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Landscape structure and composition define the body condition of dung beetles (Coleoptera: Scarabaeinae) in a fragmented tropical rainforest

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ABSTRACT

Environmental disturbance generates changes in local abiotic and biotic conditions, which affect the physiological condition of the organisms. However, most of the studies dealing with environmental disturbance have focused only on species diversity, and often ignore the species' health to evaluate habitat quality. Recently, through tools that evaluate the body condition of individuals, some studies have demonstrated that it is possible to know how species respond to environmental changes. In this study, we evaluated the effect of local and landscape parameters on different indicators of body condition and abundance of three dung beetle species in a fragmented Tropical rainforest in Mexico. We measured beetle's body size and three indicators of physiological condition (body dry mass, lipid and muscle mass) in 15 sites with different vegetation configuration. In general, abundance, body size and physiological condition of all species were sensitive to different landscape features. *Onthophagus rhinolophus*, a species typically found in conserved forest, unexpectedly showed a positive relation of body condition with landscape diversity and amount of edge, and the presence of altered sites remnants favored its body dry mass, muscle mass and body size. Nevertheless, *Onthophagus batesi* and *Canthon cyanellus*, mostly found in disturbed areas, exhibited better body condition when there were conserved habitats nearby. Therefore, we showed that *O. rhinolophus* is a sensitive species supporting reduced levels of habitat disturbance, while *O. batesi* and *C. cyanellus* are tolerant species that need conserved forests nearby. We highlight the importance of understanding the effect of environmental disturbance on the species' body condition in order to maintain not only abundant, but also healthy populations of wild animals in fragmented forests.

1. Introduction

Environmental disturbances, such as deforestation, hunting and land-use change, generate modifications in the structure of natural landscapes, consequently shifting both abiotic (e.g. temperature, wind, luminosity) and biotic (e.g. species composition, vegetation coverage, litter) conditions (Saunders et al., 1991; Ezcurra, 2016). As a consequence of landscape transformation, species that are not able to tolerate the new environmental conditions may disappear, whereas others may increase their populations (McKinney and Lockwood, 1999; Tabarelli et al., 2012). Changes in population or community parameters (i.e. abundance, species richness and composition, diversity) may hide the current health status of the biodiversity from disturbed sites, but measurements of individual physiological condition present immediate responses to environmental change that determine individual fitness and can help to understand the environment where a species can successfully develop (Cooke et al., 2013). Physiological measurements (e.g. muscle mass, lipid mass) allow to identify cause-and-effect relationships, allowing to generate management models able to predict how species respond to environmental change (Carey, 2005; Cooke et al., 2013). However, few studies have evaluated the physiological condition of individuals in disturbed sites, and these studies have mainly focused on vertebrates (see Ostman et al., 2001; Rimbach et al., 2013; Deikumah et al., 2015; Scheffers et al., 2016), showing that environmental factors favoring abundance do not necessarily favor the establishment of healthy individuals in good body condition. Notwithstanding, a recent work has been conducted with dung beetles (Coleoptera: Scarabaeinae), comparing physiological condition and relative abundance before and after logging activities in the Amazon forest (França et al., 2016). Interestingly, this study present contrasting responses of dung beetle abundance and physiological condition facing human activities.

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Body condition, in terms of nutrient storage, comprises amounts of energy reserves related to the physiological condition of animals, which can be measured directly (e.g. fat and muscle mass) or indirectly (e.g. body size) (Contreras-Garduño et al., 2008; Moya-Laraño et al., 2008; González-Tokman et al., 2011; França et al., 2016). Since body condition is sensitive to local environmental characteristics, such as food availability and habitat quality, this parameter may be used as effective proxy of health status (Ostman et al., 2001; Johnson, 2007). Landscape fragmentation may affect positively or negatively the body condition of the animals, depending on the species (Johnstone et al., 2010; Deikumah et al., 2015). Anthopogenic habitats surrounding natural landscapes (i.e. matrix) may influence the native communities (Nichols et al., 2007; Franklin and Lindenmayer, 2009). For some species, some landscape elements (e.g. live-fences, agricultural systems) may act as natural corridors for the native communities, thus some species from undisturbed areas can spread through disturbed sites (Nichols et al., 2007; Franklin and Lindenmayer, 2009). Species inhabiting antrophogenic matrices present contrasting body condition responses to landscape structure. For example, homogeneous matrices and small patches affect carabid beetles, resulting in individuals with reduced body size and fat reserves (Ostman et al., 2001). Similarly, landscapes with inhospitable matrices present bird species with lower masses of subcutaneous fat (Deikumah et al., 2015). As a consequence of reduced body condition, individual survival and fitness can be low (Chastel et al., 1995), which in a longer term may impact the population dynamics.

Many studies that analyze the disturbance of landscapes focus on understanding which environmental factors may affect the structure and functioning of natural communities (Saunders et al., 1991; Fahrig, 2003; Nichols et al., 2007). Size and shape of the forest remnants are descriptors commonly used to analyze how habitat configuration affects the diversity of natural communities. Usually larger and more regular fragments are associated with more conserved and diverse systems (MacArthur and Wilson, 1967; Laurance and Yensen, 1991; Bierregaard et al., 1992; Pardini et al., 2005; Portela and Santos, 2014). In addition, the matrix configuration may affect the distribution and movement of organisms through the modified sites (Pardini et al., 2005; Arellano et al., 2008; Lizée et al., 2012). In fact, native vegetation within the matrix, as natural corridors and small fragments, are also important, acting as stepping-stones, allowing the movement of individuals through the fragmented landscape (Pardini et al., 2005). Furthermore, the presence of different types of vegetation covers within matrices may favor the maintenance of natural communities (Pryke et al., 2013; Boscolo et al., 2017). The higher heterogeneity of landscapes may present modified habitats with abiotic conditions that are, in some way, similar to undisturbed sites, with greater resource diversity when compared to homogenous landscapes (Benton et al., 2003; Nichols et al., 2007; Pryke et al., 2013; Boscolo et al., 2017).

