ECOLOGICAL MELTDOWN IN PREDATOR-FREE FOREST FRAGMENTS

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The manner in which terrestrial ecosystems are regulated is controversial. The "top-down" school holds that predators limit herbivores and thereby prevent them from overexploiting vegetation, whereas "bottom-up" proponents stress the role of plant chemical defenses in limiting the depredations of herbivores. A set of predator-free islands created by a hydroelectric impoundment in Venezuela allows a test of these competing world views. Limited area restricts the fauna of small (0.25-0.9 hectare) islands to predators of arthropods (birds, lizards, anurans, spiders), granivores (rodents), and herbivores (howler monkeys, iguanas, leaf-cutter ants). Predators of vertebrates are absent, and densities of rodents, howler monkeys, iguanas, and leaf-cutter ants are 10 to 100 times greater than on the nearby mainland, implying that predators normally limit their populations. The densities of seedlings and saplings of canopy trees are severely reduced on herbivore impacted islands, providing evidence of a trophic cascade unleashed by the absence of top-down regulation.

Ecosystems are structured by the amount of energy flowing through them and how much primary productivity reaches consumers (herbivores, etc.), predators, and decomposers. Plant growth is enhanced through "bottom-up" effects exerted by light, warmth and the availability of moisture and nutrients. However, plants are subject to "top-down" forces when they are eaten by consumers.

The degree to which top-down vs. bottom-up forces regulate terrestrial ecosystems has not been resolved (*1,2)*. Proponents of a top-down view argue that the world is green because predators regulate the numbers of herbivores, thereby limiting the damage herbivores do to vegetation (*3,4).* Advocates of a bottom-up view argue that herbivores are limited by low forage quality and/or by constitutive and inducible plant defenses, which render much foliage unpalatable or indigestible *(5,6).*

A naïve test of the top-down vs bottom-up models is simple in principle but difficult in practice, because vertebrate predators and their prey operate on spatial scales lying beyond the practical reach of direct experimentation (*7).* However, if all relevant predators could be excluded from a sufficiently large experimental area, the top-down model would predict consumer populations to expand, whereas the bottom-up model would predict little change in consumer numbers. The prediction is naïve, because many ecosystems have both top-down and bottom-up components, and because prey behavior can vary greatly in response to the perceived risk of predation (*8).* Nevertheless, simple qualitative predictions are the best ecological theory can muster at present.

A second test of the top-down model is embodied in the concept of a trophic cascade, in which a perturbation at one trophic level propagates through lower levels with alternating positive and negative effects. Thus, removal or absence of predators would be expected to lead to increased densities of consumers, which, in turn, would be predicted to have negative consequences for producers *(9,10)*.

Here we report on the strength of top-down forces unleashed in a set of forest fragments through the fortuitous exclusion of predators. The fragments are islands in Lago Guri, a 4,300 km^2 hydroelectric impoundment in the Caroni valley of the state of Bolivar, Venezuela (*11,12)*. Isolated by rising water in 1986, these islands range from 0.2 to 4.9 km from the nearest point on the mainland, and are all situated at least 100 m across open water from any other landmass. The vegetation is semi-deciduous tropical dry forest.

In 1993-94 we conducted faunal inventories of 6 "small" islands (0.25-0.9 ha), 4 "medium" islands (4-12 ha), 2 "large" islands (≥150 ha), and two sites on the mainland (*13,14)*. Through these inventories we attempted to determine the presence/absence and abundance at each site of all vertebrates and selected invertebrates. The inventories revealed that small and medium islands already lacked ≥75% of the vertebrate species known to occur on the nearby mainland, whereas the two large islands retained nearly all species (*13)*. We have thus designated the two large islands along with two stations on the mainland as control sites.

Animals persisting on small islands fall into three trophic categories: predators of invertebrates (spiders, anurans, lizards, birds), seed predators (small rodents), and herbivores (howler monkeys, common iguanas, and leaf-cutter ants) (*15).* Medium islands harbor, in addition, armadillos, agoutis, and, in one case, capuchin monkeys (*16).* Apart from the island with capuchins, frugivores (the principal seed dispersers of tropical forests) and predators of vertebrates are largely to entirely absent from both small and medium islands (*17,18).* The resulting communities are thus highly aberrant, comprising a suite of consumers without predators.

