Carrion Removal Rates and Diel Activity of Necrophagous Beetles (Coleoptera: Scarabaeinae) in a Fragmented Tropical Rain Forest

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ABSTRACT Many studies have analyzed the effect of forest fragmentation on dung beetle diversity in tropical landscapes. Few of them, however, have analyzed how forest fragmentation affects the assemblage structure of necrophagous beetles and their removal rates of carrion in tropical forests. This study compares the effect of the time of the day in which carrion is offered to dung beetles (in the morning or at night) on the rates of carrion removal over time (12, 24, and 36 h) in tropical rain forest fragments of different sizes. Fragment size, time, and carrion offer had no effect on carrion removal rates in this study, but these factors affected abundance and species richness of necrophagous beetles. Carrion removal was the highest 12 h after the carrion had been offered. The average rate per hour of carrion removal in all fragments after 12 h was 4.47 g/h, after 24 h was 3.27 g/h, and 36 h later 2.64 g/h. Carrion removal rates are likely to be affected by beetle abundance and species richness. The most abundant species captured when carrion was offered at night was *Coprophanaeus telamon* Harold, a nocturnal necrophagous tunneler beetle. When carrion was offered in the morning, the most abundant species was the diurnal copro-necrophagous roller beetle *Canthon cyanellus* LeConte. Large nocturnal tunneler beetles were only found in large fragments, but small diurnal roller species were abundant in both large and small fragments. Our results suggest that different species contribute unevenly in different ways to carrion removal in tropical forest fragments. Carrion removal is not affected by fragment size per se, but by the fragmentation process.

KEY WORDS forest fragmentation, Scarabaeinae, necrophagous beetles, carrion removal rates, biomass

Nutrient cycling and decomposition of organic matter are important processes that influence ecosystem functioning (Nichols et al. 2008, Parmenter and MacMahon 2009). Removal rates of different resources, such as seeds, have been studied for different animal groups, including mammals (Forget 1996, Beck and Terborgh 2002), birds (Carlo and Morales 2008, Wenny 2000), and insects (Huges and Westoby 1990, Freymann et al. 2008). In tropical ecosystems, the analysis of dung removal rates as part of the nutrient cycling process for evaluating ecosystem functioning has received attention recently (Horgan 2001, 2005, 2006, Andresen 2001, 2003, 2005, Amézquita and Favila 2010, Norris and Michalski 2010). Carrion is a resource that has allowed the evolution of species of scavengers and decomposers, and has been shown to influence the nutrient composition of soils (Parmenter and MacMahon 2009). However, the process by which this resource is removed from forests and used by guilds of necrophagous beetles has rarely been studied.

In Neotropical forests, many Scarabaeinae dung beetle species are attracted to dung and carrion, or even to carrion alone (Halffter and Matthews 1966). It has been proposed that the shift from coprophagy to necrophagy among Neotropical dung beetles is an evolutionary process that occurred recently, because of the absence of large mammals and the relative scarcity of other groups of necrophagous insects that could constitute potential competitors (Halffter and Matthews 1966, Hanski and Cambefort 1991, Scholtz et al. 2009). The shift from dung to carrion may have been facilitated by the fact that carrion is more similar in nutrient composition to omnivore dung than to herbivore dung, and because carrion is a resource rich in nitrogen, with high nutritional quality, which is consumed by necrophagous adults for gonadic development and reproduction (Hanski and Cambefort 1991).

Carrion is a limited resource that necrophagous and copro-necrophagous beetles (Coleoptera: Scarabaeinae) use for feeding and nesting in tropical ecosystems (Hanski and Cambefort 1991). In tropical forests, carrion is a scarce resource and unevenly distributed in space and time (Halffter and Edmonds 1992, Hanski 1991, Peck and Howden 1984), which suggests that competition between carrion beetles is intense. Due to the fact that necrophagous beetles rely on ephemeral, unevenly distributed resources for reproduction,

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different species avoid competition by segregating their niches using diverse strategies. One strategy is using different hours of activity to find resources (Hanski and Cambefort 1991). Variations in diel activity allow different species to avoid direct competition. Doube (1991) observed a marked difference in diel activity among dung beetles: large tunneler species are mostly nocturnal, while smaller roller species tend to be diurnal. These variations in diel activity could be the result of adaptations the dung beetles have made to daylight (rollers) or darkness (tunnelers). In addition, nocturnal species may avoid predation by visual foragers such as birds, and tend to have a larger individual biomass than diurnal species, which may also result in greater nocturnal removal rates of carrion.