To obtain the most reliable responses of the ecological communities to habitat disturbance, some taxa such as birds and insects are considered good indicators, due to their sensitivity to environmental change (Gardner et al., 2008a,b). A remarkable example of organisms that quickly respond to habitat modifications and are successfully used as biological indicators are dung beetles (Favila and Halffter, 1997). Dung beetles are mainly copro-necrophagous (Hanski and Cambefort, 1991) and given the dependence on vertebrate dung and carrion, their communities are impoverished in sites that have lost vertebrates, mainly mammals (Nichols et al., 2009; Culot et al., 2013). In addition, dung beetle assemblages are composed by species with different habitat ranges, and some forest species are unable to cross modified habitats, or may just occupy specific elements of the disturbed matrices that are less harsh (e.g. habitats that present characteristics similar to the native forests) (Larsen et al., 2006; Gardner et al., 2008b; Nichols et al., 2007; Scholtz et al., 2009). As a consequence, some species are limited to forest remnants, whereas others successfully occupy disturbed and fragmented habitats (Klein, 1989; Nichols et al., 2007; Scholtz et al., 2009).

Both habitat loss and fragmentation drive a series of environmental changes that may impact on the suitability of habitats for dung beetles. In fragmented landscapes, these factors include the canopy cover, connectivity between fragments, forest cover, landscape heterogeneity, and edge effect of the remnants (Escobar, 2004; Nichols et al., 2007; Scholtz et al., 2009; Díaz et al., 2010). Despite some of these factors have been suggested as determinants of dung beetle diversity (Halffter and Arellano, 2002; Scholtz et al., 2009; Díaz et al., 2010), Nichols et al. (2007) highlight the importance of considering the landscape as a whole for the maintenance of dung beetle assemblages, including the vegetation elements surrounding the forest remnants. For example, the natural forest cover has been pointed as the most important attribute to maintain dung beetle diversity (Halffter and Arellano, 2002), although some studies show that conditions other than forest cover (i.e. forest structure, type of anthropogenic matrix or ecological restoration) are also important (Audino et al., 2014).

In the present study, we evaluated the effect of local and landscape parameters of a fragmented forest on the body condition and the abundance of three tropical dung beetle species that are contrasting in their preferred habitats. In particular, we compared body size, body dry mass, muscle mass, lipid content and abundance in three species of dung beetles present in sites with different degree of disturbance. Whereas one species is mostly found in conserved forests (*Onthophagus rhinolophus*) (Halffter et al., 1992; Carrillo-Ruiz and Morón, 2003), the other two species (*Canthon cyanellus* and *Onthophagus batesi*) successfully occupy both forests and open areas (Halffter et al., 1992; Kohlmann and Solís, 2001; Solís and Kohlmann, 2002). Thus, we expected *O. rhinolophus* to be benefited by the presence of primates, as they are considered important resource providers for the maintenance of dung beetle assemblages on the Neotropical region (Estrada et al., 1999; Jacobs et al., 2008; Nichols et al., 2009). In addition, we also expected that individuals of *O. rhinolophus* would have better body condition (i.e. higher body dry mass, lipid mass, muscle mass and larger body size) in sampling sites with larger forested areas. In contrast, we expected that *C. cyanellus* and *O. batesi* would show better body condition in sites with heterogeneous land cover. By analyzing these species, we can understand the effects of habitat disturbance on dung beetles with different life strategies, and the different environmental factors defining species abundance and health.

2. Materials and methods

2.1. Study area

The study was conducted at “Reserva de la Biosfera Los Tuxtlas” (RBLT), Veracruz, Mexico (18°20’N, 95°07’W and 18°43’N, 95°25’W). The climate of the region is warm and humid, with mean annual temperature of 25 °C and rainfall ranging from 3,000 to 4,600 mm year^{-1} (Soto and Gama, 1997). The reserve has 155,122 ha and the altitude ranges from sea level to 1,600 m a.s.l. (Guevara-Sada et al., 2004; García-Aguirre et al., 2010). The RBLT is on the northern limits of the tropical rainforests from the Neotropical region (Dirzo and Miranda, 1991) and is composed by a complex of different vegetation physiognomies, with tropical species in the lowlands, and species common from temperate regions in the highlands (García-Aguirre et al., 2010). The core region of the reserve is composed by three mountains: San Martín Tuxtla (9,806 ha), San Marta (18,032 ha) and San Martín Pajapan (1,883 ha) (Dirzo and Miranda, 1991; Guevara-Sada et al., 2004). Surrounding the core region, there are 125,401 ha of buffer zone, composed by a mosaic of agricultural lands and forest remnants in different successional stages (Guevara-Sada et al., 2004). The selected sampling sites for this study are located in lowlands (between 30 and 200 m a.s.l.) within the buffer zone and the core region of San Martin Tuxtla, and presented varying landscape structure (Fig. 1). The lowlands are the most disturbed area of RBLT, presenting a conversion of