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An assessment of the populations of *Sylvilagus brasiliensis meridensis* in páramos with different vegetation structures in the Northeastern Andes of Ecuador

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DEDICATION

To my husband for his love and unconditional support.

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RESUMEN

Con la captura de tres conejos de páramo, *Sylvilagus brasiliensis meridensis*, se calculó la tasa de defecación para esta especie por primera vez en Ecuador. Combinando la tasa de defecación estimada, el método de conteo de bolitas de heces de conejos y la ecuación de densidad de liebres de Novaro *et al.*(1992) las densidades de conejo de páramo se calcularon en cuatro páramos con distintas estructuras de vegetación. Los resultados sugieren que existe una correlación entre la diversidad de la vegetación de estos páramos y su densidad de conejos de páramo. Este estudio comprueba que el conteo de bolitas de heces de conejo de páramo es un método no invasivo y económico que permite la estimación de la abundancia de conejos de páramo. La abundancia de conejos de páramo puede servir como una herramienta para medir los efectos de la actividad humana sobre los tamaños de poblaciones de mamíferos pequeños de este ecosistema. Futuros estudios científicos sobre los pequeños mamíferos del páramo ayudarán a comprender mejor el funcionamiento del páramo para su manejo y conservación.

ABSTRACT

A defecation rate is calculated from three captured páramo rabbit *Sylvilagus brasiliensis meridensis* individuals for the first time in Ecuador. Combining this defecation rate, the pellet count method, and Novaro *et al.'s* (1992) hare density equation, páramo rabbit densities were calculated in four páramo localities with different vegetation structures. A correlation was found between the páramos' vegetation diversity and páramo rabbit densities. This study shows that pellet counting is an economical and non-invasive method that permits the estimation of páramo rabbit abundances in páramo ecosystems. Páramo rabbit abundances may serve as a tool to measure the effects of human activity over small mammal population sizes. Further studies of small páramo mammals will help better understand how the páramo ecosystem functions and will provide insights for its land management and conservation.

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INTRODUCTION

The páramo, a high-altitude ecosystem of Northern South America, forms a unique environment found in the Andes of Venezuela, Colombia, Ecuador, and northern Peru (Mena & Hofstede 2006 and Sklenar *et al.* 2005), between the upper limits of montane forests (3000-3500 m) and the lower limits of perpetual snow (Hofstede *et al.* 2003). At first sight, the páramo may seem empty and lifeless due to its extreme climatic conditions, yet it is home to thousands of species of native flora and fauna (Hofstede *et al.* 2003 and Sklenar *et al.* 2005) which have evolved various morphological, physiological, and behavioral traits in order to survive in this hostile yet fragile biome (Morales-Betancourt & Estevez-Varon 2006). In the páramo flora guide, for example, Sklenar *et al*. (2005) reported 127 families, 540 genera, and 3595 species of vascular plants in all of the páramo's geographical area, of which 512 genera are native to the páramo. Moreover, it is estimated that endemism levels of páramo flora can be as high as 60% for certain plant groups (Hofstede *et al.* 2003 and Luteyn & Churchill 1999). The páramo's fauna is also rich in comparison with other mountain biotas and includes at least 70 species of mammals including the mountain tapir *Tapirus pinchaque*, the spectacled bear *Tremarctos ornatus*, the white-tailed deer *Odocoileus virginianus*, and the mountain lion *Puma concolor* (Mena 2001). However, compared to the flora, our knowledge about páramo fauna is still scarce, not only in terms of its diversity and distribution, but also in terms of its basic ecology, and its sensitivity to human disturbance.

Current information about páramo mammals is limited to a few studies mostly related to the distribution, diet, and natural history of rare and large species such as the spectacled bear, the mountain tapir, and the white-tailed deer *Odocoileus virginianus* (Suárez 1988, Downer 2001, Lizcano *et al.* 2002, Kattan *et al.* 2004, Albuja 2007). In addition to these studies, some research has been done on the diversity, abundance and distribution of small mammals and birds in specific páramo localities (Vuilleumier 1992, Barnett 1999, Cresswell *et al.* 1999, Koenen & Koenen 2000, Woodman 2002, Bonaccorso 2004). In sharp contrast, there is virtually no information about the status of key mammal species in the páramo and the changes that their populations could be experiencing as a result of increasing pressure from human activities. Among these species, the páramo rabbit *Sylvilagus brasiliensis meridensis*, a sub species of the cottontail forest rabbit *S. brasiliensis* (Valero & Durant 2001 and Chapman & Ceballos 1990) is of special interest as it probably plays a critical role in structuring páramo communities, both as a pervasive herbivore consuming a wide variety of plant species, but also as an important food source for several predators such as the Andean fox *Lycalopex culpaeus*, the long-tailed weasel *Mustela frenata*, the mountain lion *Puma concolor*, and the black-chested buzzard eagle *Geranoaetus melanoleucus* (Jiménez & Jaksic 1989, Trujillo & Trujillo 2007, Hernandez-Guzman *et al.* 2011). From this perspective, the study of the páramo rabbit is likely to offer relevant information evaluating the impacts of human activities on the resource-base of the ecosystem (plant community structure) and also on the higher levels of the trophic webs. In addition, it will be increasingly important as managers, landowners, and decision makers struggle to find integrative approaches to manage and conserve páramo ecosystems in the context of the complex matrix of human intervention that they experience.

