Effects of habitat fragmentation and diel activity patterns on dung beetle communities

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Abstract: Conversion of tropical forest to pastureland could have large consequences for biological communities, but theories to predict which species will be more or less affected are not well developed. One previous study found that forest fragmentation had differential effects on the movements of nocturnal versus diurnal species of Lepidoptera. We tested whether similar patterns apply to dung beetle communities by comparing abundance and diversity by night and day between a previously grazed field and the adjacent tropical cloud forest. During the day, beetle abundance was slightly higher in the field than in the forest, but at night abundance was much higher (10-fold) in the forest than in the field. Three species were found exclusively in the field, 3 in the forest and the remaining 3 were common in both habitats. Only one of nine species was captured during both the day and night. The differential effects of habitat on diurnal versus nocturnal dung beetles suggest complex, but predictable, interactions between habitat fragmentation, behavior and community structure.

Key Words: coprophagy, mammalian dung, resource partitioning, Scarabaeidae

Introduction

Human activities are rapidly altering landscapes in many parts of the world, frequently with strong effects on biota. One major alteration in tropical ecosystems is the widespread conversion of forests to pastures. Dung beetles (Coleoptera: Scarabaeidae) are one group of organisms that could be affected by this conversion. Impacts on dung beetles could be consequential for the rest of the ecosystem because of the role they play in nutrient cycling. The elimination of forest might reduce the abundance and diversity of dung beetles (due, for example, to increased temperature and reduced humidity). Alternatively, the attendant increase in resource availability (dung from cattle) could increase the abundance and diversity of dung beetles and/or change the species composition of the community. Diel activity patterns might influence species responses to habitat alteration. For example, nocturnal Lepidoptera (moths) tend to be less affected by forest fragmentation than diurnal Lepidoptera (butterflies) (Daily and Ehrlich 1996).

We tested these hypotheses by comparing dung beetle diversity and abundance during day and night periods in a tropical cloud forest and an adjacent field that had been cleared for pasture. The field was not currently stocked with cattle, enabling us to investigate the effects of habitat conversion without the effect of increased dung from livestock. We predicted that the abundance and diversity would be higher in the forest, both because it was the natural habitat type in this area and because it presumably contained more mammalian dung, as well as more alternative food sources such as carrion and rotting fruit.

Methods

This study was conducted 20 - 21 January 2002 near La Estación Biológica, Monteverde, Costa Rica. We placed 5 baited pitfall traps in the ungrazed field 50 m south of the station and 5 more baited traps within the adjacent cloud forest (~500 m east of the field traps). Traps within each habitat were separated by 10 m. Traps were baited with fresh human feces, which is attractive to a high number of species (Janzen 1983). The dung was tied in mesh bundles and hung from the top of traps. Traps were 500 mL plastic cups filled with ~2 cm of soapy water and sunk in the ground to rim level. There were 2 trial

periods on each of the 2 days, day (09:00 to 14:00) and night (16:00 to 21:00). New bait was hung at the beginning of each trial and trap sites were constant from day to night. After each 5 h trial we collected dung beetles from each trap, divided them into morphotypes and identified them to genus or species when possible.

We tested for patterns in beetle diversity and abundance with a two-way ANOVA model that included time (day or night), habitat type (forest or field), time x habitat and trap site nested within habitat (as a random factor). Abundance per trap was log transformed ($\log_{10}$ (captures + 1)) to correct for heteroscedasticity.

To compare beta-diversity between habitats, we calculated a Shannon-Weiner diversity index (H) and equitability (J) for the aggregated captures from each habitat type. We also calculated Shannon-Weiner diversity indices for each trap (alpha-diversity), and tested for patterns with an ANOVA model that included time, habitat type and time x habitat.

Results

We captured a total of 9 species of dung beetles (Appendix). Total beetle captures were greater in the forest than in the field (n = 62 vs. 15 beetles). There were no main effects of day versus night on beetle abundance per trap ($F_{1,8}$ = 0.55, P = 0.48) or of field versus forest ($F_{1,8}$ = 1.77, P = 0.22). However, there was a strong interaction between time of day and habitat type ($F_{1,8}$ = 8.88, P = 0.018): during the day, abundance was slightly higher in the field than in the forest, but at night, abundance was much higher in the forest than in the field (Fig. 1).

