

# Nocturnality and species survival

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**ABSTRACT** Surveys of butterfly and moth diversity in tropical forest fragments suggest that nocturnality confers a dispersal, and possibly a survival, advantage. The butterfly faunas of smaller fragments were depauperate; in contrast, the species richness of nocturnal moths was similar in all fragments and even in pasture. The lack of correlation between butterfly and moth species richness among fragments ( $r^2 = 0.005$ ) is best explained by movements of moths at night when ambient conditions in forest and pasture are most similar; butterflies face substantial daytime temperature, humidity, and solar radiation barriers. This interpretation is supported by information on birds, beetles, and bats.

The human-induced extinction episode currently underway (1–3) raises the question of which taxonomic groups are best equipped to survive it. The paleontological prism through which we interpret great biotic upheavals in Earth's past affords relatively few clues to patterns of species loss today. The fossil record indicates: (i) that species survival of mass extinctions is not random; (ii) that breadth of geographical distribution confers a survival advantage; (iii) that while species richness serves as an extinction buffer for higher taxa during periods of background extinction levels, it is a poor predictor of survival during mass extinctions (this is partly because the biological attributes that accelerate speciation rates covary with other traits that increase species' vulnerability to extinction, such as low dispersal capability and narrow environmental tolerance; ref. 4); and (iv) that the very same species traits conferring a survival advantage during background periods may prove lethal during mass extinctions (5). Ecological theory and experimentation suggest that species survival today hinges increasingly upon dispersal ability among habitat fragments (6–8) in human-dominated landscapes.

Arthropods are diverse, abundant, and ecologically critical (9–12) and are excellent model systems for exploring the survival advantages and disadvantages associated with different species traits. We compared the responses of two close taxonomic and ecological relatives—diurnal butterflies and nocturnal moths (Lepidoptera)—to forest fragmentation and discovered a striking difference.

## MATERIALS AND METHODS

We surveyed lepidopteran diversity in eight tropical moist forest fragments, ranging from 0.3–227 hectares, near the Las Cruces Station of the Organization for Tropical Studies in southern Costa Rica. This region was continuously forested 30 years ago, but has subsequently undergone extensive forest clearance. A description of the fragments and the butterfly sampling (of species thought to be associated with forest interior) is reported elsewhere (13).

Light traps with 10-W fluorescent tubes (350–390 nm) were used to sample moths in February and March, 1994. To control for lunar phase and weather conditions (14, 15), all fragments were sampled five times in rounds of two consecutive nights.

Traps were placed in the same locations as used for the butterfly sampling: within 2 m of the ground behind topographic or vegetation barriers to prevent light from reaching surrounding pasture (even though evidence suggests a light radius of attraction of <10 m; ref. 16) and within 50 m of forest/pasture edge to control for edge effects. In addition, a trap was operated once, for half of a standard 4-hr sampling period, in open pasture, where it was not visible from forest habitat. Finally, a second, more intensive survey of only the largest (LC) fragment was conducted. A reference collection was made of specimens >12 mm in forewing length (the diameter of the trap opening precluded the capture of individuals larger than  $\approx 50$  mm in forewing length), consisting of 495 morphospecies in  $\geq 19$  families; 2667 individuals representing these species were captured.

## RESULTS AND DISCUSSION

Moth species richness (number of species) in light-trap samples was not correlated with fragment area (Table 1;  $r^2 = 0.04$ ,  $P > 0.45$ ) or distance from the largest fragment (LC), an approximate index of isolation ( $r^2 = 0.22$ ,  $P > 0.10$ ). [The correlation between fragment area and degree of isolation ( $r^2 = 0.67$ ,  $P < 0.005$ ) precludes testing of the relative influences of those factors on species richness.] The evenness of species abundance, reported here as  $J'$  (Table 1), was similar among fragments and pasture.

