Predators Accelerate Nutrient Cycling in a Bromeliad Ecosystem

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The availability of nutrients in ecosystems is determined by resource supply and recycling rates and affects important ecosystem properties (*1–3*). The relative roles of abiotic supply and food web configuration in determining resource-processing rates remain contentious and poorly understood. Under anthropogenic pressure, ecosystems are predicted to lose predators disproportionately, affecting ecosystem processes (*4*). Current ecological theory predicts that predator loss will affect nutrient cycling by changing prey abundance (density-mediated effects, as in a trophic cascade) (*5*) or prey foraging efficiency (trait-mediated effects) (*6*). These changes can further affect nutrient cycling by altering the species composition or size structure of the prey community. In this study, we examined the effects of predators on nutrient cycling by using the detritus-based insect community in bromeliads. We demonstrate that predation can have counterintuitive effects on nutrient cycling.

Leaves of tank-forming bromeliads (e.g., *Vriesea* and *Guzmania* genera) are tightly interlocking, forming wells that collect water and leaf litter and provide habitat for aquatic insect larvae. The detritus not only supports the insect community but also provides a source of nutrients for the bromeliad. A natural gradient also exists in predation where the major predator, a damselfly larva (*Mecistogaster modesta*), becomes more abundant as the plant grows. Although it has been hypothesized that aquatic insects increase nutrient flux to the bromeliad, this relationship has never been documented.

First, we ran fertilization experiments to determine whether nitrogen (N) or phosphorus (P) limit the productivity of the plant and insect components of this ecosystem (*7*). Both tissue nutrient ratios and fertilization experiments showed that N, rather than P, primarily limits productivity of bromeliads and can limit insect productivity [Supporting Online Material (SOM) text and tables S1 and S2], so we focused on the effects of trophic structure on N cycling. Leaf detritus enriched in ^{15}N was used to trace the movement of N through the food web in bromeliads containing either no insects, detritivores only, or detritivores and predators.

The presence of detritivores alone did not affect the amount of N entering bromeliads from the enriched detritus (Fig. 1A). However, in the presence of both detritivores and predators, there was a significant enrichment in ^{15}N in bromeliad leaves compared with plants containing detritivores alone, indicating that the presence of predators increased the flow of N from litter to bromeliads. This is surprising given that previous studies, consistent with the predictions of density- or trait-mediated effects, have shown that predators decrease litter decomposition by reducing detritivore abundance (*8*) or by decreasing the foraging rate (*9*) of detritivorous arthropods.

We hypothesize that the detritivorous insects, which pupate relatively rapidly, constitute a loss of litter-derived N for bromeliads when they emerge. A survey indicated that detritivorous insects generally have higher N:P ratios than those found in typical litter (Fig. 1B), suggesting that, as leaf litter is consumed, the insects will preferentially retain N in their body tissues and release P. Predation by longer-lived damselfly larvae converts the mobile pool of N contained in detritivores into fecal pellets that can be decomposed by microbes or leached to release N in a form available to the bromeliad. Thus, insects facilitate nutrient uptake by the plant, but only if both predators and detritivores are present.

These results emphasize the importance of the temporal and spatial scales of dispersal for nutrient flux. The emergence of adult insects means that, although detritivores increase resource flux over larval time scales by releasing nutrients from litter, these insects act as a nutrient sink for bromeliads over their entire life span. The faster emergence rate of detritivores compared with that of predators allows predation to reduce the loss of N from the bromeliad. Although we use insects in bromeliads to examine biotic effects on nutrient cycling, our results can give insights into other systems where mobility differs between trophic levels. Some trophic interactions, for instance, involve migratory and nonmigratory species or species that undergo ontogenetic niche shifts. This mechanism may also apply if the prey species has a very different range size than its predator. Given the increased extinction risk of higher trophic levels, understanding the mechanisms whereby predators drive important ecosystem processes is critical in predicting anthropogenic impacts on natural systems.

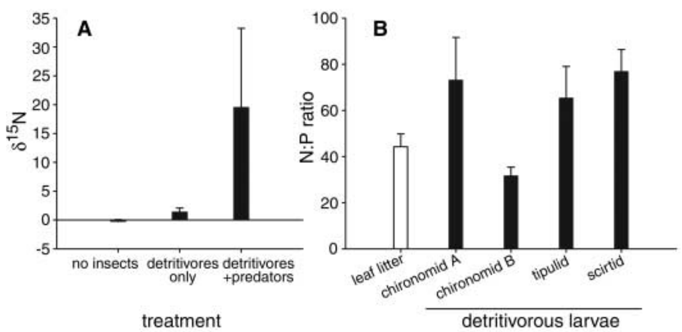

Fig. 1. (**A**) $\delta^{15}N$ in new bromeliad leaves for plants containing no insects, detritivore insects only, or detritivore and predatory insects (mean ± SEM). Bonferroni-corrected *t* test (detritivores alone versus control, $z = 0.478$ and $P = 0.63$; detritivores plus predators versus detritivores alone, $z = 2.36$ and $P = 0.018$). (**B**) Comparison of N:P ratios (by atom) for detritivore larvae and for leaf litter (mean ± SEM). Larger detritivores (chironomid A, scirtids, and tipulids) have N:P ratios higher than that of leaf litter [$F_{1,20} = 5.05$, $P = 0.04$ for linear contrast following significant analysis of variance ($F_{4,20} = 3.66$, $P = 0.02$)]. Chironomid B is a smaller detritivore that accounts for only a small proportion of detritivore biomass in bromeliads.

References and Notes

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Supporting Online Material

www.sciencemag.org/cgi/content/full/314/5801/963/DC1
Materials and Methods
SOM Text
Tables S1 and S2
References

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