In a previous study in the fragmented tropical rain forest of Los Tuxtlas, Amézquita and Favila (2010) analyzed the removal rates of two types of dung (native and exotic), and found that such rates were not affected by fragment size, but were affected by season and resource type. The removal rates of monkey dung were higher during the rainy season than during the dry season, but in the case of cow dung the removal rates were similar during both periods. The rate of dung removal was high at the beginning, but decreased over time. In this study we examined what patterns would emerge for necrophagous beetles with a scarcer and less predictable resource such as carrion. Is the removal pattern similar to that found for dung? Are carrion removal rates affected by fragment size? How do carrion removal patterns vary between nocturnal and diurnal species? Is the abundance of necrophagous beetles similar during day and night? Are there differences in necrophagous beetle biomass during the day and the night and among forest fragments of different sizes?

To answer these questions we compared the carrion removal rates by necrophagous beetles in forest fragments of different sizes when carrion is offered at night or during the day in the tropical rain forest of Los Tuxtlas, México. Our predictions were: (1) carrion removal rates should be faster the first hours after the carrion is offered to carrion beetles than later; (2) rates of carrion removed by necrophagous beetles in forest fragments should increase with fragment size; (3) rates of carrion removal should be higher when the resource is presented at night, than when presented in the morning; (4) differences during night and day are related to differences in necrophagous beetle composition, biomass, diel activity, and guild structure; (5) large nocturnal necrophagous beetle species will be mostly abundant in large fragments, while during the day, small species will be mostly found in small fragments. These predictions are based on a previous study (Amézquita and Favila 2010) in which we found that dung removal rates were not affected by fragment size, but could be affected by forest cover.

Materials and Methods

Study Area. Field work was conducted at the biosphere reserve of Los Tuxtlas, located in the Southeast of Veracruz, at 95° 04′W and 18° 34′N. This zone represents the northernmost limit of the Mexican tropical rain forest (Dirzo and Miranda 1991). The area is dominated by tropical rain forest vegetation with a mixture of cloud forest and conifers at higher elevations (Mendoza et al. 2006, Aguirre and Dirzo 2008). Temperature varies between 24 and 26°C with annual rainfall ranging from 3000 to 4500 mm. The dry season is from March to May with 111.7 mm of rain per month, and the wet season is from June to February with a monthly mean rainfall of 486.25 mm (Soto 2004). In recent decades, Los Tuxtlas has undergone transformation from primary forest to pasture or arable land, which has resulted in modification of the soil cover and landscape structure. As a result, forest fragments of different sizes and with different isolation distances dominate the landscape (Dirzo and García 1992).

Six forest fragments of different size were selected using satellite images coupled with field inspection (for more details see Amézquita and Favila (2010)). The selected fragments were: (1) 3.0-, (2) 10.3-, (3) 40.5-, (4) 112.0-, and (5) 265.5-ha fragments and (6) 700-ha of continuous undisturbed forest (Fig. 1). The percentage of vegetation cover among fragments varied between 77 and 80% regardless of size, and all fragments had similar vegetation composition with predominantly original forest species.

