highest point sampled, it is surrounded by areas in regeneration dominated by grasses, and it is near agricultural fields and pastures for cattle. This spatial configuration

may have left this area more exposed to edge effects than the other areas with Andean forest. In addition, although the Reserve is a protected zone, local hunters visit it (Sánchez *et al.* 2004), and they have better access to Hoyo Grande than to the other sites with Andean forest. These factors may explain why in this area of Andean forest we only recorded two mammal species using track stations and direct counts. Among the reforestations, the richness of mammals appeared to be lowest in the highest and youngest site sampled, El Laurel (3200 m, 16 years). However, the oldest reforestation examined, Betania (2800 m, 40 years), had lower richness than Pinares (2800 m, 20 years). This suggests that factors different from the age of the reforestation may also affect the use of these habitats by Andean mammals.

The data from the track stations also indicated that the distribution of the individuals among species was less even in reforestations than in areas with Andean forest. Thus, the data on species richness and the indices of abundance suggest that reforestations had lower diversity of mammals than areas with Andean forest. This pattern is consistent with the findings of Gutiérrez-Lamus *et al.* (2004), who reported a richer community of anurans in Andean forests than in plantations of *Quercus humboldtii*. However, the pattern found for the mammals in the Reserve differs from that of birds from another site in the Central Andes of Colombia, in that the birds did not appear to react to the differences between plantations of the exotic species *F. chinensis* and native forest (Lentijo & Kattan 2005). Lentijo and Kattan (2005) argued that the fact that small patches of reforested areas were surrounded by native forest could explain the neutral effect of plantations on the use of forest strata by birds. In our study site, reforestations are also surrounded by native forest, suggesting that differences in the pattern of diversity for birds and mammals in the Andes might be better explained by the higher mobility of birds.

Several studies in temperate and Neotropical sites show that plantations, even heavily managed ones, can increase the available area for forest-dwelling mammals (Parrotta *et al.* 1997a, Carey 2000, Foster *et al.* 2002, Harvey *et al.* 2006). Those studies have also indicated that not all forest-dwelling mammals react to the new habitat in the same way. At the Reserve, eight species of mammals have been recorded exclusively in areas with Andean forest; five mentioned in this paper, plus *Dinomys branickii*, *Dasyopus novemcinctus* and *Coendou rufescens* (Sánchez & Alvear 2003). This suggests that *A. acuminata* reforestations may act as a barrier for several mammals. Nonetheless, we recorded in the reforestations seven to nine species of medium-sized mammals. Moreover, we have reported earlier that the deer *Mazama rufina* and the sloth *Choloepus hoffmanni* have been found in both Andean forests and reforestations of the Reserve above 2500 m of altitude (Sánchez & Alvear 2003). Thus, the reforestations have increased the available area for more than half of the medium-sized mammals of the Reserve within the altitudinal range examined.

The reforestations might have even favored the abundance of several mammals. The squirrel *S. granatensis* and the coatis were found in all sampled areas, and they seemed to be the most abundant medium-sized mammals in the Reserve. The ecological flexibility of *S. granatensis* in diet and habitat use (Heaney & Thorington 1978, Glanz 1984, Nitikman 1985) probably allows this rodent to reach high abundances in some reforested areas. However, more intensive additional sampling is required to assess whether reforested areas increase the abundance of this squirrel or not. The high values obtained from the indices of abundance for coatis in reforestations might be related to the availability of food resources in this habitat. Kattan *et al.* (2006) found that during rainy seasons, Andean alder plantations have higher abundance of leaf-litter arthropods

than secondary-Andean forest areas, whereas during the low-rainfall period that difference was not found. Therefore, it is possible that invertebrate-eaters such as the coatis *Nasua nasua* and *Nasuella olivacea* (Gompper & Decker 1998, Rodríguez-Bolaños *et al.* 2000) indirectly benefited from the reforestations, via the increase in the abundance of their preys compared to native forests. Indeed, a study on a closely related species, *Nasua narica*, showed that abundance and distribution of this species is highly influenced by the abundance of invertebrate fauna inhabiting the leaf-litter (Russell 1990).

Another species that might benefit from the reforestations is the rabbit *S. brasiliensis*. This was the only mammal recorded with the track stations in the reforestations and was absent in the Andean forest. Although this species can be found in the Reserve in areas with Andean forest (Sánchez & Alvear 2003), this rabbit is known to be efficient in exploiting grass- and herb-rich open habitats (Díaz *et al.* 1997).

In conclusion, although the results from this research are preliminary due to the short time of sampling, the small number of replicates, and the lack of additional methods to verify the trends of abundance, our findings may provide important insights for understanding the effects of *A. acuminata* reforestations on the species richness and abundance of mammals in the study area: 1) the Andean alder reforestations increased the available area for several species of medium-sized mammals in the Reserve, 2) the reforestations had lower richness of mammals than areas with Andean forest, and 3) the reforestations have favored the abundance of at least one group of mammals, the coatis. Murcia (1997) recognized that the Andean alder is a good alternative for restoring forest cover on the Andes because monocultures of this species create a forest cover faster than secondary regeneration, but she also acknowledged that natural regeneration might be a better strategy to restore and to conserve biological diversity.