Knowledge about the cottontail forest rabbit is mostly limited to several studies concerning its occurrence and its role in the diet of carnivore species in savanna and tropical forest sites in the lowlands of Eastern South America (Bianchi & Mendes 2007, Kasper *et al.* 2007, Caceres *et al.* 2010, Bianchi *et al.* 2011, Borges *et al.* 2014). In contrast, the high-altitude sub-species that occurs in the Northern Andes has received little attention and our knowledge is limited to a short report on its diet (Valero & Durant 2001) and a three-year study conducted in the páramo of Mucubaji in the Venezuelan Andes (Durant 1983). The latter study described several aspects of the reproductive biology of the species and population densities of 2.2 to 3.9 individual/ha (Durant 1983). Besides theses studies, little is known about the biology of this species in other parts of its Andean distribution, and the natural or anthropogenic factors that could influence the temporal and spatial variation in its population numbers. Moreover, to the extent of our knowledge, no information exists on the potential relationships that could exist between habitat structure and the population size of this rabbit.

The Northeastern Andes of Ecuador offer an excellent opportunity to explore the factors that could influence the population status and behavior of key mammal species such as the páramo rabbit. This region exhibits a wide range of vegetation types that are related to local environmental conditions, and to varying levels of human activities from localities with little or no human intervention to areas that have been heavily impacted (Suárez & Medina 2001, Hofstede *et al.* 2002). Moreover, this region is of strategic importance for the country as it provides roughly 85% of the water for domestic use in the capital city of Quito (2.5 million people; Rosero *et al.* 2011) and a large proportion of the water used for irrigation in the inter-Andean valley. In this context, the main objectives of this study are i) to estimate population densities of the páramo rabbit in the northeastern páramos of Ecuador, and ii) to assess if páramo rabbit abundances and behavior vary among páramo localities with different vegetation structures. In the long-term, we hope that the results of this study will be useful in future studies on the ecology of páramo animal communities and also in the monitoring of restoration or conservation programs in this ecosystem.

SITE DESCRIPTIONS

Between December 2012 and July 2013, we studied four páramo sites standing along Ecuador´s northeastern cordillera (Figure 1). These sites were selected to represent a range of different vegetation types that are roughly associated with a gradient of human disturbance. These páramo sites range in altitude from 3600 to 3980 m.

Paluguillo

At 3980 m, the Paluguillo private reserve is characterized as a moderately impacted páramo area since private farms mostly surround it. Paluguillo is fragmented by a secondary dirt road that connects to a major highway less than 1 km away. Hunting is not allowed at this site although control is sporadic and some infrequent hunting could take place. In addition, feral dogs have been observed roaming this land.

Yanahurco

The Yanahurco site standing at an altitude of 3600 m is located in the Yanahurco Private Reserve. The Yanahurco Private Reserve consists of 26,000 hectares of protected páramo located in the buffer zone of Cotopaxi National Park. This páramo is considered a moderately low anthropogenic impacted páramo due to the presence of cattle and invasive wild horses. Human presence is frequent since the reserve annually receives hundreds of local and international tourists. However, hunting is banned on this reserve and the presence of invasive dogs has not been observed.

Amulanga

At 3980 m, Amulanga is also located within the Yanahurco Private Reserve, 5 km away from the Yanahurco study site. Although this site is close to the Yanahurco site, it is separated from Yanahurco by a river and mountains. Human presence here is very scarce since access to this site is possible only by foot or horseback riding. Amulanga was classified as a moderately low human impacted páramo. This area still shows signs of previous fires that have consumed the vegetation. Although wild horses and cattle are still present in this páramo, hunting has been strictly banned and no evidence of feral dogs has been noted.

Chorrera

At the outskirts of the Yanahurco Private Reserve, the Chorrera study site (3600 m) was selected to represent a páramo with very low levels of human disturbance. This study site is reachable only after traveling 14 km from the Yanahurco cabins after a day of horseback riding or hiking. Here, hunting is also banned, invasive dogs have not been observed, and no signs of recent burning have been observed. The Chorrera páramo likely illustrates what a pristine páramo might have looked like after hundreds of years without human intervention.