Field Work. Field work was conducted from the 17 to 23 August 2009. Measurements of removed carrion were taken at 12 h intervals over a 36 h period, and expressed as time (H). We considered 36 h to be a sufficient time interval to evaluate overall carrion removal because, due to the intense competition between fly larvae, ants, and vertebrates (Hanski and Cambefort 1991), the resource tends to be consumed quickly. A 200 g piece of fresh fish was placed in the center of a 17 cm diameter × 17 cm deep plastic container, which was three-fourths filled with soil. Each container was buried at ground level and covered with a plastic plate to avoid flooding in the event of rain. Six containers were placed at the center of each fragment to minimize edge effects and positioned 50 m apart to avoid possible interference between traps (Larsen and Forsyth 2005). To estimate carrion removal rates over time, two containers were removed every12 h in each fragment, and the removed carrion was weighed using a precision scale ±0.1 g. To control for loss of weight by dehydration, a 200 g piece of fresh fish was placed in one container per fragment, as above described, but covered by a mesh to avoid dung beetle activity, and weighed every 12 h over a 36 h period. Necrophagous beetles captured were counted and identified to species level in the laboratory at Los Tuxtlas Biological Station and subsequently released at the end of the experiment. To obtain each species biomass, we followed the same methodology used by Amézquita and Favila (2010). Ten individuals

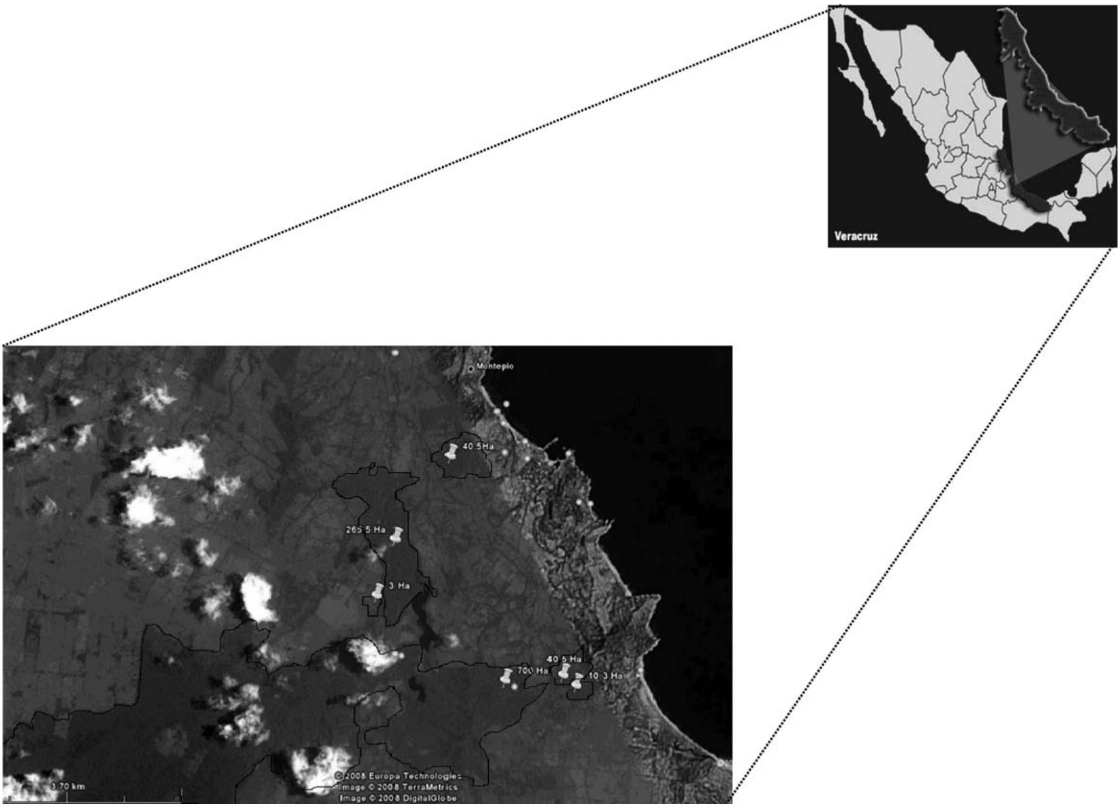

Fig. 1. Study site.

per species were dried at 120°C for 48 h, after which they were weighed, and an average individual mass for each species was obtained. Each species captured was classified according to its diel activity (diurnal and nocturnal) and food relocation behavior (tunnelers, rollers, dwellers) for each site and trap, using the species list for Los Tuxtlas by Favila (2005).

