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Original investigation

Use of early and late successional forest patches by the endangered Lowland tapir *Tapirus terrestris* (Perissodactyla: Tapiridae)

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ABSTRACT

Large herbivores play crucial ecological roles, affecting the structure and function of terrestrial ecosystems. Their effect, however, depend on how they select plants and vegetation patches for foraging. At the landscape scale, succession is one of the processes that should generate vegetation patches with different nutritional quality, affecting selection by herbivores. Earlier successional stages should be preferred as they are dominated by plants with nutritious and palatable leaves. Here, we investigate if the Lowland tapir prefers early compared to late successional forest patches, aiming at contributing to the understanding of the ecological role of the largest terrestrial South American herbivore, and to conservation strategies for this endangered species. We sampled 12 vegetation patches varying in successional stages across a 20.000-ha continuously-forested landscape in the Brazilian Atlantic Forest, recording tapirs through standardized camera trap and track surveys, and quantifying vegetation structure and treefall gaps. Whereas the number of individuals using each patch was not influenced by successional stage, intensity of use was higher in patches in earlier successional stages, in particular patches with higher density of smaller trees and higher cover of treefall gaps. Although inferences on the effects of tapir on plant community depends on future, smaller-scale studies, our results suggest herbivory by tapirs affects forest regeneration, potentially contributing to the maintenance of plant diversity. Results also point out to the potential of mosaics encompassing old-growth and secondary forests for the conservation of the Lowland tapir.

Introduction

Large herbivores play crucial ecological roles, affecting the structure and function of terrestrial ecosystems. Through herbivory, they influence plant germination and growth, composition and diversity of plant communities, and ecosystem function, such as nutrient cycling, carbon storage and primary production (Danell et al., 2006). However, the effects of large herbivores depend on how they select plants or parts of plants for feeding, and areas or patches for foraging. According to the optimal foraging theory, foraging strategies result from individuals maximizing the net rate of energy intake, depending on the availability and quality of food and environmental heterogeneity. Thus, food resource selection is associated with the balance between energy gain and energy expenditure with the search, capture and ingestion of food (Stephens and Krebs, 1986).

Large herbivores are faced with a wide variety of plants species and plants parts that differ in their nutritional and defense properties (Coley and Barone, 1996), taking foraging decisions on a range of spatial (from bites to landscapes) and temporal (from seconds to years) scales (Senft et al., 1987). They select plants, feeding stations or micro patches within plant communities, plant communities or large vegetation patches within landscapes, and, in the case of nomadic or migratory species, landscapes within regions. At the landscape scale, one of the processes that can generate vegetation patches with different nutritional qualities for herbivores is vegetation succession, which leads to changes in vegetation composition associated with varying plant strategies (McCook, 1994).

Compared to late sucessional communities, plant communities in earlier sucessional stages are dominated by species that present higher growth rates and dispersal ability, but shorter life cycles, lower heights, lower tolerance to grow under the shade of other plants (McCook, 1994), and invest less in defense against herbivory (Herms and Mattson, 1992). Generally, early successional plants produce short-lived leaves with higher specific leaf area, higher nutrient concentrations and higher photosynthetic rates (Reich et al., 1992; Poorter and Bongers, 2006). These thin and

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tender leaves, with higher water content and lower lignin concentration, are preferred by herbivores in tropical forests (Poorter et al., 2004). Therefore, earlier successional stages should represent vegetation patches with higher palatability for herbivores (Coley and Barone, 1996), and this has been well established for insects. For instance, in early successional stages, 93% of the insect community consists of herbivores and this proportion decreases as succession progresses (Schulze et al., 2005). Furthermore, herbivory rates by insects are higher for light-demanding plants compared to shade-tolerant plants (Ruiz-Guerra et al., 2010), declining with species successional position (Poorter et al., 2004).

Although the impacts of large mammalian herbivores on vegetation regeneration is widely acknowledged (Danell et al., 2006), few studies have focused on the effects of successional stages on patch selection by these species. In boreal and temperate forest, these large herbivores do indeed select early successional stages for foraging (Pastor and Naiman, 1992), including treefall gaps (Kuijper et al., 2009). In tropical forests, however, studies on plant and patch selection by large mammalian herbivores are limited. Nonetheless, the selection of early successional stages for foraging may explain the commonly observed pattern of higher abundance of ungulates in secondary compared to primary tropical forests (Parry et al., 2007).

Here, we investigate if the Lowland tapir (*Tapirus terrestris*) prefers early compared to late successional forest patches, aiming at contributing to the understanding of the ecological role of the largest terrestrial South American herbivore, and to conservation strategies for this endangered species. By sampling 12 vegetation patches across a 20.000-ha continuously-forested landscape in the Brazilian Atlantic Forest, we tested the hypothesis that tapirs use more intensively vegetation patches in earlier succession stages and/or with more treefall gaps, as expected by the optimal foraging theory.