METHODOLOGY

In order to characterize the structure of the plant community we used a combination of primary and secondary information. First, in each site we randomly established between one and six 50 meter long transects. Fewer transects were established in Amulanga and Chorrera due to the presence of a more homogenous vegetation structure and the presence of extreme climatic conditions that made the elaboration of field work difficult. All transects were located in areas with gentle slopes (<30°), in altitudinal ranges between 3600 and 3980 m, and were at least 100 meters apart from each other. Along the length of each transect, taxonomic identity, life-form (Ramsay & Oxley 1997) and percent coverage of each plant life-form was recorded. In the case of dense mat-forming species in which individual identification was difficult, percent coverage was recorded for the whole mat, disregarding the identity of individual species. These mat-forming communities usually consisted of several species, including *Lachemilla orbiculata*, *Azorella pedunculata*, *Disterigma empetrifolium*, and *Gunnera magellanica*, among the most representative. From this information we derived parameters such as percentage of bare ground coverage and Shannon diversity index for plant life-forms. Secondary information concerning the ease of human access to each site by road access was noted.

In order to estimate the densities of páramo rabbits we used a pellet-count method (Novaro *et al.* 1992 and Murray *et al.* 2002). Although direct rabbit observation during line transect sampling or live trapping could be used to estimate páramo rabbit density because it provides absolute numbers, these methods are time-consuming and rabbit densities cannot be estimated when abundances are low (Palomares 2001 and Forys & Humphrey 1997). In addition, live trapping is invasive as the method involves direct manipulation of the animals (Forys & Humphrey 1997). Thus, a less intensive and less invasive method such as counting pellets can be used to estimate rabbit densities (Palomares 2001 and Forys & Humphrey 1997). This method is based on i) the estimation of defecation rates of the páramo rabbit and ii) direct counts of páramo rabbit pellets in different field locations, over a standard period of time. Pellet counts are widely used to monitor rabbits and other lagomorphs (Palomares 2001) and have been shown to provide information on habitats with varying rabbit abundances.

In order to estimate defecation rates, this study required the capture and short-term confinement of a few páramo rabbits. Capture efforts were carried out in Paluguillo and Yanahurco due to easy access. Páramo rabbits were captured with Tomahawk live-traps following Barnett's (1999) trapping procedure. Bait consisted of a mixture of bananas, apples, peanut butter, oatmeal, alfalfa, lettuce, carrots, and apple cider. Captured rabbits were penned individually in a 1x2 m holding pen. The pen was closed off with metal fencing on all lateral sides (buried 50 cm into the ground) and the top to prevent rabbit escape and predator infiltration. The floor of the pen consisted of natural páramo covered with vegetation of known páramo rabbit consumption such as Poaceae and Cyperaceae (Valero & Durant 2001).

Each individual rabbit was confined for one day. Before entering its pen, the floor was checked to assure that all previous rabbit pellets and other animal feces had been removed. Water was provided at all times and the natural floor vegetation acted as shelter and food for the rabbit during its brief stay. Captured rabbits were weighed, observed, and released. Further manipulation of these individuals was avoided in order to prevent stress and death.

Following each rabbit's confinement, the individuals were released back into the same location they were originally captured from. Immediately after the rabbit's release, its pellets were collected and quantified. A defecation rate was calculated for the individual using its body weight, time penned, and number of pellets produced. Individual defecation rates were combined to obtain an average defecation rate for páramo rabbits that was utilized in the second part of this study. Several studies have utilized this confinement procedure (Forys & Humphrey 1997, Green & Flinders 1980, Martínez-García *et al.* 2011, Simonetti 1989) in order to calculate rabbit defecation rates since calculating defecation rates utilizing free roaming individuals in the wild is logistically difficult and expensive.

Pellet counts were carried out along six 50 m long transects randomly established at least 100 meters apart from each other. Along each transect, circular plots (1 m in diameter) were established at 10 m intervals (six plots per transect). Plots were not placed on páramo rabbit latrines. The center of each plot was permanently marked with a flagged pole in order to easily identify plots during re-visits. Large circular plots were used since this configuration has been shown to intercept as many or more pellets as did the rectangular plots, implying that the larger plot surface area reduced the likelihood of a Type II statistical error, the variability in pellet counts, and time required to establish the plots. Sites were sampled during 5 to 8 months.

During the first visit to each site, all existing rabbit feces were removed from the pellet count plots. One month later, the plots in each study site were re-visited and the new rabbit pellets in each plot were quantified. Transects were re-visited monthly for a duration of 5 to 8 months per site. Rabbit abundances were estimated with the equation developed by Novaro *et al.* (1992).

$$D = 10000m^2 / (\text{ha } X / TRA)$$

where *D*= rabbit abundance (individuals/ha), *X*= mean number of pellets per plot, *T*= time between plot pellet clearing and pellet count (days), *R*= defecation rate (number of pellets dropped per animal per day), and *A*= area of each plot (m^2). Finally, a mean páramo rabbit density was calculated for each location by grouping the rabbit densities calculated per transect. Differences in the mean densities among locations were tested with Kruskal-Wallis non-parametric test, followed by Dunn's pairwise comparisons. Linear correlations were analyzed between páramo rabbit densities and varying diversity of plant forms. All statistical analyses were carried out with software Jmp.9.0.1.