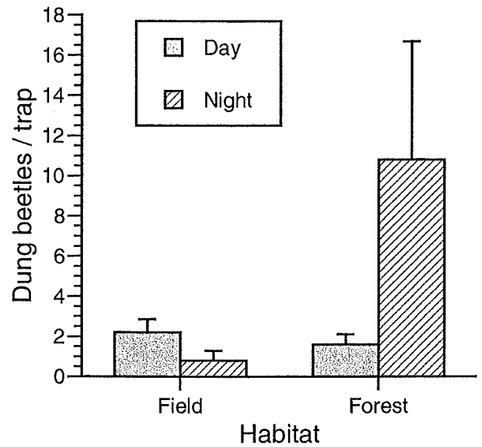

FIG. 1. Average number of individual dung beetles (+ SE) captured per trap in the field and forest during the day and night.

Species richness was similar between habitats, but species composition differed (Table 1). Six species were found only in 1 habitat (3 restricted to the field and 3 to the forest), while 3 other species were captured in both habitats. Four species were captured exclusively during the day and 4 others captured exclusively at night; only 1 species was captured during both time periods. Species evenness was higher in the field (J = 0.87) than in the forest (J = 0.48). Diversity per trap was not affected by habitat ($F_{1,8}$ = 0.22, P = 0.65), time of day ($F_{1,8}$ = 1.58, P = 0.24) or the interaction between habitat and time ($F_{1,8}$ = 1.39, P = 0.27).

TABLE 1. Number of individuals of each morphotype (A – I) by habitat and time of day.

Habitat	Time	A	B	C	D	E	F	G	H	I	Total
Field	AM	0	0	6	0	1	1	3	0	0	11
Field	PM	1	3	0	0	0	0	0	0	0	4
Forest	AM	0	0	5	3	0	0	0	0	0	8
Forest	PM	3	48	1	0	0	0	0	1	1	54

Discussion

Daily and Ehrlich (1996) argued that nocturnal Lepidopteran species are less affected by habitat conversion because at night, the microclimate differences between forest and field are less severe and individuals can easily move between and among habitat patches. Our results support this hypothesis. Of the 4 nocturnal species in our study, 2 occurred in both habitat types. The other 2 were rare (n = 1 individual of each), making it difficult to determine whether they are confined to either habitat type. In contrast, all 4 diurnal species were confined to 1 habitat type; none crossed between the forest and field. Microclimate differences could account for the habitat x time of day interaction we observed in dung beetle abundance. If so, we would predict that diurnal dung beetles are sensitive to microclimate changes and that at night, these differences (such as temperature and humidity) would be reduced or eliminated between the cloud forest and nearby field.

Other factors could also influence this pattern. Daytime predators of dung beetles, such as birds, could cause beetles to forage more actively at night, as we found in the forest. We did not see this pattern in the field habitat, perhaps because birds are less common due to the shortage of perching and nesting sites. Competition among beetles could also be driving the day versus night specialization, with species having evolved different times of peak activity to minimize interspecific resource competition. Diel patterns in the availability of fresh mammalian dung is presumably important, and must depend upon the relative abundances of nocturnal versus diurnal mammals in the forest and field, but our study was unable to evaluate these patterns.

Although species richness was equal in both habitats, beta-diversity and species evenness were higher in the field than in the forest. In the forest, *Uroxys B* accounted for 48 out of 62 individuals, while the other 5 species were relatively rare. In the field, there was no single dominant species; instead, all 6 species were about equally common.

Not only does forest conversion change physical habitat structure, but it has the potential to alter the composition of the biological community as well. Studies in both Lepidoptera and Coleoptera communities suggest that diurnal species distributions may be more severely altered by deforestation. It is possible that these effects extend to other groups of organisms as well, and further studies should look at possible relationships between habitat fragmentation, behavior and species diversity.

Literature Cited

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APPENDIX. Morphotypes of dung beetles (Scarabaeidae) collected in this study.

Species ID	Length, mm (mean ± SD)	Number collected	Description	Roller (R) or Tunneler (T)	Probable taxon[a]
A	2.7 ± 0.18	4	black, narrow body	T	*Uroxys A*
B	4.5 ± 0.10	51	brown, narrow body	T	*Uroxys B*
C	3.6 ± 0.35	12	round body, iridescent	T	*Canthidium A*
D	5.2 ± 0.53	3	round body, iridescent	T	*Canthidium B*
E	5.0	1	dull black, round body	T	*Onthophagus "anthracinus"*
F	8.2	1	green iridescent, round body	R	*Canthon viridius*
G	8.7 ± 0.55	3	shiny black, grooved elytra	T	*Onthophagus incensus*
H	13.0	1	dull black, round body	R	*Deltochilum parile*
I	17.9	1	black, red hairs, grooved elytra	T	*Dichotomius satanas*

[a]Based on comparisons with pinned, identified specimens in insect collection at Monteverde Biological Station.