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# Effects of collared peccary (*Pecari tajacu*) exclusion on leaf litter amphibians and reptiles in a Neotropical wet forest, Costa Rica

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ABSTRACT

Peccaries are known to shape vegetation structure and create important breeding habitat for some pond-breeding amphibians in Neotropical forests. Because peccaries are also important agents of disturbance and microhabitat variation in the litter, peccary loss could have important consequences for litter amphibians and reptiles that depend entirely upon the litter for shelter, foraging and reproduction sites, and thermoregulation. However, very little is known about the effects of peccaries or their loss on litter amphibians and reptiles. We experimentally reduced peccary density in 20 × 50 m fenced exclusion plots ($n = 5$). We compared standing litter structure and amphibian and reptile abundance where peccaries were excluded to paired, open-forest control plots that had natural peccary densities. We encountered 16% more amphibian and reptile individuals in open control plots, and we encountered more juveniles of the most common anuran species in control plots than on peccary exclusions. Control plots had more compacted litter than peccary exclusion plots, indicating that peccaries alter the physical structure of the standing leaf litter in a way that promotes greater recruitment of juvenile anurans. Our results demonstrate that peccaries should be viewed not just as seed predators or ecosystem engineers for palms and pond-breeding amphibians, but also as important agents that affect leaf litter structure and abundance of terrestrial amphibians and reptiles. Peccary extirpation from overhunting or habitat degradation could have unexpected negative consequences for litter amphibians and reptiles, a diverse group already severely threatened by habitat loss, climate change, disease, and other anthropogenic effects worldwide.

## 1. Introduction

The world's tropical forests are under unrelenting pressure from human activities, resulting in the tragic loss of plant and animal species (Bradshaw et al., 2009). The goal of considerable ecological research has been to quantify how biodiversity loss affects ecosystem structure and function (Hooper et al., 2005; Hector et al., 2007; Thebault and Loreau, 2006; Isbell et al., 2011; Wardle et al., 2011). Many Neotropical rainforest mammals affect plant diversity and structure, yet habitat loss, diseases, pollution, and overhunting threaten mammal populations with extirpation (Bodmer et al., 1997; Peres, 2001; Grelle, 2005; Wilkie et al., 2011). Worldwide, many otherwise intact tropical forests are at least partially defaunated (Peres and Palacios, 2007; Michel and Sherry, 2012). The elimination or reduction of large mammals, especially frugivores and seed predators, poses a serious threat to biodiversity and complicates forest conservation (Wright et al., 2000, 2007; Terborgh et al., 2001; Wright and Duber, 2001; Bodmer and Ward, 2006; Peres and Palacios, 2007; Terborgh et al., 2008; Estes et al., 2011; Farwig and Berens, 2012).

Most research on mammal defaunation has focused on its effects on plant diversity and distributions. Tapirs and peccaries are important seed dispersers and predators (Galetti et al., 2001; Beck, 2005; Keuroghlian and Eaton, 2008) and structure plant communities through seed dispersal, seed predation, and seedling trampling (Beck, 2006, 2007; Clark and Clark, 1989; Fragoso, 1997; Wright et al., 2000; Guariguata et al., 2000; Roldán and Simonetti, 2001; Silman et al., 2003; Paine and Beck, 2007; Keuroghlian and Eaton, 2009). Defaunated and partially-defaunated forests may undergo shifts in plant diversity and density that, over time, could lead to changes in forest structure, ecosystem function, and regeneration (Dirzo and Miranda, 1990; Redford, 1992; Terborgh et al., 2001; Wright et al., 2007). Because partial defaunation may result in mesoherbivore release with increased consumption of seeds and seedlings, mammal loss might have positive or negative effects on seed fate and seedling recruitment (Dirzo and Miranda, 1990; Asquith et al., 1997; Wright et al., 2007). The effects of large mammals likely go beyond impacts on tropical

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forest vegetation to the entire ecosystem and we expect mammal defaunation to have strong direct and indirect effects on other animals in tropical forests as well (see Wardle and Bardgett, 2004).

Peccaries (collared, *Pecari tajacu*, and white-lipped, *Tayassu pecari*) are model systems to study the impact of large mammal loss from Neotropical forests. Peccaries are large, often abundant mammals that contribute substantially to the mammalian biomass in Neotropical forests, and have large home ranges (McCoy et al., 1990; Judas and Henry, 1999; Keuroghlian et al., 2004). Given the rapid rates of deforestation and the potential for overhunting by humans, the extirpation of collared and white-lipped peccaries is a possibility throughout the Neotropics (Beck, 2005; Beck et al., 2008; Gongora et al., 2011; Altrichter et al., 2012). The cascading effects of peccary extirpation on Neotropical forests would likely be substantial but only a handful of studies have investigated the effects of peccaries on other animals. For example, peccaries reduce bruchid beetle populations through consumption of palm fruits (Beck, 2005; Wright et al., 2007). White-lipped peccaries in the Amazon are considered to be ecosystem engineers because they create wallows that hold water longer into the dry season than do natural depressions. For many amphibians, wallows support reproductive activities and increase the anuran biodiversity of forests with peccaries (Gascon, 1991; Beck et al., 2010). Peccary loss would leave wallow-breeding anurans without access to critical reproductive habitat ("habitat split", Becker et al., 2009), and could result in population declines if pools are limited reproductive resources for forest frogs.