In contrast, butterfly species richness was significantly correlated with fragment area (Table 2;  $r^2 = 0.55$ ,  $P < 0.025$ ). This correlation may be spuriously weakened by satyrine butterflies, many of which feed on grasses associated with human disturbance (13, 17); their exclusion strengthened the correlation ( $r^2 = 0.72$ ,  $P < 0.005$ ). There was weak negative correlation of butterfly species richness and distance from the LC fragment (including satyrines,  $r^2 = 0.26$ ,  $P < 0.10$ ; excluding satyrines,  $r^2 = 0.40$ ,  $P < 0.05$ ). Butterfly species evenness,  $J'$ , is low in the small fragments (Table 2), primarily due to the superabundance of certain satyrine species, and forest butterflies are almost never observed in the pastures.

Several possible explanations could account for the lack of correlation between moth and butterfly species richness ( $r^2 = 0.005$ ,  $P > 0.50$ ). First, moths may be less host-specific than butterflies, but this appears unlikely (18, 19). An extensive survey in northern Costa Rica, (20) revealed that  $\approx 50\%$  or more of the moths had only one local host plant species and that  $\geq 80\%$  of the remainder had just a few chemically or taxonomically related hosts. Moreover, brief sampling in pasture revealed high moth species richness—certainly not supported by the pasture grasses, principally *Melinis minutiflora* P. Beauv. and the African import *Cynodon nlemfuensis* Vanderyst.

Second, vagile, generalist species may have accounted for a disproportionately large fraction of moth samples from small patches. If so, one would expect a nested subset distribution of moths among fragments, as exists for the butterflies (13); however, no such distribution was found. Moreover, the species richness and evenness sampled in the second, more

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Table 1. Moth species richness and evenness in forest fragments and pasture

	Location								
	LC	CAS	RRR	VV	UGS	LGS	LSL	LSTR	Open pasture
Fragment size, hectares	227	20	25	20	1	1	0.3	0.3	—
No. of samples	5	5	5	5	5	5	5	5	0.5
No. of species									
Apatelodidae	1	0	0	0	0	0	0	0	0
Arctiidae	19	5	7	23	17	22	25	4	27
Bombycidae	3	1	2	2	0	1	1	0	0
Geometridae	32	16	16	28	25	33	34	4	20
Hedylidae	1	0	0	0	0	0	0	0	0
Hepialidae	4	3	1	1	3	3	1	0	0
Lasiocampidae	3	1	1	3	1	2	0	0	1
Limacodidae	1	0	0	0	0	0	0	0	0
Lymantriidae	1	1	0	1	1	1	1	0	0
Megalopygidae	0	0	0	0	1	0	0	0	0
Noctuidae	25	10	16	30	23	23	19	6	40
Notodontidae	3	1	1	2	3	2	2	1	1
Oxitenidae	0	0	0	1	0	0	0	0	0
Psychidae	3	0	0	0	0	1	1	0	0
Pyralidae	4	0	5	9	6	6	6	0	5
Saturniidae	1	0	0	1	0	2	2	1	2
Tortricidae	1	0	0	0	0	0	0	0	0
Unclassified	7	1	1	2	4	2	4	0	3
Total no. moth species	109	39	50	103	84	98	96	16	108
Moth evenness index, $J'$	0.91	0.90	0.88	0.86	0.74	0.90	0.81	0.92	0.88

Data on LC are from the first survey only. In all, 1616 individuals of 351 species are represented.  $J'$  measures the relative evenness of species abundance and is calculated as  $-\sum p_i \ln p_i / \ln S$ , where  $p_i$  is the proportion of a sample made up of the  $i$ th species and  $S$  is the total number of species in the sample (32). Fragment areas are corrected over those reported in ref. 13.

intensive survey of LC (Table 3) was comparable to that sampled elsewhere in the forest-pasture habitat matrix (Table 4), suggesting that the movement of moths was not strongly influenced by vegetation structure. Species richness per unit sampling effort was slightly higher throughout LC (Tables 3 and 4), but this is attributable in part to the placement of forest edge traps, so vegetation and topography prevented light from reaching the pasture. Trap lights at interior sites were not comparably shielded. This biased the sampling against the small patches, since the numbers of species and individuals captured were highly correlated ( $r^2 = 0.95$ ,  $P \ll 0.001$ ) and appeared, in retrospect, determined by the exposure of the light trap. [At the extremes, the trap locations in LSTR were in a very deep, narrow stream bed, whereas that at TJ (in the interior of LC) was high on a slope overlooking the forest. Most spectacularly, the open pasture trap accumulated as many species as the richest fragment (LC) in one-tenth the time.]

