Ecological Indicators 57 (2015) 164–170

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Variations in dung beetle assemblages across a gradient of hunting in a tropical forest

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ARTICLE INFO

Article history:
Received 14 November 2014
Received in revised form 17 April 2015
Accepted 20 April 2015

Keywords:
Body size
Dung beetles
French Guiana
Hunting
Mammals
Trophic cascades

ABSTRACT

Populations of large mammals are severely depleted by hunting in tropical forests, with direct effects on plant regeneration. But indirect consequences on commensal taxa depending on them for food resources, like coprophagous beetles, are less documented. Cascading effects of species loss across Scarabaeinae are expected, with likely significant negative implications for ecosystem functions. We examined dung beetle assemblages using pitfall traps at three rain forest sites in French Guiana ranging from intact mammalian fauna (Nouragues) to moderate (Kaw) and heavy (Matoury) defaunation. The site with the most depauperate mammalian fauna showed significantly lower dung beetle species richness than the two other two sites, which were not different from each other. Mean abundance and biomass per trap were not different across sites whereas community composition strongly differed among sites. A positive correlation was observed between body size and the individual contribution to dissimilarity between Nouragues and Kaw. The species contributing the most to dissimilarity were large. By contrast, one medium-sized species, dominant in Matoury, contributed the most to dissimilarity between Matoury and other sites. Diurnal genera of large tunnellers showed a higher diversity and abundance in Nouragues compared to other sites, whereas a nocturnal genus showed no differences. Large rollers were more abundant in Kaw compared to other sites. None of the groups of small beetles but one were affected by defaunation. Our results suggest that loss of large mammal populations affects dung beetle assemblage structure and causes decreasing abundance or disappearance of large tunnellers species that have a major impact on several dung beetle-mediated ecological processes.

1. Introduction

Human disturbances induce biodiversity loss through habitat degradation and overexploitation. Research has focused on the direct causes of extinction such as hunting or forest fragmentation because the effects are easy to predict (Barlow et al., 2006; Brook et al., 2008). But besides direct effects, human perturbation may also have indirect effects which, in complex co-evolved systems, can lead to a cascade of extinctions (Rezende et al., 2007). The decline or loss of a keystone species or a species group can provoke local extinction of dependent taxa, with dramatic implications for community structure associated with disruption of ecosystem functioning (Larsen et al., 2005; Eklof and Ebenman, 2006). Overhunting has caused severe declines or local extinctions in many medium and large-sized rain forest mammals, increasing concern about the consequences for plant communities, for example through zoochory (Stoner et al., 2007). However, another cascade effect of defaunation is the secondary extinction of dependent groups and the related ecological functions.

Scarabaeine dung beetles rely on mammalian dung as an adult and larval food resource (Hanski and Cambefort, 1991) and are likely to suffer from a shortage of dung when mammals are depleted (reviewed by Nichols et al., 2009). Impoverishment of dung beetle communities implies a disruption in the important ecological services that dung beetle provide to the ecosystem, such as recycling of nutrients into the soil, soil bioturbation, parasite and pathogen control and secondary seed dispersal (reviewed by Nichols et al., 2008). Dung beetles are sensitive to forest disturbance and have been widely used as an indicator group related with ecological functions (Barragán et al., 2011; Braga et al., 2013; Edwards et al., 2013). But the specific effect of mammal abundance remains poorly documented. Several studies showing the effects of tropical forest fragmentation partially attribute the decline in the dung beetle fauna to an impoverished mammal assemblage (Klein, 1989; Estrada et al., 1993, 1999; Vulinec, 2000; Andresen, 2003; Feer and Hingrat, 2005). However, it is difficult in this

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http://dx.doi.org/10.1016/j.ecolind.2015.04.034
1470-160X/

context to speculate on relationships between mammals and beetles because fragment area and isolation influence both groups (Nichols et al., 2007a,b). The determination of the relative importance of landscape and dung resource availability in structuring dung beetle communities along a gradient of deforestation suffered from the same problem (Gardner et al., 2008; Harvey et al., 2006). Yet, Barlow et al. (2010), by examining the potential conservation value of forest strips for Amazonian dung beetles, showed a positive relationship between large mammal activity and dung beetle abundance independent of isolation and forest structure.

Only two tropical forest studies have documented the effects of hunting and decline of mammal fauna on dung beetle communities by comparing similar continuous forest sites along a gradient of selective defaunation. In Panama, Andresen and Laurance (2007) reported that species richness and abundance of dung beetles declined with decreasing overall mammal abundance. Culot et al. (2013) recently reported in the Brazilian Atlantic forest that dung beetle abundance increased but species richness and body size decreased with declining mammal biomass. In addition, they highlighted that the composition of the mammal community, independently of overall mammal biomass, structured the dung beetle community.

Here we report changes in dung beetle communities across a gradient of mammal abundance and richness induced by hunting pressure. All study sites presented similar forest structure and microclimatic conditions, minimizing thereby the effect of habitat. We asked (1) whether changes in mammal fauna affect overall dung beetle species richness and abundance, (2) what is the pattern of community turnover between sites, (3) what are the relationships between the contribution of species to community turnover and body size and (4) how species abundance changes across sites within different genera and tribes.

