



Research Article

Activity patterns and habitat use of mammals in an Andean forest and a *Eucalyptus* reforestation in Colombia

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Abstract

To mitigate deforestation effects, reforestation programs with native and/or exotic species have been implemented in the Colombian Andes, but little is known about how such reforestations affect wildlife. Using camera-traps, we studied the species richness, activity patterns, and habitat use of middle and large mammals in two adjacent forests, a native forest and a *Eucalyptus grandis* reforestation located at the Colombian Central Andes. Since the two forests were adjacent, we expected no differences between species richness in the two forests. The reforestation was a monoculture and an artificial ecosystem, thus we expected differences in activity and habitat use by mammals in the two forest types. We did not find significant differences in the species richness between the forests. The activity of *Sciurus granatensis* and *Mazama rufina* was influenced by the time of the day, and there was a temporal and spatial segregation among the soil forager species *Nasua nasua*, *Nasuella olivacea* and *Dasypus novemcinctus*. The species *N. nasua* and *D. novemcinctus* used the Andean forest more than the reforestation, whereas *N. olivacea* used the reforestation more. *D. novemcinctus* and *N. olivacea* were mainly nocturnal and/or crepuscular, whereas *N. nasua* was mainly active during daytime. This suggests that the creation of a new habitat, such as the reforestation, might influence the interactions among some species and apparently, could reduce interspecific competition and thus contribute to their co-existence at the study zone though niche differentiation in time and space.

Introduction

The transformation and deforestation of Andean ecosystems have resulted in biodiversity loss (Aubad et al., 2010; Etter and van Wyngaarden, 2000) and isolation of wildlife populations (Kattan et al., 2004). To recover fragmented ecosystems and mitigate the deforestation effects, reforestation programs with native and/or exotic species have been implemented in the Colombian Andes (Etter and van Wyngaarden, 2000; Hofstede et al., 2002; Etter et al., 2006; Günter et al., 2009). Reforestation with exotic species, such as the conifers brought from Europe and North America, can generate soil desiccation and may decrease its micro biota (Hofstede et al., 2002). Conifers may promote plants diversity loss (Cavelier and Santos, 1999), but these effects are not always predictable (Cavelier and Santos, 1999; Hofstede et al., 2002). In spite of the potential negative effects of *Eucalyptus* reforestations over the soil microbiota (Chen et al., 2013; Martins et al., 2013), it might present less threat to local plant diversity in the Colombian Andes than other exotic species, and even compared to Neotropical native species such as the Andean alder, *Alnus acuminata* (Murcia, 1997; Cavelier and Santos, 1999). *Eucalyptus* plantations have been broadly used throughout the Colombian Andes, but we know very little about their impact on wildlife (Mendoza and Sánchez, 2014). Therefore, understanding the potential effects of these plantations on the native biodiversity could contribute to the development of management and conservation plans. In particular, in this work, we evaluated whether a *Eucalyptus* reforestation can affect the species richness, activity patterns, and habitat use of non-volant mammals in the Central Andes of Colombia.

The use of time constitutes a fundamental aspect in the ecology of an organism, since time is an unique dimension in which organisms have to maximize their fitness (Pianka, 2000; Kronfeld-Schor and Dayan, 2003; Bennie et al., 2014). In non-volant mammals, activity patterns and habitat use may depend on climate, availability of food resource, habitat structure and interactions such as competition and predation (Kotler, 1984; Morris, 1989; Abramsky et al., 2001, 2002; Morris, 2003b; Kotler et al., 2004; Bennie et al., 2014). For instance, preys and predators come into a “game” when one wants to hunt and the other wants to be not hunted, and therefore the prey adjusts its time activity to avoid the predator (Brown et al., 1999, 2001). Also, similar habitat use in competing species could cause allopatric distributions or different activity patterns to facilitate their co-existence (Kotler et al., 1991; Bouskila, 1995; Abramsky et al., 2001; Jaksic and Marone, 2007; Di Bitetti et al., 2013). Thus, habitat selection and activity patterns are product of manifold interactions which are related to different environmental characteristics (Halle and Stenseth, 2000; Wong et al., 2004; Kolowski and Alonso, 2010; Morris, 2011). Therefore, their study could be used to understand the animal responses to the effects produced by human activity (Morris, 2003a).