Data Analysis. Generalized linear models (GLM) were used to analyze (1) abundance, (2) species richness, (3) biomass (*biom*) of necrophagous beetles, and (4) total carrion removal rates per 12 h period (*carr*) as dependent variables. In all cases, fragment size (*Fr*, six fragments as a continuous variable); time (*H*, with three levels: 12, 24, and 36 h); carrion offer (*CO*, with two levels *N:* night and *D:* day), and their interactions were the independent factors. For the GLM analysis of abundance and species richness, we used a Poisson distribution, and for the biomass and carrion removal analysis, we used a normal distribution. To obtain the optimal model, Akaike Information Criteria (AIC) was used. The best-supported model has the lowest AIC compared with the other models (Crawley 2002). Statistical analyses were carried out using R 2.9.0 software for Windows (2006) and Statistica 7.0 (StatSoft, 2004). For traps in which the bait disappeared or was invaded by ants (*Camponotus sericeiventris* Guerin, *Labidus sp* Jurine, and *Pachycondyila impressa* Roger), the missing values were replaced with the overall mean carrion removal values (Little and Rubin 1987).

Results

A total of 632 individuals from eight different species were captured during the sampling period. The most abundant species were *Canthon cyanellus* LeConte, with 406 individuals, *Deltochilum pseudoparile* Harold, with 98 individuals, *Coprophanaeus telamon* Harold, with 75 individuals (all necrophagous species), and *Onthophagus rhynolophus* Harold, a generalist or copro-necrophagous species (Halffter et al. 2007, Scholtz et al. 2009), with 41 individuals (Table 1). The first two species belong to the roller guild and the last two species belong to the tunneler guild.

Carrion Removal Rates. A GLM revealed that fragment size ($P = 0.09$), time ($P = 0.08$), carrion offer ($P = 0.94$), and the interaction between time × carrion offer ($P = 0.39$), had a nonsignificant effect on carrion removal (Table 2). Removal rates were similar whether the carrion was offered at night or in the morning. Removal rates were not significantly different over time, the average removal rate per hour in all fragments was 4.47 g/h after 12 h, 3.27 g/h after 24 h, and 2.64 g/h after 36 h.

Abundance and Species Richness. Fragment size did not have a significant effect on abundance and species

Table 1. Abundance and species richness captured in each fragment when traps where set (a) nocturnally, and (b) diurnally

	Fragment area (ha)							Guild/diel[a]
(a)								
Species/fragment size	3	10.3	40.5	112	265.5	700	Total/species	
Ateuchus illaesum Harold	1						1	t/d
C. cyanellus LeConte	60		24	14	13	6	117	r/d
C. morsei Howden	4			1			5	r/d
Canthon vasquezae Martínez, Halffter y Halffter					2		2	r/d
C. telamon Harold	4	1	6	3	6	19	39	t/n
D. gibbosum Fabricius						1	1	r/n
D. pseudoparile Paulian		2	2	3	17	13	37	r/n
O. rhynolophus Harold	7		1		7	12	27	t/n
Total/fragment	76	3	33	21	45	51	229	
(b)								
Species/fragment size	3	10.3	40.5	112	265.5	700	Total/species	
Ateuchus illaesum			1	1			2	
C. cyanellus	176		15	95		3	289	
C. morsei			1				1	
Canthon vasquezae								
C. telamon	5		4	11	4	12	36	
D. gibbosum								
D. pseudoparile	2		1	15	40	3	61	
O. rhynolophus	12			1		1	14	
Total/fragment	195	0	22	123	44	19	403	

[a] Guild: r, roller; t, tunneler, activity (d, diurnal; n, nocturnal).

richness ($P = 0.300$ and $P = 0.094$, respectively). Time had a significant effect on necrophagous beetle abundance ($P = 0.024$) and species richness ($P = \leq 0.01$). Abundance and species richness increased gradually from 12 to 36 h. The highest abundance and species richness of necrophagous beetles was found after 36 h (Fig. 2). Carrion offer had a significant effect on species richness ($P = 0.049$); when carrion was offered at night, more species (eight) were captured than when it was offered in the morning (six species).