In the light of the above, we suggest that a combined approach using natural regeneration as the predominant managing strategy for restoration, and plantations only at highly deteriorated places (preferably polycultures of native species), could be one of the best ways to increase the habitat available for Andean forest-dwelling mammals and to preserve the diversity of Andean communities.

ACKNOWLEDGEMENTS

We are grateful to Rimma Gluhik, and two anonymous reviewers for their constructive comments on early versions of the manuscript. Dinesh Rao and Orly Razgur provided comments to improve the English of the paper. F. Sánchez would like to thank the families living at the Reserve and the field assistants for their help during the fieldwork. In particular, to Alsonso Uribe for sharing his knowledge on the tracks of Andean mammals. F. Sánchez also thanks the Fundación Ecológica Gabriel Arango Restrepo for financial assistance to the project “Mamíferos de la Reserva Río Blanco” and to Corpocaldas for the permits to do the research.

LITERATURE CITED

- ALVEAR, M. 2000. Flora y vegetación de la Reserva Torre Cuatro (Manizales, Colombia). Tesis de pregrado. Departamento de Biología, Universidad Nacional de Colombia, Bogotá.
- ANONYMOUS. 1983. Sustaining tropical forest resources: reforestation of degraded lands. Background paper 1. Congress of the United States, Office of Technology Assessment OTA, Tropical Forestry Staff, Washington, D. C.
- ANONYMOUS. 1987. Cartografía integrada del medio natural: Chinchiná - Manizales. Análisis Geográficos - Instituto Geográfico Agustín Codazzi 8, Bogotá, D.C.
- ARANDA, J. M. 1981. Rastros de los mamíferos silvestres de México: Manual de Campo.

- Instituto Nacional de Investigaciones sobre Recursos Bióticos, Xalapa, México.
- AUGUST, P. V. 1983. The role of habitat complexity and heterogeneity in structuring tropical communities. *Ecology* 64:1495-1507.
- CADENASSO, M. L., S. T. A. PICKETT, K. C. WEATHERS & C. G. JONES. 2003. A framework for a theory of ecology boundaries. *BioScience* 53:750-758.
- CAREY, A. B. 2000. Effects of new forest management strategies on squirrel populations. *Ecological Applications* 10:248-257.
- CAVELIER, J. 1995. Reforestation with the native tree *Alnus acuminata*: Effects on phytodiversity and species richness in an upper mountain rain forest area of Colombia. Pages 125-137 in: L. S. Hamilton, J. O. Juvik & F. N. Scatena (eds.). *Tropical montane cloud forest*. Springer-Verlag, New York.
- CAVELIER, J., T. M. AIDE, J. M. DUPUY, A. M. EUSSE & C. SANTOS. 1999. Long-term effects of deforestation on soil properties and vegetation in a tropical lowland forest in Colombia. *Ecotropicos* 12:57-68.
- CAVELIER, J. & A. ETTER. 1995. Deforestation of montane forests in Colombia as a result of illegal plantations of opium (*Papaver somniferum*). Pages 125-137 in: S. P. Churchill, H. Balslev, E. Forero & J. L. Luteyn (eds.). *Biodiversity and conservation of Neotropical montane forests*. The New York Botanical Garden, New York.
- CAVELIER, J. & A. TOBLER. 1998. The effect of abandoned plantations of *Pinus patula* and *Cupressus lusitanica* on soils and regeneration of a tropical montane rain forest in Colombia. *Biodiversity and Conservation* 7:335-347.
- COLWELL, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- COLWELL, R. K. & J. A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London* 345:101-118.
- COLWELL, R. K., C. X. MAO & J. CHANG. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85:2117-2727.
- CUATRECASAS, J. 1958. Aspectos de la vegetación natural de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 10:221-268.
- DÍAZ, A., J. E. PÉFAUR & P. DURANT. 1997. Ecology of South American páramos with emphasis on the fauna of the Venezuelan páramos. Pages 263-310 in: F. E. Wielgolaski (ed.). *Polar and Alpine tundra, Ecosystems of the World* 3. Elsevier, Amsterdam.
- DURÁN, S. M. & G. H. KATTAN. 2005. A test of the utility of exotic tree plantations for understory birds and food resources in the Colombian Andes. *Biotropica* 37:129-135.
- EMMONS, L. H. 1997. Neotropical rainforest mammals. 2nd edition. The University of Chicago Press, Chicago.
- ETTER, A. 1998. Mapa general de Colombia (1:1.500.000). Informe nacional sobre el estado de la biodiversidad en Colombia 1997. Ministerio del Medio Ambiente - Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá.
- FOSTER, D. R., G. MOTZKIN, D. BERNARDOS & J. CARDOZA. 2002. Wildlife dynamics in the changing New England landscape. *Journal of Biogeography* 29:1337-1357.
- GLANZ, W. E. 1984. Food and habitat use by two sympatric *Sciurus* species in central Panama. *Journal of Mammalogy* 65:342-347.
- GOMPPER, M. E. & D. M. DECKER. 1998. *Nasua nasua*. *Mammalian Species* 580:1-9.
- GUTIÉRREZ-LAMUS, D. L., V. H. SERRANO & M. P. RAMÍREZ-PINILLA. 2004. Composición y abundancia de anuros en dos tipos de bosque (natural y cultivado) en la Cordillera Oriental colombiana. *Caldasia* 26:245-264.
- HARVEY, C. A., J. GONZÁLEZ & E. SOMARRIBA. 2006. Dung beetle and terrestrial mammal

- diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. *Biodiversity and Conservation* 15:555-585.
- HEANEY, L. R. & R. W. J. THORINGTON. 1978. Ecology of Neotropical red-tailed squirrels *Sciurus granatensis*, in the Panama canal zone. *Journal of Mammalogy* 59:846-851.
- HERNÁNDEZ-CAMACHO, J. I. 1992. Caracterización geográfica de Colombia. Pages 45-53 in: G. C. C. Halffter (ed.). *Diversidad biológica de Iberoamérica I*. Instituto de Ecología, Xalapa, México.
- HERNÁNDEZ-CAMACHO, J. I. & H. SÁNCHEZ. 1992. Biotas terrestres de Colombia. in: G. C. C. Halffter (ed.). *Diversidad biológica de Iberoamérica I*. Instituto de Ecología, Xalapa, México.
- KATTAN, G. H. & H. ALVAREZ-LÓPEZ. 1996. Preservation and management of biodiversity in fragmented landscapes in the Colombian Andes. Pages 3-18 in: J. Schelhas & R. Greenberg (eds.). *Forest patches in tropical landscapes*. Island Press, Washington, D. C.
- KATTAN, G. H., D. CORREA, F. ESCOBAR & C. MEDINA. 2006. Leaf-litter arthropods in restored forests in the Colombian Andes: A comparison between secondary forest and tree plantations. *Restoration Ecology* 14:95-102.
- LENTIJO, G. M. & G. H. KATTAN. 2005. Estratificación vertical de las aves en una plantación monoespecífica y en un bosque nativo en la Cordillera Central de Colombia. *Ornitología Colombiana* 3:51-61.
- LUGO, A. E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99:9-19.
- MACARTHUR, R. H. & J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42:594-598.
- MURCIA, C. 1995. Edge effects in fragmented forests: Implications for conservation. *Trends in Ecology and Evolution* 10:58-62.
- MURCIA, C. 1997. Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forest in Colombia. *Forest Ecology and Management* 99:163-170.
- NITIKMAN, L. Z. 1985. *Sciurus granatensis*. *Mammalian Species* 246:1-8.
- PARROTTA, J. A., O. H. KNOWLES & J. M. WUNDERLE, Jr. 1997a. Development of floristic diversity in 10-year-old restoration forests on a bauxite mined site in Amazonia. *Forest Ecology and Management* 99:21-42.
- PARROTTA, J. A., J. W. TURNBULL & N. JONES. 1997b. Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99:1-7.
- RODRÍGUEZ-BOLAÑOS, A., A. CADENA & P. SÁNCHEZ-PALOMINO. 2000. Trophic characteristics in social groups of the mountain coati, *Nasuella olivacea* (Carnivora: Procyonidae). *Small Carnivore Conservation* 23:1-6.
- RUSSELL, J. K. 1990. Influencia de las fluctuaciones alimentarias sobre la época de reproducción de los coatíes (*Nasua narica*). Pages 481-499 in: E. G. Leigh, Jr., A. S. Rand & D. M. Windsor (eds.). *Ecología de un bosque tropical: Ciclos estacionales y cambios a largo plazo*. Smithsonian Institution, Washington, D. C.
- SÁNCHEZ, F. & M. ALVEAR. 2003. Comentarios sobre el uso de hábitat, dieta y conocimiento popular de los mamíferos en un bosque andino de Caldas, Colombia. *Boletín Científico, Museo de Historia Natural, Universidad de Caldas* 7:121-144.
- SÁNCHEZ, F., P. SÁNCHEZ-PALOMINO & A. CADENA. 2004. Inventario de mamíferos en un bosque de los Andes centrales de Colombia. *Caldasia* 26:291-309.
- TELLERÍA, J. L. 1986. *Manual para el censo de los vertebrados terrestres*. Editorial Raíces, Madrid.
- ZAR, J. H. 1999. *Biostatistical analysis*. 4th edition. Prentice Hall, Upper Saddle River, New Jersey.

Recibido: 07/03/2007

Aceptado: 21/02/2008