Indeed, we could expect that changes associated to human activity in Andean environments could affect habitat selection and activity of wildlife species. Previous studies that evaluated the impacts of reforestations upon Andean mammals were focused on evaluating composition and species diversity (Roncancio Duque and Estéves Varon, 2007; Sánchez et al., 2008; Tirira and Boada, 2009). However, it has been reported for forest fragments of the Brazilian Amazon that some nocturnal mammals become crepuscular in small, <1000 ha, forest fragments (Norris et al., 2010). Moreover, in forests of Argentina several felid species preferred forests with the lowest human disturbance

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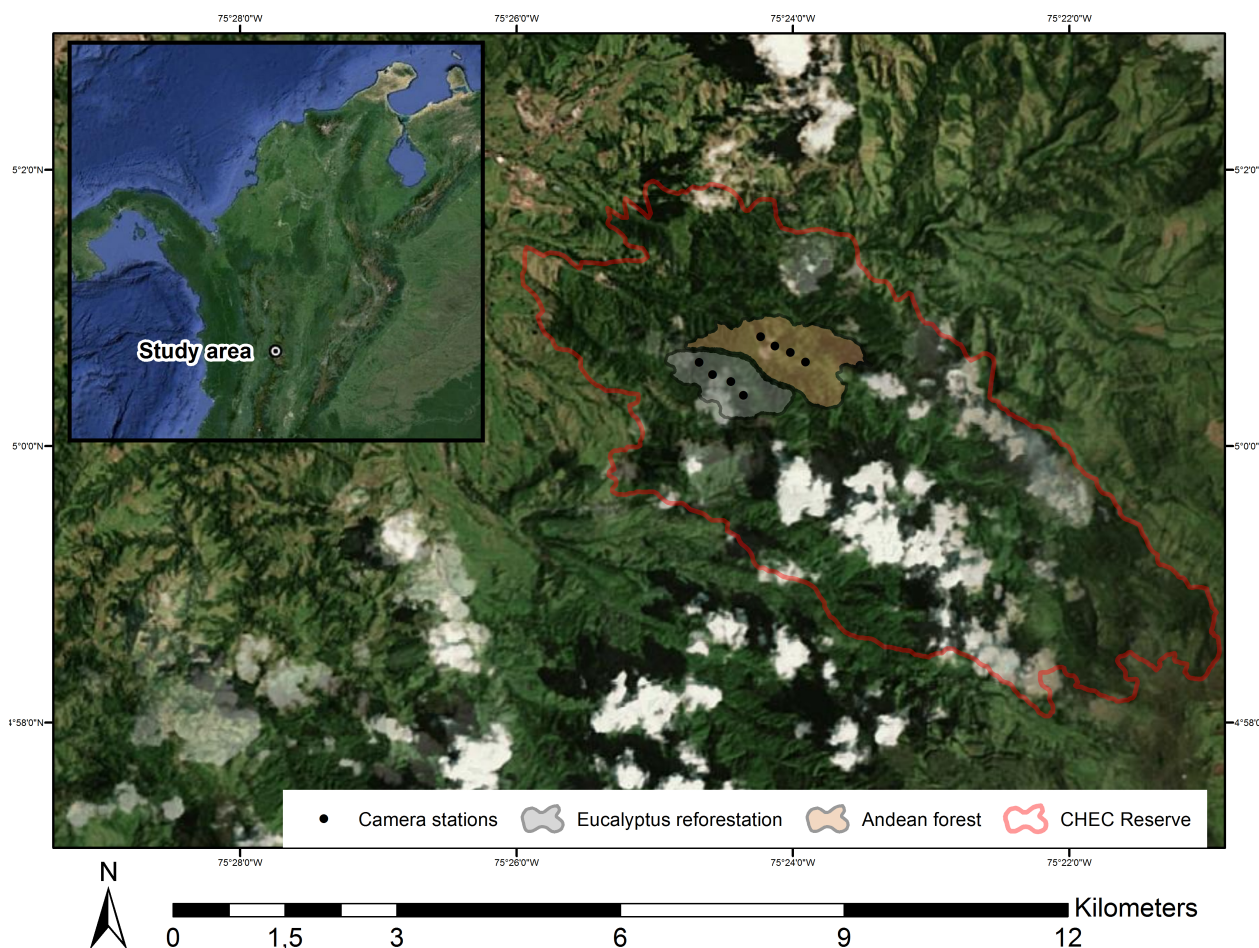


Figure 1 – Location of the study area at the Colombian Central Andes and the sample stations at CHEC Reserve. Central point of the Reserve is located at the coordinates $75^{\circ}24'0''\text{N} - 4^{\circ}52'30''\text{W}$. The Andean forest and the *Eucalyptus grandis* reforestation cover an area of 145.75 and 92.93 ha, respectively. The camera-trap density was 0.027 cam/ha in the Andean forest and 0.043 cam/ha in the reforestation.