Consumers able to persist on small and medium islands are typically hyperabundant in relation to control sites. The mean number of rodents captured per 100 station-nights on 3 medium and 6 small islands was 35 times greater than at 3 sites on a large island and one on the mainland (*19).* Transect counts of iguana dung indicated a 10-fold increase in abundance relative to the mainland (*13).* Beyond these density estimates, we have little information on iguanas because they live in the canopy where they are almost invisible. Howler monkeys on some small islands persist at densities equivalent to 1000 per km^2 (20-40 per km^2 is normal for the mainland), and the density of mature leaf-cutter ant colonies is roughly two orders-of-magnitude higher than on large landmasses (Tables 1 and 2) (*20).*

Reproduction of howler monkeys appears to be suppressed where they are hyperabundant, suggesting strong density dependence and bottom-up regulation. On one 0.6-hectare island, a group of howlers containing two adult females produced only one young in four years (0.125 birth per female-year) whereas on a 350-hectare island, 10 adult females belonging to two groups produced 5 infants in 2001 (0.5 birth per female-year).

On medium islands, rodents were as abundant as on small islands, but densities were less for common iguanas, howler monkeys and especially, leaf-cutter ants (Tables 1 and 2) *(20,21).* The difference in the density of leaf-cutter colonies on small and medium islands was investigated by placing wire cages over entrances to young colonies. On medium islands, cages resulted in significantly increased colony survivorship by excluding armadillos. Cages had no effect on small islands where armadillos were not present (*20).*

The truncated animal communities of small and medium Lago Guri islands are ideal for revealing the strength of top-down regulation because the principal herbivores (howlers, iguanas, leaf-cutter ants) all feed mainly or exclusively on the foliage of canopy trees and lianas. Moreover, none of these animals has a juvenile stage which feeds at a lower trophic level, a factor that frequently complicates the interpretation of food web interactions in aquatic systems (*22).*

The presence of hyperabundant consumers on predator-free islands supports the näive prediction of the top-down hypothesis and could signal the operation of a trophic cascade. To investigate this possibility, we established plots for monitoring vegetation change on each of the 6 small and 4 medium islands, and at 5 sites on large landmasses (*23).* Concurrently, we tested a second hypothesis proposed to account for the rapid loss of tree species on small islands in Lake Gatun, Panama, namely, that plant recruitment had been suppressed by desiccating dry-season winds (*24).* Accordingly, the small-stem subplots were situated within each site so that half had a windward exposure and half a leeward exposure.

Counts of small (≥1 m tall, <1 cm dbh) and large (≥1 cm dbh, <10 cm dbh) saplings in exposed and sheltered subplots on small, medium and large landmasses were analyzed by ANOVA, with orientation (exposed vs sheltered) nested within landmass. There proved to be a highly significant effect of landmass size on the number of small saplings (F=8.0[2], p=0.003), and a marginally significant effect on the number of large saplings (F=3.7[2] , p=0.046). Small saplings were less than half as dense on small islands than on larger landmasses (cf. Tables 1 and 2). There was no effect of windward vs. leeward exposure on either stem size class (F=0.57[1], p=0.64). These stem counts probably do not accurately reflect current rates of plant recruitment, because it is likely that many of the stems became established prior to isolation of the islands in 1986 (*25).*

A better representation of recruitment under current conditions is provided by the smallest class of plants, those <1 m tall. Small islands proved to have low numbers of stems in this class ($4.7/m^2$ vs. 13.1 $stems/m^2$ on a large landmass, F=41.5[1], $p<10^{-6}$). Numbers of stems representing species of canopy trees were only 20% of the control value ($0.86/m^2$ vs. $4.25/m^2$, F=14.7[1], p<0.001). More than half the stems on the small islands were of lianas (especially Bignoniaceae, Leguminosae, and Malphigiaceae), and most of the rest were understory shrubs and bambusoid grasses. Recruitment of canopy trees appears to be severely depressed, providing further evidence of a trophic cascade on these small islands.

