10-2001

Essays on Ecological Classics: Discovering an Effect of Insect Floral Herbivory on Plant Population Density and Distribution in a "Green World"

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Bulletin of the Ecological Society of America, Vol. 82, No. 4 (Oct., 2001), pp. 229-231

DEPARTMENTS

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DISCOVERING AN EFFECT OF INSECT FLORAL HERBIVORY ON PLANT POPULATION DENSITY AND DISTRIBUTION IN A "GREEN WORLD"

Introduction

Could insect herbivory be a significant factor influencing the population density of some native plants? I first asked this question in 1971, and this led me to the research that was acknowledged by the 1982 Mercer Award. The question occurred to me in the context of studying the controversy over trophic structure dynamics (Hairston et al. 1960, Murdoch 1966, Ehrlich and Birch 1967, Slobodkin et al. 1967). At the time, herbivory was not considered an important factor affecting either the abundance or the distribution of plant populations.

The only direct evidence of the role of insect herbivory in plant dynamics that I found before initiating my studies in 1973 was published by Cantlon (1969). Preliminary results from an insecticide exclusion of foliage-feeding insects by Cantlon and colleagues showed that recruitment and population density of *Melampyrum lineare* Desr. (Scrophulariaceae) increased when insects, especially the shield-backed katydid (*Atlanticus testaceous*), were excluded. No evaluation of the effect of insect feeding in inflorescences ("predispersal seed predation") on plant regeneration had been done. However, Janzen (1971) had collected evidence illustrating the ubiquity and magnitude of such interactions. In addition, even the protagonists of the "Green World hypothesis"—who argued that herbivores did not limit primary producers—agreed that seed consumers might be an exception (Slobodkin et al. 1967).

Furthermore, it seemed obvious to me that a fundamental, unevaluated assumption was involved in extending the conceptual argument for resource limitation of the primary producer trophic level to population limitation of all species composing that trophic level. This implicit assumption was that the mechanisms of population limitation were identical to the mechanisms of trophic limitation—an assumption for which no experimental substantiation existed. So I set out to test whether flower- and seed-feeding insect herbivores ("predispersal seed predators") could be limiting *populations* of native plants composing the first trophic level, even if resources limited the level as a whole.

The system on which I chose to work in the coastal scrub of southern California presented me with a second fundamental question: Could changes in insect feeding pressure on the flowers and developing seeds of closely related plant species lead to the replacement of one plant species by another along an environmental gradient? The abundance of the plant on which I first observed floral herbivory, *Haplopappus squarrosus* (now called *Hazardia squarrosa*), varied along an 80-km environmental gradient from mountains to ocean in San Diego County, California. Although this species was common in the interior mountains of the coastal portion of the county, I found that its abundance decreased dramatically near the coast. At the same time, I observed that insect herbivory increased near the coast. In fact, this goldenbush species was so sparse in the coastal portion of the ocean-to-mountain gradient that I decided to work on a second species as well, the closely related, quite similar *Haplopappus venetus* (now called *Isocoma veneta*). This species was abundant near the coast but sparse or absent farther inland toward the mountains. The two species thus replaced each other along the 80-km gradient.

The prevailing hypothesis to explain such species replacements, for both plants and animals (see Cody and Diamond 1975), was that selection on similar, related organisms led to physiological differentiation and resource use specialization on the gradient, leading to the competitive displacement of one by the other as environmental conditions and resources changed along the shared gradient. However, my observation of higher levels of floral herbivory on *H. squarrosa* in that portion of the gradient where its abundance was lowest (Louda 1982*a*) suggested another potential mechanism. So, I hypothesized that higher levels of herbivory in one portion of the gradient

limited plant recruitment, leading to systematic variation in plant density along the environmental gradient. If a consistent difference in significant herbivore pressure existed among congeneric species along the gradient, then such herbivory would provide a plausible alternative mechanism to competition in explaining such species replacements.

The research

In my experiments (1973–1978), I compared seed production and subsequent seedling and juvenile densities for plants on which I treated inflorescences with insecticide vs. with water, for both *H. squarrosa* (Louda 1982*a*,*b*) and *I. veneta* (Louda 1983). These experiments, plus my data on the survival of older plants and my finding that there was essentially no permanent seed bank for these two species, allowed me to quantify the demographic consequences of floral herbivory for both species. By doing the same exclusion experiment for each species at multiple sites along the coast-to-mountain gradient, I also was able to quantify the spatial variation in the intensity of floral herbivory, and evaluate its effects on plant densities along the environmental gradient.