(Di Bitetti et al., 2010). In some areas of Europe, adult brown bears, *Ursus arctos*, modified their daily activity of 24h cycles to become predominantly nocturnal, which appears to be a strategy to avoid humans (Kaczensky et al., 2006). In degraded natural ecosystems in Argentina, some carnivore species travel larger distances than in non-degraded ecosystems (Forsey and Baggs, 2001; Manfredi et al., 2011). Atlantic forests of Brazil present similar non-volant mammals richness compared to *Eucalyptus* sp. reforestations, and some carnivore species could even prefer the reforestations (Da Silva and De Almeida, 2002; Lyra-Jorge et al., 2008). Furthermore, in the Colombian Andean forest some species of terrestrial and volant mammals appear to prefer reforestations of Andean alder, *A. acuminata*, over natural Andean forests (Roncancio Duque and Estéves Varon, 2007; Sánchez et al., 2008).

In this study, we evaluated the species richness, activity, and habitat use of non-volant mammals in two adjacent forests in the Central Cordillera of Colombia: a native forest and a *Eucalyptus grandis* reforestation. Both forest types should offer different resources to mammals. On one hand, reforestations are monospecific, novel ecosystems created by humans. Also, *Eucalyptus* spp. can decrease plants diversity (Murcia, 1997; Cavelier and Santos, 1999), and therefore a plantation with this plant species may affect the interactions among the mammal species that are present (Kronfeld-Schor and Dayan, 2003). On the other hand, the native forest is the environment where the mammal populations evolved, and accordingly we expected differences in the activity and habitat use of at least some species, as suggested by studies in other areas of the Central Andes (Roncancio Duque and Estéves Varon, 2007; Sánchez et al., 2008). In addition, we also expected moonlight illumination to affect the activity of some species, since it may increase their risk perception (Brown et al., 2001; Brown and Kotler, 2004; Kronfeld-Schor et al., 2013). Finally, since the forests are adjacent, we expected

travelling costs to be negligible (Morris, 1989) and, consequently, to find a similar species richness and composition in both forests.

Materials and methods

Study site

We carried out the study at the Caldas' Central Hydroelectric (CHEC) Reserve, located in the western slope of the Colombian Central Andes, in Manizales and Villamaría municipalities at the Caldas department (Fig. 1). The CHEC Reserve has 3893.34 ha (CHEC, 2007) and its central point is at $75^{\circ}24'0''\text{N} - 4^{\circ}52'30''\text{W}$ (Roncancio Duque and Estéves Varon, 2007). The Reserve comprises different types of vegetation cover, since it ranges from 2400 to 4000 m of altitude (CHEC, 2007), and we focused our study in a region between 2450 to 2550 m of altitude. This zone was declared as a reserve to protect the highest part of the Chinchiná River basin, since it provides water for more than 500 000 people (Corpocaldas, 2000), and because water availability from the river varied considerably during the 1960's (Pérez-Arbeláez, 1966). In the same decade, the most degraded zones of the region were reforested with eucalyptus (*Eucalyptus* spp.), pine (*Pinus* spp.), acacia (*Acacia* spp.), cypress (*Cupressus* spp.), and Andean alder (*Alnus acuminata*) as the only native species (CHEC, 2007). Currently, the Reserve's vegetation is a mosaic of several small reforestations, grasslands and Andean forest in different states of ecological succession.

Since the Reserve was acquired by CHEC in 1968, the native forest has received relatively little human intervention, but small scale wood extraction and poaching still occur. The native forest around 2450 m of altitude (Fig. 2a) includes species such as *Fareamea flavicans*, *Guettarda hirsuta*, *Guarea kunthiana*, *Rhodostemonodaphne laxa* and *Ocotea* aff. *calophylla* (CHEC, 2007). The understory includes species



Figure 2 – Study zone at the CHEC Reserve. A. Andean forest, 2400 m of altitude. B. *Eucalyptus grandis* reforestation, 2400 m of altitude. Note the homogeneity in the physiognomy of reforestation compared with the Andean forest. The researcher in the pictures is 1.75 m tall.

such as *Hedyosmum bonplandianum*, *Alsophila erinacea*, *Chamaedorea linearis*, *Geonoma undata*, *Piper archeri*, *Miconia* spp., and *Critoniopsis ursicola*, among others. Also, there is a high frequency of vascular epiphytes of the families Gesneriaceae, Orchidaceae, Araceae and Bromeliaceae, as well as non-vascular plants (CHEC, 2007). We selected this forest since it was the largest patch of natural vegetation without intervention on the Reserve, covering an area of 145.75 ha (Figs. 1 and 2a).

The *Eucalyptus grandis* reforestation was planted in the 1960's decade (CHEC, 2007), and at the time of the study the trees had a height between 30 to 35 m, and there were usually 4 m between neighbouring trees, but occasionally there were 8 m. Its understory was composed of native plants with heights between 7 and 10 m (Fig. 2b). In particular, this reforestation was selected because it was the largest (92.93 ha) and oldest in the study site (Figs. 1 and 2b).