The potential of predation pressure on the páramo rabbit from the páramo fox *Lycalopex culpaeus* and feral dogs was estimated for a total of 15 field work days at each study site. Presence of predation pressure was measured by the direct observation of individuals or by the observation of canid feces along pellet transects. Feces were removed and discarded from study sites in order to avoid recounting the same feces on different observation days.

RESULTS

All our study sites were dominated by tussock grasses (*Calamagrostis* sp.) which average percent cover ranged between 45 % ±23 (mean ± standard error) and 73 % (Table 1; Figure 4). Yanahurco was the site with the highest diversity of plant life-forms (Shannon diversity index; H = 0.53), and included not only a high cover of tussock grasses (61% ± 12), but also an important layer of shrubs and erect herbs, which covered 6% and 5% of the ground, respectively (Table 1; Figure 4). The site with the second highest diversity of plant life-forms was Paluguillo (H = 0.42), where shrubs and mosses covered between 8% and 4% of the ground, respectively. The remaining two sites had lower diversity of plant life-forms (Amulanga: H = 0.25; Chorrera: H = 0.35), which reflects a simpler vegetation structure with only two or three life-forms, as compared to the seven found in Yanahurco and Paluguillo.

The total trapping effort was 100 trap nights consisting of 90 trap nights at Paluguillo and 10 trap nights at Yanahurco. Trapping efforts were carried out only in these two study sites since live-trap transportation was facilitated by the access of roads at both sites. In total, three rabbits were captured, all of them sub-adult individuals in good body condition. Further body measurements were not taken to avoid further stress from confinement. The average páramo rabbit defecation rate was 280.3± 35 pellets/individual/day (mean ±standard error).

Mean rabbit densities ranged from 23 to 92 ind/m^2 and were significantly different between sites (χ^2= 21.7, p <0.0001; Figure 2). Yanahurco had the highest calculated páramo rabbit abundance 92 ± 25 ind/ha (mean ± standard error) followed by Paluguillo

(76 ± 18 ind/ha). Páramo rabbit densities at these sites were between two and four times higher than corresponding values at the (Chorrera 34 ± 17 ind/ha) and Amulanga (23 ± 6 ind/ha) sites (Figure 2). In all study sites, the estimated páramo rabbit densities tended to increase during summer months (June and July) especially in Paluguillo, Chorrera, and Yanahurco, where the densities of rabbits between June and July were between two and four times higher than densities between December and February (Figure 3). Although our number of sites was low, we found a strong and significant correlation (non-parametric Spearman´s correlation: $\rho=0.95$; $p<0.001$) between the mean density of páramo rabbits and the Shannon index of diversity of plant life forms at each site. According to this analysis, the highest densities of páramo rabbits were found in the sites with higher diversity of plant life-forms.

Regarding the presence of canids, the total number of observations (direct sightings and signs) ranged from 15 (Yanahurco) to 2 (Paluguillo). No correlation was found between the number of canid observations and páramo rabbit densities.

DISCUSSION

The main objective of this study was to estimate the densities of *S. brasiliensis meridensis* in páramo localities with different plant community structures in Northeastern Ecuador. Mean páramo rabbit densities at our study sites ranged from 23 to 92 ind./ha and are similar to densities estimated for *Oryctolagus cuniculus* in southern Italy (26 to 95 ind./ha; Siracusa & Petralia 2013). In the latter study, rain was negatively correlated with the density of rabbits. Similarly, in all our study sites, rabbit densities peaked during the summer near the end of the sampling period (June and July of 2013), reaching values that were between 2 and 2.6 times higher than at the beginning of the study, except for Amulanga where the differences were considerably smaller (Figure 3). Other studies have also reported significant changes in rabbit densities probably related to seasonal changes in rabbit activity. For example, Novaro *et al.*(1992) reported higher European hare (*Lepus capensis*) densities during summer months. However, this pattern is unlikely to explain the contrasting densities that we report here, as the seasonality at our study sites is not comparable to that of temperate areas. Although our study was not long enough to allow a better understanding of the temporal changes in páramo rabbit densities, they are sufficiently large to suggest that this pattern could have important ecological consequences. For example, a large increase in rabbit densities could result in spread of disease and stronger competition for food, which could then affect population dynamics.