The most likely explanation for the lack of correlation between butterfly and moth species richness, however, is that, unlike butterfly movement, the movement of nocturnal moths

is relatively uninhibited by forest-pasture edges. A butterfly's ability to fly is primarily determined by solar radiation, whereas moths are endothermic (21, 22). In both clear and overcast weather, temperature and humidity differed substantially between forest ( $\approx 100$  m from edge) and pasture diurnally ( $3.3 \pm 0.9^\circ\text{C}$  cooler and  $12 \pm 4\%$  higher humidity in forest;  $n = 4$  days), but little at night ( $0.2 \pm 0.1^\circ\text{C}$  warmer and  $1 \pm 1\%$  higher humidity in forest;  $n = 3$  nights); year-round data from a nearby site substantiate this (K. Holl, personal communication). Thus, demographic units (23) of many moth species may occupy several square kilometers of a complex matrix of forest fragments and pasture, whereas those of diurnal forest butterflies appear to be much more restricted to the fragments. We expect that more intensive sampling would eventually reveal higher moth species richness in LC than in the smaller fragments, a trend that may be apparent in our sampling (Table 4), simply because some moth species will be too sensitive to microhabitat conditions or will have insufficient vagility to cross open areas. But the absence of a nested subset of highly vagile "tramp" species makes the key point that the patterns in butterflies and moths are different; nocturnality is the prime suspect for the source of that difference.

Table 2. Butterfly species richness and evenness in forest fragments

	Location							
	LC	CAS	RRR	VV	UGS	LGS	LSL	LSTR
Family								
Charaxinae	$\geq 8$	$\geq 4$	2	$\geq 2$	1	0	1	1
Nymphalinae	3	4	1	0	0	0	0	1
Morphinae	1	1	1	1	0	0	1	0
Brassolinae	5	5	$\geq 4$	2	2	2	2	2
Satyrinae	6	$\geq 6$	4	4	2	4	9	3
Total no. butterfly species	$\geq 23$	$\geq 20$	$\geq 12$	$\geq 9$	5	6	13	7
Total no. nonsatyrine species	$\geq 17$	$\geq 14$	$\geq 8$	$\geq 5$	3	2	4	4
Butterfly evenness index $J'$	0.73	0.80	0.21	0.21	0.10	0.20	0.42	0.36

In all, 1070 individuals of  $\geq 32$  species in five subfamilies are represented. Approximate numbers reflect the escape of a few individuals before positive species identification had been made.

Table 3. Number of moth species found in the second survey of the LC fragment

Family	Location					Total
	GP	S1B	JBW	RJ	TJ	
Apatelodidae	0	1	0	0	1	2
Arctiidae	12	21	6	20	53	74
Bombycidae	0	1	0	0	6	7
Epiplemlidae	0	0	1	0	0	1
Geometridae	12	31	10	19	42	74
Hepialidae	1	3	2	1	4	7
Lasiocampidae	0	2	3	3	12	13
Limacodidae	1	0	0	2	2	4
Lymantriidae	0	1	1	1	1	1
Megalopygidae	0	0	0	0	1	1
Noctuidae	8	18	12	10	35	57
Notodontidae	0	2	0	2	5	6
Psychidae	0	1	0	0	0	1
Pyralidae	5	4	3	7	7	17
Saturniidae	0	0	1	1	3	4
Sphingidae	0	0	0	1	1	2
Tortricidae	0	0	0	1	1	1
Unclassified	1	3	3	2	8	11
Total no. moth species	40	88	42	70	182	283
Moth evenness index $J'$	0.98	0.94	0.94	0.91	0.84	0.84

Sampling was at five locations within LC on two nights each; in all, 1051 individuals of 283 species are represented.