Photo-trapping of mammals

We sampled from September 2013 to February 2014. We employed four camera-traps Bushnell 8 MP Trophy Cam HD® at the same time in each type of forest, with 200 to 250 m space between consecutive cameras, and placed them 30 to 40 cm from the ground (Díaz-Pulido and Payán Garrido, 2012). We defined the location of the cameras after searching for signs of mammals, e.g., signs of foraging, claw marks, footprints, among others (Tobler and Powell, 2013); those sample points were fixed during the study. We synchronized time and date in the cameras, and programed them to take 20 second videos at intervals of five seconds in case the animal continued to be present in the camera's range and we considered each mammal record as a capture. We categorized captures as diurnal when taken between 08:00–18:00h, nocturnal between 19:00–06:00h, and crepuscular between 06:00–07:00h and 18:00–19:00h. During the fieldwork, sunrise and sunset occurred around 06:00h and 18:15h, respectively. Cameras functioned continuously throughout the study, i.e., a sampling effort of 752 camera-traps days in each type of forest.

Statistical analyses

We compared species richness in both forests using individual-based rarefaction curves (Colwell et al., 2012) and estimated total species richness with the non-parametric estimators of Chao2 and Jack1. We used Estimates 9.0 to obtain the rarefaction curves and the total species richness estimators after randomizing the samples 100 times (Colwell et al., 2012).

We evaluated the effect of *Eucalyptus* reforestation on the habitat use and activity pattern of non-volant mammals assemble using a logistic regression (Quinn and Keough, 2002; Lewis, 2004), with presence/absence of captures as a response variable, and hour (diurnal, nocturnal, crepuscular), type of forest and moon illumination as independent variables. We included illumination of the moon, since it has been reported that moon phase may affect activity patterns of nocturnal mammals probably affecting the perception of predation risk (Halle and Stenseth, 2000; Brown and Kotler, 2004). The predictors hour and moon illumination were included in the statistical analyses as categorical and continuous exploratory variables, respectively. To evaluate the goodness of fit of each model, we used the Hosmer-Lemeshow test (Quinn and Keough, 2002). We obtained the moon illumination data from the web site www.timeanddate.com. Finally, we used logistic regression models only on those species recorded more than 20 times.

To test the hypothesis of a potential effect on the activity patterns of competitor species sharing similar food resources, we quantified their coefficient of activity overlap Δ in both forests (Linkie and Ridout, 2011). We considered activity patterns as probability density functions (Linkie and Ridout, 2011), and used R version 3.2.3 to build the functions with the package *overlap* (Meredith and Ridout, 2016; R Core Team, 2015). The overlap coefficient ranges from 0 (no overlap) to 1 (complete overlap), and is strongly influenced by sample size. Thus, following Ridout and Linkie (2009) we used $\hat{\Delta}_1$, which is recommended for small sample sizes. We also calculated confidence intervals for $\hat{\Delta}_1$ after using 1000 bootstrap samples (Ridout and Linkie, 2009). Additionally, we used non-parametric Spearman correlations (Zar, 1999) to examine the possible relationship among the activity pat-

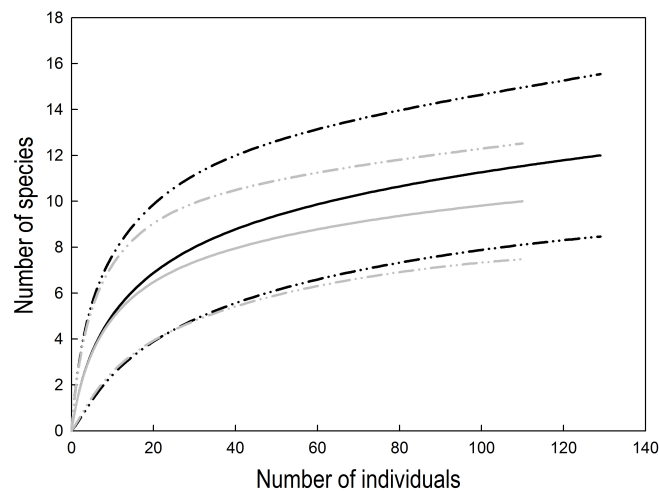


Figure 3 – Rarefaction curves of Andean forest (black line) and *Eucalyptus* reforestation (gray line) at the CHEC Reserve. The black and gray dashed lines represent the lower and upper confidence intervals of 95%. The intervals in both forest overlap, indicating that there were no differences in the number of species.

terns of those potential competitors using the percentage of records of each species per hour in each type of forest.

Results

Species richness

We analyzed 239 videos and recorded nine species in the *Eucalyptus* reforestation and 11 species in the Andean forest; *Puma concolor* (order Carnivora) and *Cuniculus taczanowskii* (order Rodentia) were the only species exclusive to the Andean forest. We did not find significant differences in the species number between the forests using rarefaction (Fig. 3), and this result was consistent with those of the estimators of total species richness (Andean forest, Chao 2 – 95% confidence interval [CI] = 12.49±52.62 and Jack 1 mean±SD = 14.98±1.71; *Eucalyptus* reforestation, Chao 2 – 95% CI = 10.18±31.95 and Jack 1 mean±SD = 11.98±1.39).