Our páramo rabbit densities are higher than other documented leporid species throughout the world reported in studies including densities of 0.85 to 2.7 ind./ha for *Oryctolagus cuniculus* in Iberian Mediterranean habitats (Fernández de Simon *et al.* 2011) and of 5 to

35 ind./ha for *Sylvilagus palustris* in the Florida Keys. Our estimate is also much higher than the only other density reported in the literature for *S. brasiliensis* (2.2 to 3.9 ind./ha) in the high Andes of Venezuela (Durant 1983). Although some of these differences could be attributed to the field methods used in different studies, previous research has shown that density estimates generated through pellet counts and live trapping methods are closely correlated. For example, Forys and Humphrey (1997) concluded that both live trapping and pellet counting were accurate and effective methods for estimating marsh rabbit (*Sylvilagus palustris hefneri*) densities since they were significantly correlated and both offered an accurate estimate of the density calculated from radio-tracking data. However, the previous study does mention that a defecation rate calculated with captive rabbits could be a possible source of error since rabbits may defecate more when they are not captive. In this context, the wide range of densities that we report in this study probably reflects important differences in vegetation structures between sampling sites that result in significant differences in the population dynamics of *S. brasiliensis*.

Some studies show that rabbit populations could exert a significant negative impact on the plant community, as has been shown in previous studies in Italy (Bell *et al*. 1998) and Australia (Bird *et al*. 2012). In these studies, increased rabbit numbers were related to crop damage in cultivated land versus this study's natural habitat settings. In our study, the mean density of páramo rabbits was highly correlated to the diversity of plant life-forms (*i.e.* the complexity of the vegetation) in each site. Although we do not have specific field information to explain this pattern, we speculate that the higher rabbit density in areas that have heterogeneous vegetation could be explained by at least two main factors. First, a more complex vegetation could offer better protection against predators such as the

Andean Fox (*Lycalopex culpaeus*), the black-chested buzzard eagle (*Geranoaetus melanoleucus*), or the long-tailed weasel (*Mustela frenata*) that are common in the northeastern Ecuadorian Andes. Such patterns have been previously reported for *Oryctolagus cuniculus*, a species that showed higher abundance at sites with more woodland versus sites where grass, scrub, and crops were dominant (Trout *et al.* 2000). Second, the higher diversity of the vegetation could result in a more reliable and diverse food-source for the rabbits. For example, Durant and Valero (2001) suggest that the páramo rabbit may be an opportunistic species that eats three to 12 vegetation species abundantly each month in addition to eating other available plants. Finally, the level of heterogeneity of the vegetation could be an outcome of the histories of human use in each site. In this regard, several studies have shown that one of the main impacts of burning and grazing is the simplification of vegetation structure and, more specifically, the elimination or reduction of the shrub layer in the plant community (Ramsay & Oxley 1997, Keating 2000, Suárez & Medina 2001, Ríos 2013). From this perspective, the lower abundances of páramo rabbits in sites where vegetation structure was less diverse could reflect the cumulative effect of the lower availability of food sources and hiding places, and the direct impacts that fires might have on the population dynamics of this species. The distinction between the influences of all these factors clearly deserves further attention. Moreover, it is likely that large population fluctuations in páramo rabbit densities could have cascading impacts throughout the food web because of their roles as primary consumers, seed dispersers, and as a food source to a wide assemblage of predators and scavengers. Despite their potential importance, the nature of these interactions remains largely unexplored for the Tropical Andes.

The data collected on canine pressure was not sufficient enough to find out if predation is a factor affecting páramo rabbit population size since a greater sampling effort should be carried out. Likewise, other mammal or avian predators were not taken into account. However, this does not imply that predation pressure is not an important factor affecting páramo rabbit populations. In addition, Trout *et al.* (2000) indicate that high rabbit numbers may lead to more predators therefore making it difficult to distinguish between cause and effect.

Another important factor related to the ample temporal and spatial variability that we report in the populations of *S. brasiliensis meridensis* is the potential existence of large population cycles as those that have been reported for other small mammal and leporid species. For example, in northern Canada's boreal forest the snowshoe hare (*Lepus americanus*) fluctuates in cycles with a 10 year periodicity and in tundra regions lemmings fluctuate in cycles with a 3–4 year periodicity (Krebs 2011). Although the short-term nature of our study does not allow a proper evaluation of this possibility, during this research we talked to several park-rangers and local people from Andean communities of the study area, and they all mentioned the existence of 5 to 7 years cycles in the populations of páramo rabbits. In fact, these cycles are the theme of local tales that involve "games" between mountains in which the mountain that wins takes all the páramo rabbits of the region for 7 years. Moreover, local people believe that the appearance of a white páramo rabbit in the population foretells an upcoming crash in the number of páramo rabbits or, as local people call it, end of the "time of rabbits". Interestingly, during this study both, local park rangers and owners of páramo haciendas stated that every seven years, when the páramo rabbit numbers crash, most individuals will show signs of an unidentified disease characterized by patches of bare skin, fungus-like skin lesions, and signs of malnutrition (Fernando Cobo, pers. comm.). Coincidental or not, Cobo and other páramo experts stated that during this investigation páramo rabbit numbers were recuperating after a recent drastic drop, which is consistent with the increase that we reported during this study. Additional studies are needed to characterize the nature of these perceived population cycles, their causes and ecological consequences, and the potential presence of disease. The latter point is specially important, considering that previous research has shown that rabbit populations can be affected by outbreaks of myxomatosis and rabbit hemorrhagic disease (Williams *et al.*2007 and Trout *et al.* 2000). Likewise, páramo mammals like the páramo rabbit, white-tailed deer, alpacas, cattle, and sheep can be affected by hepatic fasciolosis, a parasitic trematode transmitted through infected snails (White 2001).