Biomass. Fragment size ($P = 0.007$) and Time ($P = 0.007$) had significant effects on necrophagous beetle biomass. Like abundance and richness species, the highest necrophagous beetle biomass was captured 36 h after the carrion was offered (Fig. 3). Beetle biomass tended to increase from the smallest fragments to the continuous forest (Fig. 4). Carrion offer had no significant effect on biomass (Table 2). When carrion was offered at night, the accumulated necrophagous beetle biomass in all fragments was 19.86 g; when carrion was offered in the morning, 20.92 g of necrophagous beetle biomass was accumulated in all of the fragments.

Although the accumulated biomass of necrophagous beetle in all fragments was similar regardless of whether carrion was offered (at night or in the morning), the contribution to the biomass accumulation was different according to the species, especially in the continuous forests. *C. telamon* was the species that contributed the highest biomass accumulation in all of the fragments during the night, especially in the continuous forest. *C. cyanellus*, the most important diurnal species, did not present a defined pattern of biomass accumulation in space and time. It was found in most of the fragments in a similar biomass both at night and during the day, but mainly in small- and medium-size fragments.

Discussion

We could not corroborate the hypothesis that carrion removal increases with fragment size. We also found that abundance and species richness were not affected by fragment size. Thus, the similarity in carrion removal rates in all of the fragments studied suggests that the process of reincorporation of carrion

Table 2. GLM to evaluate the effect of fragment size, sampling period (12, 24, and 36 h) and carrion presentation (night and day), on necrophagous beetle abundance, richness, biomass, and carrion removal rates

	Removal rates			Abundance			Richness			Biomass		
	DF	F	P	DF	F	P	DF	F	P	DF	F	P
Fr	1	2.90	0.090	1	1.06	0.30	1	2.79	0.094	1	8.25	0.007
H	2	2.69	0.08	2	7.39	0.002	2	17.00	<0.001	2	5.76	0.007
CP	1	0.005	0.94	1	1.58	0.20	1	3.86	0.05	1	0.02	0.87
H*CP	2	0.96	0.39	2	1.58	0.45	2	5.20	0.07	2	1.11	0.34
D.F error	29			29			29			29		

Fr, fragment size; H, sampling period; CP, time of carrion presentation; H*CP, interaction between sampling period × time of carrion presentation.

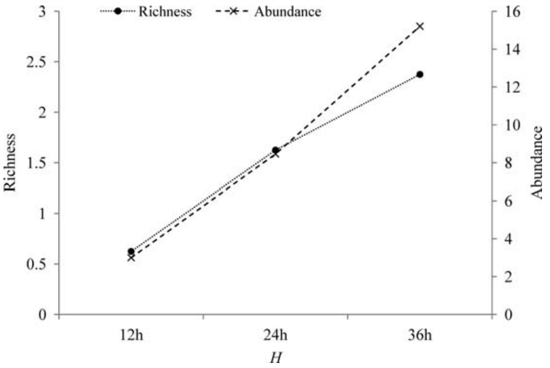

Fig. 2. Abundance and species richness of necrophagous beetles captured in time (H) 12 h, 24 h and 36 h.

into the soil by the carrion beetles is being maintained in the fragments by compensation in abundance and biomass of some of the species (Rosenlew and Roslin 2008). Contrary to our findings here, Amézquita and Favila (2010) found that in small fragments the removal rate of native dung was higher than in large fragments. Differences in response to the removal of a food resource by coprophagous and necrophagous beetles suggest that each guild responds in different ways to forest fragmentation or that different factors related to the effect of forest fragmentation exist for coprophagous and necrophagous beetles.