Activity patterns and habitat use

The nine-banded armadillo, *Dasyurus novemcinctus* (order Cingulata), the Andean white-eared opossum, *Didelphis pernigra* (order Didelphimorphia), the margay *Leopardus wiedii* (order Carnivora), the on-cilla, *Leopardus tigrinus* (order Carnivora), the mountain paca *C. taczanowskii*, and the cougar, *P. concolor*, were recorded almost exclusively at night (19:00–06:00h). The last four species were registered less than ten times and were not taken into account for the statistical analysis. The jaguarondi, *P. yagouaroundi* (order Carnivora), and the tayra, *Eira Barbara* (order Carnivora), were recorded during daytime, once and five times respectively, and we did not include them in the statistical analysis either. In all the logistic regressions, neither moon

illumination nor any of the interactions between factors were significant (Tab. 1), whereas type of forest and/or hour had a significant effect on the occurrence of four of the tested species (Tab. 1). We found a significant effect of the type of forest and hour on the presence of *D. novemcinctus* (logistic regression $p<0.01$; Tab. 1), and this armadillo used more the Andean forest (30 records) than the reforestation (10 records). There was a high overlap ($\hat{\Delta}_1=0.61$) in the armadillo's activity in both forests and it was active mainly throughout the night (Fig. 4). The South American coati, *Nasua nasua* (order Carnivora), and the red-tailed squirrel, *Sciurus granatensis* (order Rodentia), were mainly diurnal and crepuscular (Fig. 4). The type of forest and the hour affected the frequency of occurrence of *N. nasua* (logistic regression $p<0.01$; Tab. 1), using more the Andean forest (48 records) than the reforestation (23 records). For *N. nasua* there was high activity overlap ($\hat{\Delta}_1=0.7$) between the forests, but there were two peaks in the reforestation absent in the native forest (Fig. 4). The squirrel *S. granatensis* was significantly more active during the day (06:00–12:00h) than in other period and there was a high overlap in its activity pattern between both forests (Fig. 4 and Tab. 1). Activity of the little red brocket deer, *Mazama rufina* (order Artiodactyla), was not affected by any of the factors (logistic regression all $p>0.05$; Tab. 1), and it was predominantly nocturnal (Fig. 4). We recorded diurnal, nocturnal and crepuscular activity in the Andean coati (Fig. 4), *Nasuella olivacea* (order Carnivora), and its frequency of occurrence was influenced by both type of forest and hour (logistic regression $p<0.01$; Tab. 2). This coati used more the reforestation (43 records) than the native forest (10 records). Also, we found a high overlap in the activity of this species between both forests, $\hat{\Delta}_1=0.73$, but in the reforestation its activity appeared more spread throughout the night and morning.

Activity of species sharing similar food resources

Since *D. novemcinctus*, *N. nasua* and *N. olivacea* consume soil invertebrates, we evaluated the overlap of their activities in both forests. The species *N. olivacea* and *D. novemcinctus* were mainly nocturnal (Fig. 4), and there was a high overlap of their activities in both forests, (Fig. 5). The coati *N. nasua* was diurnal (Fig. 4), and showed low overlap of its activity with *N. olivacea* and *D. novemcinctus*, i.e., there was a clear temporal separation among them (Fig. 5). Additionally, we found negative correlations between the activities of *N. olivacea* – *N. nasua* and *N. nasua* – *D. novemcinctus* in the Andean forest, and between *N. olivacea* – *N. nasua* in the native forest (Tab. 2). The activity of *N. nasua* and *D. novemcinctus* was not correlated in the reforestation (Tab. 2).

Discussion

Species richness

We have previously reported 19 species of mammals for the CHEC Reserve between 2400 and 2700 m of altitude (Ramírez-Mejía and Sánchez, 2015). Of those species, 11 were registered also in this study at 2450 to 2550m of altitude, and we recorded a similar number of species in native forest and *Eucalyptus* plantation. Previous studies have also shown that *Eucalyptus* reforestations and native Neotropical forests present similar richness and species composition of mammals (Da Silva and De Almeida, 2002; Lyra-Jorge et al., 2008; Lantschner et

Table 1 – Summary of logistic regression models for five species of mammals at the CHEC Reserve. The p -value of the Hosmer lemeshow goodness of fit test (HLGOF) is included. A non-significative p -value of HLGOF denotes that the model fit well. (d.f.) Degrees of freedom. (NA) not applicable.