Our study reports the first population density estimates for *S. brasiliensis meridensis* for the high Andes of Ecuador, and the first attempt at understanding the factors that control the large temporal and spatial variability of its population numbers. This survey suggest that the population densities of *S. brasiliensis meridensis* is strongly associated with the structure of the páramo vegetation, although further studies are needed to establish the nature and prevalence of this relationship. Furthermore, our data strongly suggest that long-term sampling is urgently needed to understand the temporal cycles of the populations of the páramo rabbit, and their ecological causes and consequences in páramo ecosystems.

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FIGURES AND TABLES

Figure 1. Map of study sites.

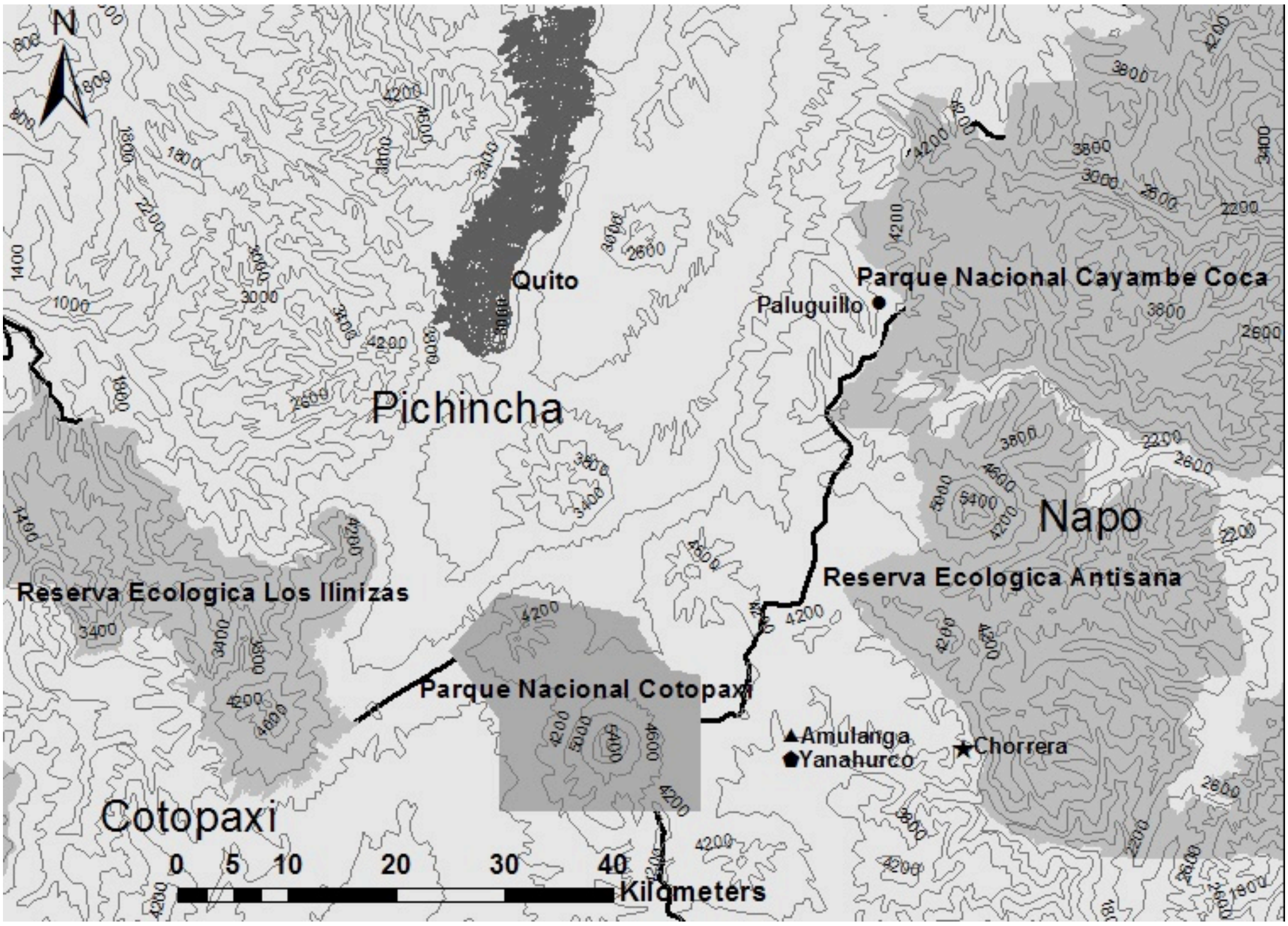

Figure 2. Mean rabbit density (rabbits/ha) and standard error in four study sites calculated with Novaro *et al.'s* (1992) hare density formula. N= number of months pellet count took place (Amulanga N=5, Paluguillo N=8, Chorrera N=7, and Yanahurco N=7). Sites that do not share a letter were significantly different (*p*< 0.05) according to Dunn's non-parametric test of pairwise comparisons.