We expect that processes set in motion at the time of isolation will run their course on most small islands in another few decades. Hyperabundant folivores threaten to reduce species-rich forests to an odd collection of herbivore-resistant plants (*26).* Along the way, much plant and animal diversity will probably be lost. The endpoint will be a biologically impoverished system, much like that found today on 85 year-old islands in Lake Gatun, Panama (*24).*

In a parallel situation, long-term overgrazing of semi-arid range is well-known to convert grassland to thornscrub or shrub steppe *(27,28).* Intense grazing predictably reduces the ratio of palatable to unpalatable species, thereby increasing the resistance of the vegetation and reducing the carrying capacity for grazers. Our results show that these same processes can operate in forests, with similar implications for reduced diversity, increased plant defenses, and lowered carrying capacity for consumers. Similar, if less extreme, processes have been unleashed in parts of the U. S., where hyperabundant ungulates have massively impacted natural vegetation (*29,30).* Wild pigs (*Sus scrofa*) are severely reducing plant recruitment in a remnant forest in Malaysia where they lack predators (*31).* These observations are warnings, because the large predators which impose top-down regulation have been extirpated from most of the continental U. S. and, indeed, much of the earth's terrestrial realm.

It has long been known that herbivores explode on predator-free islands to the detriment of natural vegetation (*32).* But in the absence of controlled experiments, many ecologists have passed off such accounts as unreliable anecdotes, rather than as convincing evidence of top-down regulation. By taking advantage of a fortuitous experiment, we show that the absence of predators consistently frees certain consumers to increase many times above "normal," unleashing a trophic cascade.

The extreme hyperabundance of herbivores on small Lago Guri islands demonstrates that food availability (and by implication, plant defenses) does not limit these consumers in the presence of predators (*33).* Where predators depress herbivore populations, plant species with relatively low investments in chemical and mechanical defenses can attain high densities, because such plants grow faster and compete better than species which invest heavily in anti-herbivore defenses (*34).* Herbivores explode in the absence of predators, but only as a transient phenomenon, until the species composition of the vegetation adjusts to impose regulation from the bottom-up *(35).* Herbivore pressure has been weak over much of the earth since the eradication of megafauna by Stone Age hunters, so bottom up regulation has become widespread, creating aberrations that have spawned the top-down vs. bottom-up controversy (*36).*

Table 1. Tree species diversity, and densities of saplings, howler monkeys, and mature leaf-cutter ant colonies on 6 small Lago Guri islands (1996-1997).

	Island					
	Baya	Cola	Colón	Iguana	Perímetro	Palizada
Area (ha)	0.25	0.7	0.3	0.6	0.5	0.9
No. trees ≥10 cm dbh	203	490	290	381	301	403
No. tree species	32	40	33	47	54	55
No. stems ≥1 m tall, <1 cm dbh/500 m^2	39	84	147	90	156	301
No. howler monkeys	2	6	3	6	-	-
Howler monkeys per ha	4.0	8.6	10.0	10.0	-	-
No. leaf-cutter colonies	1	3	2	4	2	1
No. leaf-cutter colonies/ha	4.0	4.3	6.7	6.7	4.0	1.1

Table 2. Tree species diversity, and density of saplings and mature leaf-cutter ant colonies on medium and large Lago Guri landmasses.

	Landmass								
	Medium				Large				
	Ambar	Chota	Lomo	Pano	DM-15	DM-12	Grande	TF-1	TF-2
Area (ha)	8	5	11	12	350	350	150	∞	∞
No. tree species per 300 stems ≥10 cm dbh	63	42	49	51	50	55	46	51	50
No. stems ≥1 m tall, <1 cm dbh/500 m^2	214	311	375	236	304	-	379	340	-
No. leaf-cutter colonies	2	1	2	2	≥4	≥4	≥2	-	-
No. leaf-cutter colonies/ha	0.25	0.20	0.18	0.17	≥0.01	≥0.01	≥0.01	≤0.04	≤0.04

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16. Armadillos are *Dasypus novemcinctus*, agoutis are *Dasyprocta leporina*, and capuchins are *Cebus olivaceus*.
17. Several small raptors and two small owls do occur on the small and medium islands inventoried, but none of them are known to prey regularly on mammals or other large forest vertebrates.
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