	<i>Nasua nasua</i>		<i>Nasuella olivacea</i>		<i>Dasyurus novemcinctus</i>		<i>Mazama rufina</i>		<i>Sciurus granatensis</i>		
	p -value	HLGOF	p -value	HLGOF	p -value	HLGOF	p -value	HLGOF	p -value	HLGOF	d.f.
Forest	<0.01		<0.01		<0.01		0.367		0.527		
Hour	<0.01	0.210	<0.01	0.053	<0.01	0.298	0.097	NA	<0.01	0.747	3
Moon	0.648		0.965		0.226		0.218		0.683		
Forest * Hour	0.647		0.025		0.543		0.952		0.993		
Forest * Moon	1		1		1		0.520		1		
Moon * Hour	0.375	NA	0.668	<0.01	1	NA	0.692	NA	0.548	NA	6
Forest * Hour * Moon	0.954		0.470		1		0.547		0.6		

Table 2 – Spearman non-parametric correlations of the activity of three soil forager invertebrate mammal species at the CHEC Reserve.

	<i>Nasua nasua</i>	<i>Nasuella olivacea</i>	<i>Dasylops novemcinctus</i>
<i>Nasua nasua</i>	–	$r_s = -0.707$; $p < 0.01$ Andean forest	$r_s = -0.737$; $p < 0.01$ Andean forest
<i>Nasuella olivacea</i>	$r_s = -0.596$; $p = 0.02$ <i>Eucalyptus</i> reforestation	–	$r_s = 0.471$; $p = 0.02$ Andean forest
<i>Dasylops novemcinctus</i>	$r_s = -0.303$; $p = 0.15$ <i>Eucalyptus</i> reforestation	$r_s = 0.486$; $p = 0.02$ <i>Eucalyptus</i> reforestation	–

al., 2012; Mendoza and Sánchez, 2014). In addition, some carnivores appear to use the reforestation more, which may be explained by the opportunistic habits of these species, suggesting they can adapt easily to new habitats created by humans (Da Silva and De Almeida, 2002; Lyra-Jorge et al., 2008). In a study site near ours, coatis and squirrels used Andean alder reforestations more than native Andean forests (Sánchez et al., 2008).

Habitat use and activity patterns

In our study site, although all mammal species were recorded in the Andean forest, we recognized differences in habitat selection by some species. Indeed, *N. nasua* and *D. novemcinctus* selected the Andean forest over the reforestation, whereas *N. olivacea* did the opposite. *Eucalyptus* reforestations may decrease understory plant diversity on the Andes (Murcia, 1997; Cavelier and Santos, 1999) as well as the biomass of edaphic arthropods (Mboukou-Kimbatsa et al., 1998; Pellens and Garay, 1999). Therefore, is likely that the differences in habitat selection by *N. nasua* and *D. novemcinctus* is product of differences in food availability between the forests examined, i.e., the Andean forest

may offer more food resources for *N. nasua* and *D. novemcinctus* than the reforestation. However, the separation in space and time between *N. nasua*, *N. olivacea* and *D. novemcinctus* may also be indication of an additional effect derived from the interactions among those species.

Our results confirmed that the activity pattern of the squirrel *S. granatensis* is mainly diurnal-crepuscular (Nitikman, 1985; Emmons, 1997; Gómez et al., 2005). Our findings on *M. rufina* activity are in agreement with those of Lizcano and Alvarez (2008), who mention that this deer is mostly active during the final hours of the afternoon until night. These results are also similar to the activity patterns described for *Mazama americana* in the Bolivian Amazon (Gómez et al., 2005). We have previously recorded the presence of cougars at the Reserve, including hunting episodes by this species during the daytime (at 12:57 h; Ramírez-Mejía and Sánchez, 2015). Thus, the activity of *M. rufina* during 17:00 and 23:00 h might be related to the activity of the largest predator in the study site (Ferrari et al., 2009), a hypothesis that needs further studies.

McBee and Baker (1982) and Reis et al. (2006) described *D. novemcinctus* as a nocturnal and crepuscular mammal, and this species may