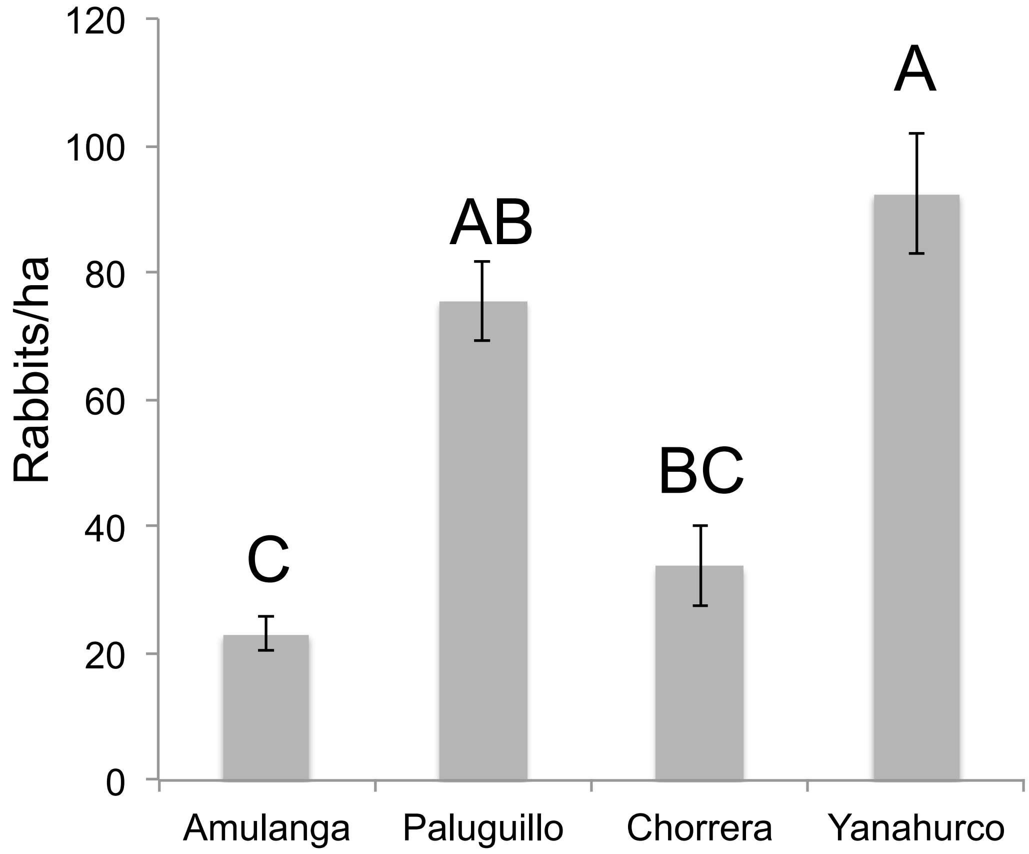

Figure 3. Study sites' grouped mean rabbit densities and standard errors during pellet counting period.