Peccaries alter soil and leaf litter through their foraging activities which include rooting, redistributing leaf litter, and trampling of soil and litter (Beck, 2005; Keuroghlian and Eaton, 2009). If ecosystem engineering by peccaries alters litter dynamics and the detrital food web, peccary loss could affect the organisms that depend on the leaf litter as primary habitat. The diverse leaf litter amphibians and reptiles of moist tropical forest use leaf litter for foraging, reproduction, and retreat (Scott, 1976; Lieberman, 1986; Heinen, 1992). Litter amphibians are dominated by direct-developing species in the families Eleutherodactylidae, Strabomantidae, and Craugastoridae that lack an aquatic tadpole stage; adults and juveniles co-occur in the leaf litter covering the forest floor. Litter amphibians and lizards are prominent among the top predators of invertebrates involved in the detrital food web (Whitfield and Donnelly, 2006) and litter-dwelling pit vipers are among the top predators in tropical forests. Litter amphibians and reptiles contribute substantially to the biomass of the detrital food web and represent important trophic links among the detrital, aquatic, and arboreal food webs (Donnelly, 1991; Whitfield and Donnelly, 2006). Litter amphibians and reptiles are sensitive to changes in microhabitat structure because the leaf litter ameliorates the effects of desiccation and daily thermal fluctuations (Scott, 1976; Heinen, 1992). If peccary foraging activities create sites for reproduction or thermoregulation, or promote the availability of arthropod prey, we would expect peccary loss to have a negative effect on amphibian and reptile populations. Over time, defaunation or partial defaunation of peccaries could affect the abundance and demography of litter amphibian and reptile populations.

To determine if collared peccary loss can affect litter amphibian and reptile populations, we compared the relative abundance and community assembly of litter reptiles and amphibians in plots where peccaries were experimentally excluded and open control plots that allowed access by peccaries. Because litter amphibian and reptile populations depend on litter for habitat and food, we also examined correlates of litter quality (standing litter mass, complexity, depth, and moisture), and understory vegetation density.

## 2. Methods

### 2.1. Study site

Our research was conducted at the La Selva Biological Station (hereafter La Selva), located in the Caribbean lowlands of northeastern Costa Rica in Heredia Province (10°26′N, 84°00′W). The primary forest is described as lowland wet forest, located between 35 m and 137 m asl, and receives ~4 m of precipitation annually with a mild dry season from January to April. See McDade and Hartshorn (1994) for a complete description of the site. La Selva is home to a robust collared peccary population. Collared peccaries weigh 17–35 kg (Emmons, 1997; Desbiez et al., 2009) and at La Selva can form groups of up to 30 individuals (K. Reider, pers. obs.). Collared peccary density estimates for La Selva are 13–15 individuals/km$^2$ derived from radio-telemetry of a few peccary groups (Torrealba-Suárez and Rau, 1993). Estimates from long-term camera trapping show that collared peccary relative abundance is 3–4 times higher at La Selva than the more seasonal and isolated forests at Barro Colorado Island and Gigante, Panamá (N. Michel, personal communication). White-lipped peccaries (*T. pecari*) were extirpated from the region by the mid-1900s (Timm, 1994).

### 2.2. Experimental design

We used five mammal exclusion plots established in June 2000 in primary forest (Appendix I in Supplementary Material). Since March 2009, the exclusion fences have been maintained to prevent access to plots by peccaries. The plots are 20 m × 50 m and are surrounded by a 2 m high chain-link fence which is expected to exclude large, non-arboreal and non-volant mammals (e.g., deer, tapir, peccaries). Deer and tapir density at La Selva is very low (Timm, 1994) and we did not observe deer or tapir sign near the plot locations during the 10 months of our study. Small terrestrial mammals like agoutis and armadillos have access to all exclusion plots through openings at the soil surface that extend under the fences. To compare the effects of collared peccary presence and absence, we paired exclusion plots with five control plots, which are completely open. All control and exclusion plots were located 15–25 m from each other on the same soil type to avoid confounding effects of soil on the litter amphibians and reptiles (Watling, 2005), on level ground, and at least 50 m from streams. All data were collected from randomly determined points. Measurements on controls and exclusions were collected by the same observer on the same day. No data were collected within 1 m of the fences inside the exclusion plots to avoid fence effects. All plot locations will hereafter be referred to by their La Selva trail acronyms (LOC2300, LOC2650, LS, SHO, and SSO).

### 2.3. Mammal activity

To ensure that peccary activity and use of area inside exclusion plots was lower than control plots, we deployed a pair of motion-activated cameras (Bushnell Trophy Camera Model 119405) in the LOC2300, LOC2650, SHO, and LS control and exclusion plots in July–August 2010, and June–July 2011. The cameras failed when they were placed in the SSO control and exclusion, and we were not able to redeploy cameras there because of time constraints. We placed the camera traps simultaneously inside peccary exclusion plots at tunnels under fences, and outside the fences on control plots. Cameras were attached to trunks of trees at a height of approximately 50 cm. The cameras were set to take three photographs after each trigger event, with a 1 min. delay between trigger events. When individuals appeared in multiple photos of the three taken, they were only counted once. Individuals may have been