Material and methods

Study species

The Lowland tapir (*Tapirus terrestris*) is the largest terrestrial mammalian herbivore in South America. They are solitary browsing ungulates that feed on a wide variety of species and plant parts (Hibert et al., 2011; Tobler, 2002). Although there are many studies on the diet of the Lowland tapir, the vast majority is based on the identification of seeds in feces and stomach contents (e.g. Bodmer, 1990). However, most of the ingested food is composed of fibers and leaves (Hibert et al., 2011; Tobler, 2002) of tree species (Simpson et al., 2013). Thus, the Lowland tapir should play a key ecological role in structuring plant communities via herbivory given their body size (Padilla and Dowler, 1994), relatively large home ranges (Cabrera et al., 2016), high percentage of activity time (∼90%) spent on foraging (Medici, 2010), and the large amount of consumed food (Clauss et al., 2009).

The number of studies on the use and selection of vegetation patches by tapirs, however, is considerably lower than those dedicated to their diet. Some studies have addressed habitat characteristics, such as slope, water availability, and vegetation types (e.g. Salas, 1996; Tobler, 2002). Some of them indicate that *T. bairdii* and *T. terrestris* frequently use secondary forests and treefall gaps (Foerster and Vaughan, 2002; Naranjo, 1995; Salas, 1996). In contrast, Medici (2010) noted that *T. terrestris* avoids secondary areas, preferring riparian and tall mature forests in the Atlantic Forest, and other studies also reported that primary forest was more frequently used by *T. pinchaque* (Lizcano and Cavelier, 2000). Nevertheless, none of these studies was specifically designed to compare the use of forest patches in different successional stages by tapirs.

Study area

The study was conducted in an area of about 20,000 ha within the largest tract of continuous Atlantic Forest in Brazil (Fig. 1), located in the plateau of Serra do Mar, a coastal mountain range in the State of São Paulo covered by dense ombrophilous forest, at about 900 m of altitude. The area is situated within one of the most humid regions in Brazil. Despite the seasonal variation in temperature and rainfall – January is the month of highest temperature and precipitation (average 22 °C and 246 mm) and July the coldest and driest month (average of 15.1 °C and 46 mm) – there is no hydric deficit (Peel et al., 2007), and the forest is evergreen.

The 20,000-ha area encompasses part of a protected area (Serra do Mar State Park) and neighboring forested areas in private land, and it is covered mainly by old-growth forest that has not been clear-cut in the past, but may have suffered selective logging of the Juçara palm *Euterpe edulis*. Interspersed within the old-growth forest, there are patches of secondary forest that regenerated after clear-cutting or intense logging in the past.

The study area is home to a significant population of *T. terrestris*, and tapirs are often seen in the study area. However, the species is considered extinct in 14% of its original range, including extensive areas in Argentina, Brazil, Colombia and Venezuela. In the Atlantic Forest, the species is currently absent in many remnants outside protected areas (Canale et al., 2012).

Sampling design

Within the 20,000-ha study area, we stablished 12 sampling sites (Fig. 1), six located in forest patches in earlier successional stages (i.e. patches of secondary forest that regenerated after clear-cutting or intensive logging in the past) and six in patches of later succession stages (old-growth forests that were not clear-cut or intensively logged) (see Appendix S1 in Supplementary material). Forest patches in different successional stages were first identified from satellite images (Google Earth ™ Digital Globe/2010 Geoeye) and aerial photographs, and, subsequently, visited to check the successional stage in the field. We chose the largest available patches (minimum size 12-ha) with no sign of hunting activity found in the field, which were structurally connected to continuously-forested areas (with no paved roads, eucalyptus plantations or human settings isolating them) and at least 1000 m a part from each other (Fig. 1). All patches were accessible on foot, being at most 1000 m from dirty roads.

In each sampling site we established two 320-m long perpendicular transects, marked every 20 m from the central point (33 sampling points in total), defining 32 20-m long sampling sectors (Fig. 1).

Use of forest patches by Tapirus terrestris

At each of the 12 sampling sites, we carried out six sampling sessions between March and August 2011. In the first sampling session, each site was sampled for seven nights (excepting one sampled for 10 nights), and in the remaining five sessions, for four nights (excepting one sampled for eight nights in the third session). The interval between sampling sessions within the same site ranged from 16 to 27 nights.

In each sampling session, each site was visited twice. On the first visit, two camera traps were installed in front of each other in the central point, and transects were inspected to erase tracks of *T. terrestris*. At the end of each session, the sites were revisited to uninstall the camera traps and map the new tracks found within 1.5 m from both sides of the transects.

For each site, we quantified (1) capture history along the six sampling sessions (presence-absence of tapir in each session as