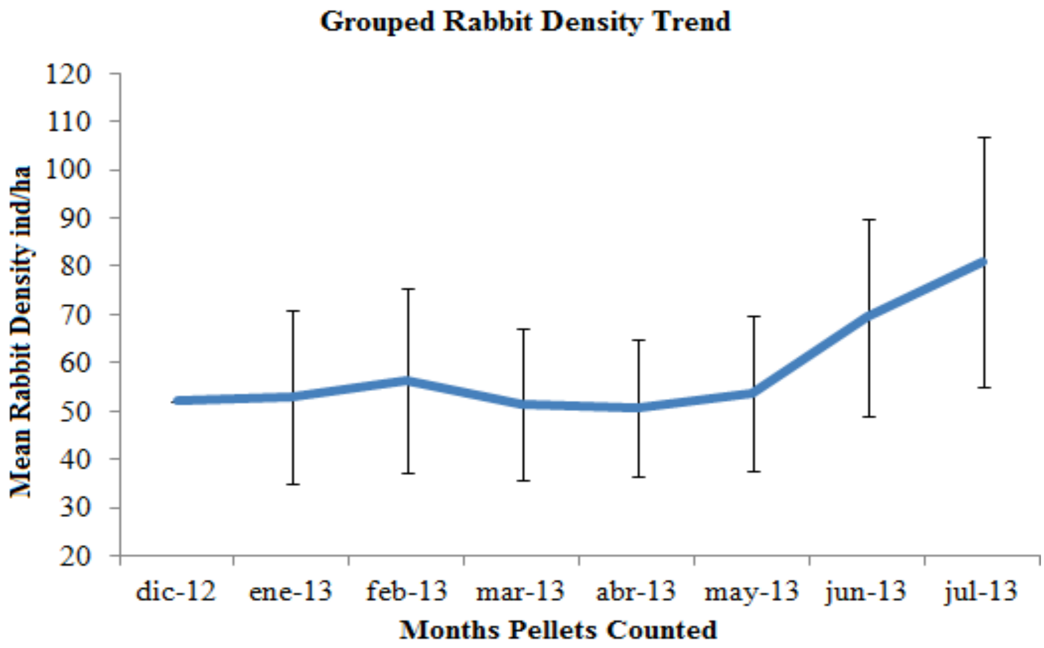

Figure 4. Mean percent coverage of vegetation life-forms and bareground with corresponding Shannon diversity index (H) in four páramo sites in northeaster Ecuador.

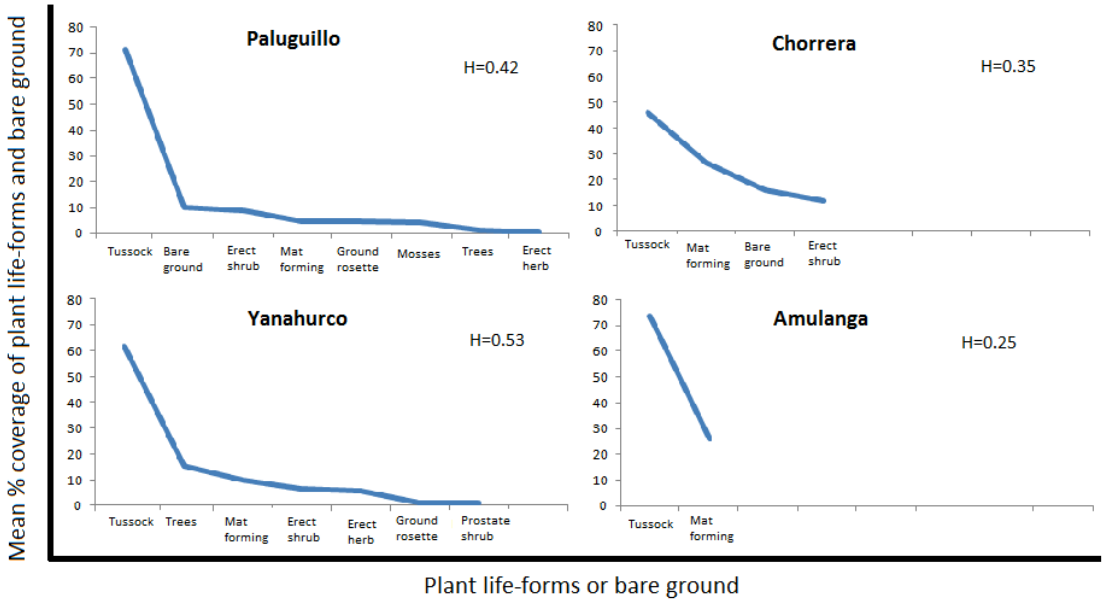

Table 1. Mean percentages of plant cover by various vegetation life-forms and bare ground in four páramo sites in northeastern Ecuador. Standard errors are shown in parenthesis, except for sites in which no replicates were available. Means were calculated from cover data along six line-transects in Yanahurco and Paluguillo, two transects in Chorrera, and one transect in Amulanga.

	Tussoc kgrass	Erect shrub	Matt forming	Ground -rosette	Erect herb	Prostate shrub	Mosses	Trees	Bare-ground
Amulanga	73.85	0.00	26.15	0.00	0.00	0.00	0.00	0.00	0.00
Chorrera	45.87	11.56	26.47	0.00	0.00	0.00	0.00	0.00	16.10
	(23.81)	(4.58)	(3.13)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(16.10)
Paluguillo	71.00	8.84	4.47	0.48	0.13	0.00	4.08	1.03	9.96
	(5.18)	(4.47)	(3.48)	(0.48)	(0.13)	(0.00)	(2.20)	(1.03)	(3.37)
Yanahurco	61.58	6.26	9.82	0.93	5.47	0.81	0.00	15.13	0.00
	(12.35)	(1.36)	(4.42)	(0.64)	(2.18)	(0.31)	(0.00)	(15.13)	(0.00)

Table 2. Monthly páramo rabbit density estimates (rabbits/ha) among sites calculated with Novaro *et al.'s* (1992) hare density equation.

Date	Amulanga	Paluguillo	Chorrera	Yanahurco
December 2012		52		
January 2013		74,7	17,4	66,6
February 2013		57,5	22,8	88,5
March 2013	24,2	67,6	26,3	87,4
April 2013	24	79,9	28,9	69,8
May 2013	22,3	76,7	29,7	85,8
June 2013	14,3	87,4	66,5	109,3
July 2013	30,6	108,6	44,5	139,4