The hypothesis that carrion removal would be higher during the night also was not confirmed. The absence of differences in carrion removal rates in this study is related to the fact that abundance and biomass of necrophagous beetles during night and day were similar. However, the species which were present when carrion was offered at night or during the day were not the same. Large nocturnal species, such as *C. telamon*, *P. endymion*, and *D. gibbosum* (Favila 2005, Favila and Díaz 1997), were found more often during the night and, as expected, small diurnal species such as *C. cyanellus*, *D. pseudoparile*, and *O. rhynolophus*, were mostly found during the day, and also in a lower proportion during the night. Morón (1987) observed diel variations in the abundance and diversity of necrophagous beetles in a coffee plantation and in a rain forest in Chiapas, Mexico. Large tunnelers such as species belonging to *Coprophanaeus* genus were more abundant during the night, whereas small rollers like *Canthon* species were abundant both during day and night. Such resource partition in diel activity reduces species competition for resources (Hanski 1989), but according our findings it is not eliminated. If carrion is found for first time at night by nocturnal beetles or by other competitors diurnal beetles will have few opportunities to consume the resource, and vice versa.

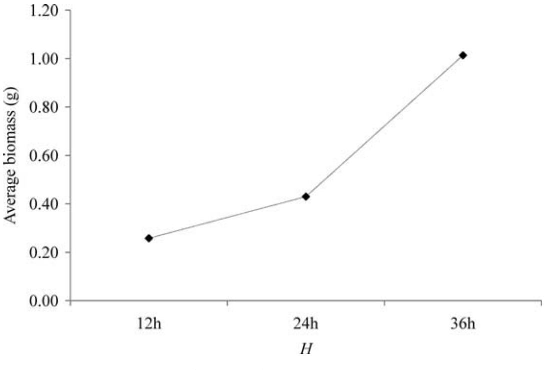

Fig. 3. Average beetle biomass captured during each sampling period (H): 12, 24, and 36 h.

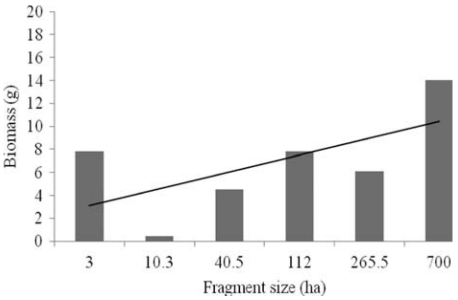

Fig. 4. Overall necrophagous beetle biomass captured by fragment size.

A lottery dynamic in which all individuals have equal opportunity to obtain a portion of the resource or a territory seems to apply in dung and carrion beetles. The strongest competition is for the part of the resource appropriated by the beetle, while the remaining resource is disposed of by other individuals and species (Hanski 1991). Under these circumstances a continuous process of colonization of the food resource by consumers should be expected. We found that both abundance and species richness increased over time, suggesting that a continuous process of colonization occurred in the food resource offered to the carrion beetles. In addition, the fact that the average removal rate per hour in all fragments was similar over time suggests that some individuals obtained a fragment of food and then allowed other individuals to use the remaining resource. While these results suggest that in the fragments studied the lottery dynamic is maintained, more studies are necessary to analyze the competitive dynamics of dung and carrion beetles in fragmented landscapes.

Our results corroborate the hypothesis that biomass of necrophagous beetles increases with fragment size. This finding differed from that of Amézquita and Favila (2010) in which fragment size had no effect on dung beetle biomass. Necrophagous dung beetles in this study appear to be more sensitive to fragmentation than are coprophagous species, with large tunneler species confined to large fragments. This was due, perhaps, to the relative scarcity and unpredictability of breeding resources relative to dung produced by primates and other vertebrates with predictable spatial and temporal defecation patterns.