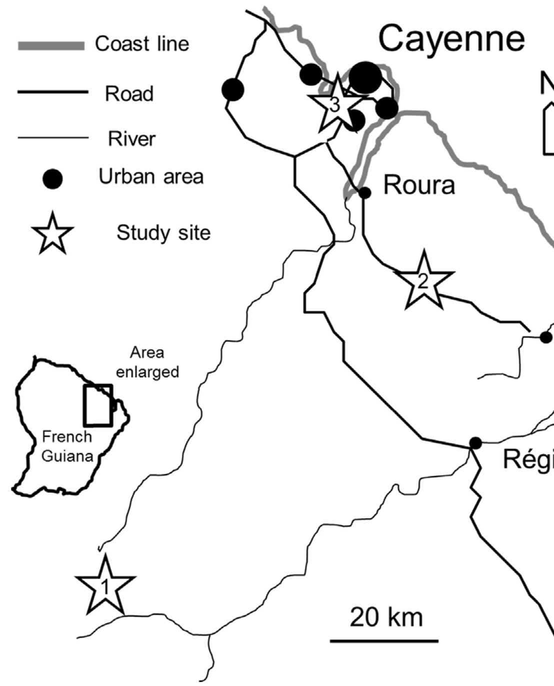

Fig. 1. Study sites in French Guiana: 1. Nouragues National Nature Reserve (protected), 2. Montagne de Kaw (intermediate disturbance), 3. Mont Grand Matoury National Nature Reserve (heavy disturbance).

2. Methods

2.1. Study area

We sampled dung beetles in three sites that show a gradient of hunting pressure (Fig. 1). The most protected forest site is located nearby Nouragues Research Station at the ‘inselberg’ site (hereafter Nouragues) (4°05′ N, 52°40′ W), in the 105,800 ha Nouragues National Nature Reserve, French Guiana (Charles-Dominique, 2001). The climate is of equatorial type and is characterized by one dry (August–November) and one wet season (December–July), with a slight decrease in precipitations around March. The average annual rainfall is 2690 mm (2001–2011), and daily temperatures range between 20 and 35 °C, with an average value of 27 °C (2003–2011, Nouragues Research Station). The elevation ranges from 60 to 200 m above sea level. The site is located 100 km upriver from the nearest settlement, the town of Régina (830 inhabitants).

Montagne de Kaw (hereafter Kaw) is located 70 km north-east of Nouragues. The seasonal distribution is the same as at Nouragues, but with higher mean annual rainfall (4099 mm). It is a 40-km-long ridge, reaching 309 m in elevation, and located 45 km from the capital town Cayenne and adjacent to the village of Roura, (2800 inhabitants). A road following the ridge is used by hunters to access numerous forest tracks. The sampling site Amazone Nature Lodge (4°33′ N, 52°12′ W) is situated between Kaw-Roura National Nature Reserve and Trésor Regional Nature Reserve. Commercial logging occurs outside the reserves. The sampling site is on the upper slope, which is part of the same forest landscape unit as Nouragues (Richard-Hansen, 2010).

Mont Grand Matoury National Nature Reserve (hereafter Matoury) is located 20 km to the North-West of Kaw, in the vicinity of the town of Cayenne (4°51′ N, 52°21 W). It is an isolated hill, reaching 234 m. The mean annual rainfall is 3686 mm. The habitat is moderately disturbed primary forest on the hill, surrounded by old secondary forest on the slopes. It is less than a kilometer away from an inhabited place and the forest is almost completely surrounded by anthropized land. The site was granted national nature reserve status in 2006 (area 2129 ha).

The habitat at the three sites is 20–35 m high forest with closed canopy and open understorey (Poncy et al., 1998; Ek et al., 2000; INPN, 2014). Air humidity and temperature recorded at each study site at 0.8 m high during a minimum of two periods of sampling presented very similar values (Feer unpublished). Average maximum humidity varied between 95.7% and 97.4% with pairwise differences smaller than 1.7% and minimum varied between 83.6% and 86.1% with pairwise differences smaller than 2.4%. Average maximum temperature varied between 26.2 °C and 28.6 °C with pairwise difference smaller than 2.4 °C and minimum varied between 22.3 °C and 25.2 °C with pairwise difference smaller than 2.8 °C. Larger microclimate changes were recorded with warmer and drier condition under lower and discontinuous canopy, such as at forest edges or after disturbance (Feer, 2008; Harper et al., 2005), negatively affecting species richness and abundance of the dung beetle assemblages (Feer, 2008).

2.2. Mammal fauna

At Nouragues the fauna is intact, being effectively protected from hunting due to permanent presence of researchers and/or staff. Although parts of Kaw are protected, the forest is submitted to moderate levels of hunting (O. B. *personal observation*; C. Richard-Hansen, *personal communication*). At Nouragues and Kaw, relative and absolute densities of mammals were estimated in 2000 and 2011 along two-kilometer-long line transects (Boissier, 2012). Large-bodied mammals like atelid monkeys and Ungulates exhibited strong signs of decreased abundance at Kaw relative to Nouragues (mean encounter rates along linear transects, 0.03 contact per km versus 0.67, 0.04 versus 0.47, respectively; Boissier, 2012). These species are known to be sensitive to harvesting and