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The Ecological Complexities of Biological Control: Trophic Cascades, Spatial Heterogeneity, and Behavioral Ecology

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Abstract: Biological control can be considered an intentional induction of a trophic cascade, whereby the addition of herbivores' natural enemies or other habitat manipulations effectively enhance natural enemy populations, lead to reduced herbivore populations or feeding damage, and indirectly improve or protect plant health, agricultural yield, or the condition of some other biotic population or community of interest to man. The following set of papers (Denno et al., 2008; Ram et al., 2008; Stuart and Duncan, 2008; Spence et al. 2008) offer insights into the broad- and fine-scale factors that ultimately contribute to the success of biological control efforts. Many of the ideas herein were presented and discussed during a special session at the 2007 Annual Meeting of the Society of Nematologists. The goal of this session was to examine explicitly the ramifications of spatial and temporal heterogeneity in the context of effective biological control. The biological focus was primarily on interactions involving entomopathogenic nematodes (EPN), although many of the authors' conclusions are applicable to other types of nematodes, soil fauna and natural enemies in general.

Key words: Bioassay, biological control, bush lupine, citrus, entomopathogenic nematodes, meta-analysis, plant parasitic nematodes, trophic cascade.

It is universally acknowledged that ecosystems are heterogeneous in space and time. Even within agricultural ecosystems, where we typically attempt to minimize variability and thereby increase the predictability of yield, we often see variability of an order of magnitude or more in nutrient availability at both broad and sub-meter spatial scales, resultant differences in plant rooting behavior, and spatial and temporal shifts in the populations of soil micro- and macrofauna. Relationships among these kinds of factors create the exceedingly complex and multidimensional milieu that is the soil, and the specifics of how to integrate the reality of this heterogeneity into biological control approaches remain obscure and decidedly murky. The authors in this special feature make strong arguments for the prominent role of soil variability in driving interactions between plants and their soil-borne herbivores and natural enemies; they also focus on potential strategies for improving the probability of successful biological control in these heterogeneous systems.

The opening paper (Denno et al., 2008) uses a meta-analytical approach to assess the tendency of entomopathogenic nematode applications to induce a trophic cascade, a negative effect on herbivores that translates into an increase in crop production. These authors draw on the extensive literature on aboveground intraguild, multiple-enemy interactions to develop hypotheses regarding such interactions involving EPN and other predators and pathogens in the soil. Studies of trophic cascades per se in soil systems are rare, but the authors identified 35 published articles that provided data on both arthropod hosts and plant responses to EPN additions. The results of this meta-analysis showed strong evidence of EPN-induced trophic cascades: consistent, negative effects of EPN additions on their hosts and a consistent, positive, indirect effect of EPN additions on herbivore associated plants. However, as the authors described, intra-guild interactions can interfere with the effectiveness of cascades, and the paper ends with a call for research specifically focused on how, where and when antagonistic effects due to EPN additions and multiple-enemy interactions might affect soil food webs.

The second manuscript in this series (Stuart and Duncan, 2008) shows examples of how such multiple-enemy interactions might generally take place within Florida citrus groves infested by the citrus root weevil, *Diaprepes abbreviatus* (L.). This paper begins to dissect the complex temporal and spatial linkages between soil texture, endemic EPN communities, EPN additions, EPN antagonists, such as nematophagous fungi, and free-living, bacterial-feeding nematodes. The authors found, for example, that chicken manure mulch applications can cause short-term reductions in EPN prevalence that can then be followed by long-term increases in EPN prevalence. These same mulch applications resulted in a long-term reduction in free-living, bacterial-feeding nematodes that compete for insect cadavers and a reduction in densities of nematophagous fungi. Future research by this group promises to continue exploring these complex paths. From a somewhat different perspective, these authors also present results of a soil manipulation experiment in which the soil texture around young citrus trees was altered in an effort to create "hotspots" of persistent EPN abundance. This experiment involved creation of 1-m-diam. "islands" of coarse-textured Central Ridge sand for planting trees within a citrus grove located on the finer sands of the Flatwoods region of Florida. Growers began using this

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strategy to improve drainage, reduce pathogen prevalence and enhance tree growth, but it appears to have the side effect of increasing persistence of inoculated EPN in the zone immediately around the roots of the young trees. This suggests a technique for cultural biological control that might improve the long-term effectiveness of applied EPN in Florida and elsewhere.

The next paper in the series (Ram et al., 2008) summarizes 13 years of data and presents new findings from the bush lupine—ghost moth—EPN system at Bodega Marine Reserve. This system represents one of the best-documented examples of a terrestrial trophic cascade driven by an EPN. One of the most intriguing aspects of this system is the significant differences observed in long-term EPN incidence at stands of bush lupine within the Reserve, with long-term incidence differing by more than an order of magnitude between low- and high-incidence sites, but with no observable linkage in the availability of lupines or ghost moths. The authors review a range of mechanisms that might drive this persistence, including differences in survivorship, dispersal and metapopulation dynamics. Survivorship appears to be similar among high- and low-incidence sites, but the authors observed evidence of significantly higher rates of colonization-extinction at high-incidence sites that might underlie patterns of persistence at these sites. Further, at high-incidence sites, there is also evidence of intra-annual vertical migration, which might also contribute to persistence. Within a given site, they have observed significant intra-annual variation in the horizontal extent of EPN patches, with patches swelling to large size during the wet season and contracting to the moist lupine rhizospheres in the dry season. Thus, both horizontal and vertical changes in population distributions could play a major role in the biology of the EPN *Heterorhabditis marelatus* and the interactions between these three closely associated species within the trophic cascade.

The final paper in the special feature (Spence et al., 2008) addresses the question of nematode behavioral complexity in response to a range of soil-borne cues. Specifically, it addresses the always relevant issue of the transferability of the results of laboratory and greenhouse bioassays to predictions of EPN effectiveness in the field. One of the attractions of nematological research is the ability to conduct assays in the laboratory—the organisms typically are small, often with short life cycles, and experiments typically can be conducted without many of the constraints imposed by field conditions. However, as the authors point out, such assays must be conducted with explicit consideration of (i) the physical and biological context in which the nematode-host interaction takes place within the soil, and (ii) the potential differences in the role of cues in long-range host finding, during short-range host finding, and after the nematode has come into contact with the host organism. This paper broadens the focus of the feature beyond consideration of EPN and examines the responses of both plant- and animal-parasitic nematodes. The authors finish by stressing that while the simplified arenas typically used to examine host finding most certainly will continue to play a prominent role, researchers should more explicitly consider whether the gradients in such assays represent the kinds of realistic exposures that the organisms encounter in the natural environment. Only when laboratory assays properly focus on nematode responses to the range of cues and cue strengths found within the soil can we address how the spatial heterogeneity in such cues acts to structure interactions between these nematodes and their hosts.

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