Our results concur with Rosenlew and Roslin (2008) who examined the consequences of habitat fragmentation on the decomposition of dung by temperate dung beetles assemblages. They concluded that although landscape fragmentation can affect the composition of dung beetle assemblages, this is not reflected in ecosystem function because the loss of biomass of the most common species is compensated by a direct increase in the biomass of other species. In our study, the majority of species with the largest biomass belonged to the nocturnal tunneler guild, the most important guild in carrion and dung removal (Morón 1987, Klein 1989). Beside, the higher richness of carrion beetles during night than during the day has no effects on the carrion removal rates, suggesting that some diurnal species compensate the abundance and biomass of nocturnal species.

The presence of a high biomass and abundance of *C. telamon,* a nocturnal species in Los Tuxtlas (Favila and Díaz 1997), in large fragments corroborates the hypothesis that large species tend to persist in large conserved fragments (Larsen et al. 2006, Halffter et al. 2007). Navarrete and Halffter (2008) found a high abundance of small-bodied necrophagous species in small forest fragments and pastures in the Lacandon tropical rainforest (Chiapas). In Los Tuxtlas, the small fragments also had a high biomass and abundance of small roller species. In this way, necrophagous beetles are a useful indicator to evaluate the "health" of different forest patches and modified areas in tropical landscapes (Halffter et al. 2007).

Necrophagous as well as coprophagous beetles exhibit some degree of specificity with respect to food resources (Hanski 1989, Tshikae et al. 2008, Scholtz et al. 2009). In the current study, the presence of species like *C. cyanellus, D. pseudoparile,* and *C. telamon* corroborates the hypothesis that these beetle species prefer carrion. Favila (1993) has reproduced successfully *C. cyanellus* in laboratory only with fish or cow meat, which indicates that this species is strictly necrophagous, although dung is used for feed. However, it is also possible to find *C. cyanellus* and *D. pseudoparile* in monkey dung baited traps (Amézquita and Favila 2010), which suggests that when alternative resources are available, these species use them for feeding and not for reproduction. In particular, the high abundance of *C. cyanellus* in small fragments confirms that it is an opportunistic species that can feed on both dung and carrion, and can move from the forest interior to the edges, showing its adaptability to environmental and temperature changes. This species moves among forest fragments searching for available resources (Halffter et al. 1992, Favila and Halffter 1997, Favila 2005) and, in the case of males, for females (Arellano et al. 2008).

In Neotropical forests, necrophagous beetles are less abundant and less diverse than coprophagous beetles (Hanski and Cambefort 1991). At Los Tuxtlas Favila and Díaz (1997) reported 37 species of Scarabaeinae beetles, and near 11 of these species were caught in necrotraps. Some of these necrophagous forest species prefer specific types of resources, such as lizards, frogs and other small vertebrate species. *C. morsei* Howden, for example, is a necrophagous species that consumes dead miriapods (Bedoussac et al. 2007). It would be interesting to evaluate the removal rates of carcasses of small mammals, lizards, and other tropical forest vertebrates, as well as the removal rates of carcasses of insects and millipedes, to determine how forest fragmentation affects the removal of native resource by Scarabaeinae necrophagous beetles in tropical forests (Amézquita and Favila 2010).

One question remains. Why we did not find an increase in carrion removal with increasing fragment size? In the conserved forests of Los Tuxtlas, it is possible to find an average of 24 dung beetles species (Favila 2005). Many of these are copro-necrophagous and they seem to be redundant species (Halffter et al. 1992, Favila and Halffter 1997). According to Yachi and Loreau (1999), the more diverse the assemblage, the more likely it is to contain redundant species that are able to cope with a particular stressor. As a consequence of the process of fragmentation in Los Tuxtlas, these redundant species seem to confine themselves to specific fragments (Favila 2005). That could explain why we did not find differences in carrion removal process in Los Tuxtlas according to fragment size. Studies that analyze complementarity and redundancy among fragments associated with the loss or modification of key ecological processes are required to better understand the ecological consequences of forest fragmentation on dung and carrion beetle assemblages (Nichols et al. 2008, Rosenlew and Roslin 2008).

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