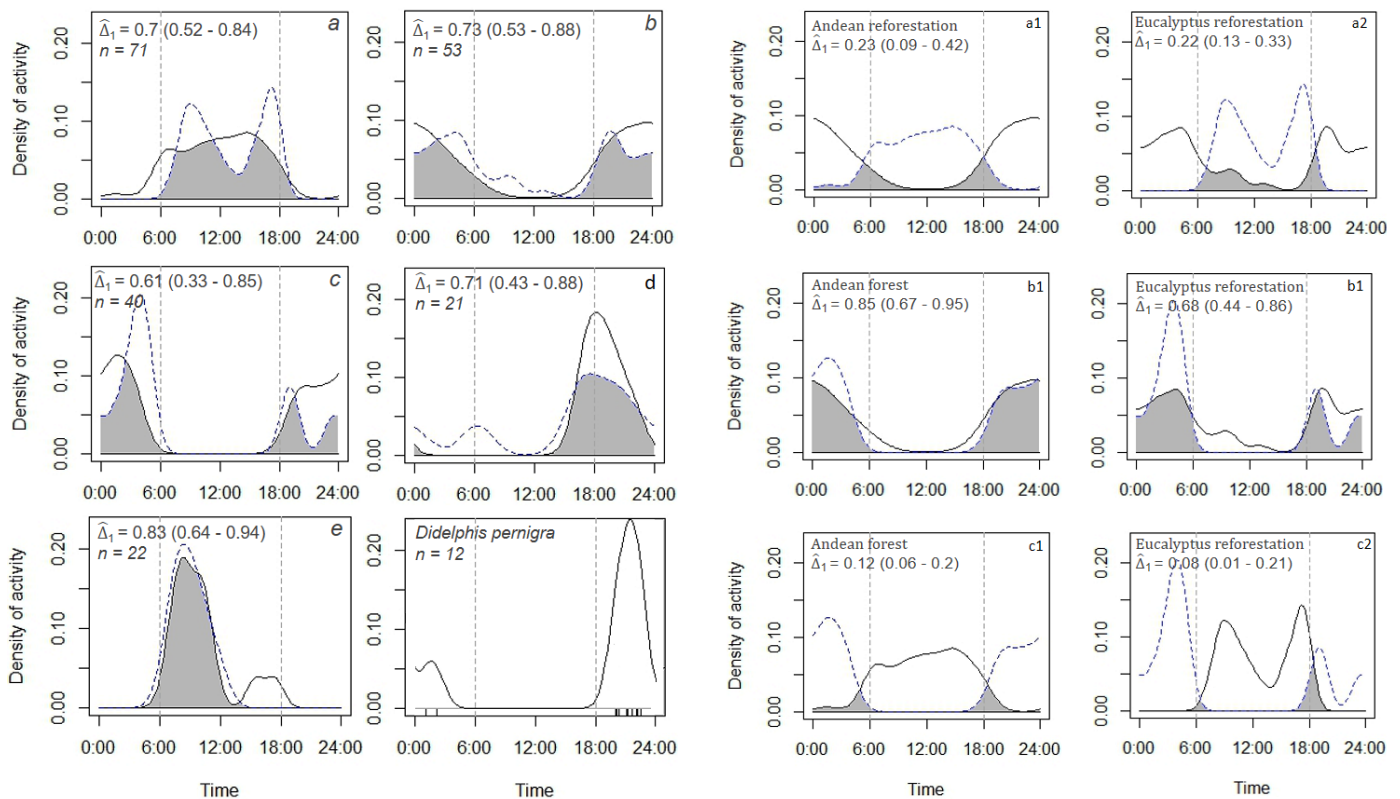


Figure 4 – Mammal activity in the Andean forest (solid line) and *Eucalyptus* reforestation (discontinuous line) at the CHEC Reserve. The shaded region denotes the activity overlap of each species between the two forests. a) *N. nasua*, b) *N. olivacea*, c) *D. novemcinctus*, d) *M. rufina*, e) *S. granatensis*. Overlap coefficients (Δ_1) and 95% confidence intervals (in parentheses) are presented. Discontinuous gray lines cutting abscissa axis show the sunrise and sunset times. Overlap coefficient was not calculated for *Didelphis pernigra* since there were not enough observations, but in the figure appears its main activity peak.

Figure 5 – Activity overlapping among soil-forager invertebrate species at the CHEC Reserve. The shaded region denote the activity overlap between species. Overlap coefficients (Δ_1) and 95% confidence intervals (in parentheses) are presented. Discontinuous gray lines cutting abscissa axis show the sunrise and sunset times. a1) and a2) show the activity overlap of *N. nasua* (discontinuous line) and *N. olivacea* (solid line) in the Andean and reforested forests, respectively. b1) and b2) show the activity overlap of *D. novemcinctus* (discontinuous line) and *N. olivacea* (solid line) in the Andean and reforested forests, respectively. c1) and c2) show the activity overlap of *N. nasua* (solid line) and *D. novemcinctus* (discontinuous line) in the Andean and reforested forests, respectively.