This interpretation is supported by the distribution of crepuscular butterfly species (*Caligo* spp., Brassoliniæ), found in comparable abundance in all fragments (13). It is also supported by the distribution of light-trapped nocturnal beetles and visually and aurally censused diurnal birds in these fragments, which correlated well with that of the moths and butterflies, respectively, but not vice versa (Table 5; unpublished data). Further support comes from distributions of birds and bats in tropical forest fragments and cleared areas in Amazonia and Mexico. For example, of the 248 bird species censused in a region of Amazonian forest, only 18 occurred in nearby degraded pasture; by contrast, fully half of the 14 bat species captured in the forest were also encountered in pasture (24). A survey of bats in Mexican tropical forest fragments and agricultural areas found no relationship between bat species richness and fragment area; indeed, although agricultural sites represented only 1% of the total area surveyed (and 27% of the sites studied), they accounted for 77% of all species recorded and 38% of all bat captures (25).

Our findings have two important implications. First, identifying taxa to serve as biodiversity indicators may prove

unexpectedly difficult. Butterflies and moths have been touted as potentially useful indicators of biodiversity (26–28), yet butterflies were poor indicators of moth diversity. Unlike nocturnal moths, however, the distribution of butterflies appears to reflect that of their larval foodplants, possibly making them conservative indicators of suitable larval moth habitat. Second, nocturnality may enhance survival prospects by enabling organisms to more fully utilize recently fragmented landscapes, where populations of species with restricted movement would be more prone to subdivision and extinction.

We hypothesize that, in this context, selection is acting indirectly upon nocturnality and directly upon vagility in fragmented landscapes. This interpretation prompts several testable predictions. First, the rate of faunal collapse in natural habitat fragments will be lower for nocturnal (and crepuscular) organisms than for diurnal organisms. Day-flying moths, for example, should undergo the same rate of collapse as butterflies. Second, one would expect the rate of faunal collapse to be lower among plant or animal species with nocturnal (versus diurnal) dispersal agents. Third, the extent to which the rates of faunal collapse differ among nocturnal and diurnal species will vary as a function of the spatial homogeneity of temperature, humidity, and solar radiation in the original, natural

Table 4. Comparison of eight moth samples from the interior of the largest fragment, LC, with sets of eight comparable samples drawn from the smaller patches, as indicated

Samples	Total no. individuals	Total no. species	Evenness index $J'$
Sets of eight samples from VV, UGS, LGS, and LSL			
VV-1,4; UGS-2,5; LGS-3,4; LSL-1,5	433	144	0.82
VV-2,3; UGS-4,5; LGS-1,3; LSL-2,4	234	108	0.82
VV-4,5; UGS-1,3; LGS-2,3; LSL-1,4	443	147	0.83
VV-2,5; UGS-3,4; LGS-1,5; LSL-2,3	332	124	0.83
VV-1,3; UGS-1,2; LGS-2,5; LSL-3,5	376	129	0.82
Mean	364	130	0.82
Eight samples from within LC (two each from GP, S1B, JBW, RJ)	397	182	0.91

The samples from TJ (within LC) and from LSTR are excluded because they were so anomalously large and small, respectively, apparently because of the exposure (and lack thereof) of their trap locations (see text).

Table 5. Correlation matrix (reporting  $r^2$ ) of the species richness of different taxa among forest fragments

	Butterflies	Moths	Beetles	Birds
Butterflies	1.00	0.005	0.22	0.55*
Moths		1.00	0.58†	-0.05
Beetles			1.00	-0.05
Birds				1.00

In the case of birds, the LC fragment was relatively oversampled and is excluded to be conservative.

\* $P < 0.05$ .

† $P < 0.025$ .

habitat. If the natural habitat is highly heterogeneous with respect to these conditions, one would expect organisms to have evolved means of dispersing through it or of surviving with limited dispersal. Fourth, one would expect the nocturnality advantage to be eliminated in cases where the recently converted habitat separating fragments of natural habitat has similar temperature, humidity, and solar radiation conditions, such as exotic plantation forest contiguous with native forest.

Which elements of the biota survive the current extinction episode will have profound implications for the future of humanity (29, 30). The rapid loss of populations (31) from many regions represents an opportunity to illuminate patterns of species extinction susceptibility and their consequences for ecosystem function and human well-being and perhaps to slow the decay of biodiversity in the future.

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