Several of my results continue to challenge accepted generalizations in plant ecology. First, insects, rather than resources, limited the number of viable seeds produced by both *H. squarrosa* (Louda 1982*a*,*b*) and *I. veneta* (Louda 1983) at all of the sites along the gradient, challenging the usual assumption that resources for seed maturation limit the number of seeds produced.

Second, the number of viable seeds after predispersal seed predation, rather than the number of microsites for establishment, limited the density of the seedling recruits (Louda 1982*b*), at all sites along the gradient for both *H. squarrosa* (Louda 1982*a*) and *I. veneta* (Louda 1983). These data were the first to quantify the effect of flower- and seed-feeders on the number of seedlings that established under natural conditions, and they challenge the usual assumption that the number of microsites generally limits the number and density of seedlings that establish.

Third, both floral herbivory and seed limitation of seedling density of *H. squarrosa* were greatest in the coastal zone, the area with the lowest adult plant density (Louda 1982*a*). Because the permanent seed bank was low and the survivorship of established plants did not vary across the gradient, the higher rate of seed reduction by insect consumers near the coast provided the best explanation for the greater inland abundance of *H. squarrosa* (Louda 1982*a*). These findings challenge the differential physiological adaptation and competitive displacement mechanism as the only explanation for systematic variation in a plant species' distribution along a large spatial or environmental gradient.

Fourth, the experimental evidence of greater levels of vertebrate herbivory on seedlings of *I. veneta* at inland, as opposed to coastal, sites, provided a plausible mechanism for the compression of this plant's distribution toward the coast (Louda 1983). These data demonstrated that an interaction between insect herbivory, which limited seedling establishment, and vertebrate herbivory, which limited seedling survival, could determine variation in plant density and abundance along a gradient. The outcome challenges the common assumption that if one form of herbivory (insect or vertebrate) is important for plant abundance, then the other is not.

Finally, the two studies together provided the first evidence for an alternate mechanism to competitive displacement for plant species replacement along a spatial gradient—namely, differential rates of herbivory along portions of the gradient (Louda 1989*a*,*b*).

Lessons?

Are there any lessons to be learned from my retrospective view of these studies that might help to facilitate future research? I think so. First, the diversity of my prior experiences contributed significantly to the success of this research, suggesting that breadth of experience is a positive trait and should be encouraged in our training of the next generation of ecologists. My ability to pose the questions and see what needed to be done reflected the training that I had been given by supportive but critical mentors, the help offered by enthusiastic graduate student colleagues, and the mindset stimulated by previous study of both economics and experimental marine ecology. My experience suggests that the potential for new insights is probably unique to each person, and that it may be proportional to the breadth of academic and field experience.

Second, I am convinced that some naivete and luck, combined with an enthusiasm for the challenge and a willingness to work, were crucial, suggesting that we should encourage risky, potentially difficult, but paradigm-challenging research by our students and colleagues. I had no idea that testing my ideas represented a high-risk, low assurance of success type of research endeavor (especially in the pursuit of a degree), and I feel very lucky that no one ever told me that until later! Thus, I suggest that we should go ahead and encourage risk-taking in the design of ecological research at all levels; it just might lead to something interesting!

Finally, I am not sure where I learned to ask: "What is nature trying to tell me?" However, I am convinced that asking this question helped, and that it remains fundamental to the best creative science. Subsequent experience has reinforced my observation that the preconceived theory, the original hypothesis, and even the initial question may not turn out to represent the most productive direction for research. All of these factors are important, because they get the research started. Yet, if I had not questioned the "Green World hypothesis," or if I had stayed with my original question and not questioned the reigning theory on species replacement, I would not have explored differential insect herbivory as an al-

ternative mechanism to competitive displacement for the distribution of plants along gradients. So, when things do not work out as planned (as is often the case in field research!), my experience strongly suggests that one should ask: "What is nature trying to tell me?" I am convinced that doing so has made a major difference in the quality of the resulting research done by me and my students.

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