be active during daytime depending on temperature. Also, Norris et al. (2010) reported that *D. novemcinctus* is mainly active between 22:00–04:00h in Amazonian forest fragments greater than 1000 ha, whereas in smaller fragments it shows crepuscular activity. In our study, the armadillo was mainly nocturnal in both forests, but it was also recorded during twilight hours in the reforestation. This suggests that *D. novemcinctus* may adjust its activity patterns in response to modifications to its habitat. The activity of *N. nasua* was mainly diurnal and crepuscular, which is similar to the known activity for this species (Emmons, 1997; Gompper and Decker, 1998; Gómez et al., 2005; Reis et al., 2006). At the Talamancas Cordillera in Costa Rica, *Nasua narica* showed diurnal activity with two peaks between 07:00–08:00h and 14:00–15:00h (González-Maya et al., 2009), and this is similar to our observations of *N. nasua*. Finally, in the study site, *N. olivacea* was mainly nocturnal, but was also active during crepuscular and diurnal hours. These results differ substantially with those reported by Rodríguez-Bolaños et al. (2003), who studied the movements of one individual using telemetry in the Eastern Cordillera of Colombia, 2340–3340 m of altitude, and classified this species as strictly diurnal. Therefore, it is possible that the activity of the Andean coati varies depending on its geographical location or that a greater sampling effort was needed in the Eastern Cordillera to determine the Andean coati activity pattern. In addition, in our study site, interactions with other soil-foraging species may also affect the Andean coati's activity pattern.

The Andean coati, *N. olivacea*, and the nine-banded armadillo, *D. novemcinctus* are specialized to forage on soil invertebrates (McBee and Baker, 1982; Rodríguez-Bolaños et al., 2000), and although the South American coati, *N. nasua*, has been described as an omnivorous species (Gompper and Decker, 1998), almost half of its diet is based on soil invertebrates (Gompper and Decker, 1998; Alves-Costa et al., 2004; Hirsch, 2009). Therefore, it is reasonable to assume that these three species share food resources. Divergence on the spatial and temporal distribution of species in a biological community may allow for the coexistence among competitors sharing one or more resources (Brown, 1989; Kotler et al., 1993; Abramsky et al., 2001; Morris, 2005, 2011). In our study site that is exactly the case: we found a temporal and spatial segregation among the soil-invertebrate foraging species. For instance, *N. olivacea* used the reforestation more than the Andean forest and was mostly nocturnal. In contrast, *N. nasua* and *D. novemcinctus* used the Andean forest more than the reforestation, and were mainly diurnal and nocturnal, respectively. There is evidence of Neotropical felid assemblages where poaching influences the species distribution, and they also present different activity patterns, probably to reduce competition (Di Bitetti et al., 2010). Changes in habitat use and activity patterns by small mammals are strategies to avoid possible competitors and increase fitness (Morris, 1996; Abramsky et al., 2001; Kronfeld-Schor and Dayan, 2003). In the Negev Desert of Israel, studies with two gerbil species have shown that a large species of gerbil, *Gerbillus pyramidum*, forces a smaller species, *Gerbillus andersoni*, to shift its habitat preferences and activity patterns to spend more time in low quality patches (Kotler et al., 1993; Abramsky et al., 2001). We suggest that could be the case in the CHEC Reserve, and *N. olivacea* might be avoiding in space and time the foraging site more used by *N. nasua*, a bigger species, which through interference could relegate *N. olivacea* to use foraging patches of lower food quality such as the reforestation. Also, *D. novemcinctus* may be a more efficient competitor than *N. olivacea*, and as a result the competitor less apt is relegated to use the reforestation. These ideas need more detailed testing, but if that is the case, the reforestation established since 1960's at the study site, has contributed to facilitate the coexistence among the soil invertebrate foraging species.

Conclusions

As far as we know, our study is the first to analyze the responses of mammal activity and their interactions in relation with the establishment of a new forest type in the Andes. Our results suggest that the *Eucalyptus* reforestation is not a barrier for mammals and most of them can use both types of forests. However, the reforestation could influ-

ence the spatial distribution of species feeding on soil invertebrates. Thus, the reforestation appears to influence the coexistence of the species in the community. In a previous study, it has been recorded that coatis were capable of using Andean alder reforestations and they were more abundant there than in Andean forests in Manizales, although the authors could not differentiate with certainty tracks from *N. olivacea* and *N. nasua* (Sánchez et al., 2008). In this work we demonstrate, with the use of camera-traps, that habitat selection by the coati species may not be similar and they do not overlap in time and space. Our results also show the little knowledge available about the ecology of Andean mammals and the flexibility in their activity patterns. A clear example of that situation is the Andean coati, traditionally considered as a diurnal species (Rodríguez-Bolaños et al., 2000, 2003; Balaguera-Reina et al., 2009), but that during our study was mainly nocturnal.

Finally, in the Colombian Andes, the study of the impact of reforestations with exotic species has focused mainly in the evaluation of its effect on the abundance or taxonomic diversity (Murcia, 1997; Cavelier and Santos, 1999; Roncancio Duque and Estéves Varon, 2007; Sánchez et al., 2008). Our results show that the possible effects of the reforestations go beyond those on composition, richness or abundance of species and highlight the need to continue investigating how the reforestations affect the biological communities in the Colombian Andes. Of particular interest should be the species that could be more sensitive to the habitat modification by their limited range of movements as the small non-volant mammals. ☞

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