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Vertical stratification in arthropod spatial distribution research

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Spatial heterogeneity within individual host trees is often overlooked in surveys of phytophagous arthropod abundance and distribution. The armored scale *Aulacaspis yasumatsui* is controlled by the predator *Rhyzobius lophanthae* to a greater degree on leaves at 75-cm height than on leaves at ground level within its host tree *Cycas micronesica*. The direct influence of elevation on the predator indirectly generates vertical heterogeneity of the scale insect. Arthropod sampling schemes that fail to include all strata within the vertical profile of the host tree species may generate misleading outcomes. Results indicate that submeter increments can reveal significant differences in vertical distribution of phytophagous insects, and that inclusion of observations on other organisms that interact with the target arthropod may illuminate determinants of vertical heterogeneity.

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Biological control of the invasive armored scale *Aulacaspis yasumatsui* has been ineffective in the Mariana Islands. The 2003 invasion of this scale threatens native *Cycas micronesica* trees in natural habitats and *Cycas revoluta* in the urban landscape. The successful introduction of the predator *Rhyzobius lophanthae* in 2005[1] was augmented by the unsuccessful introductions of the parasitoids *Coccobius fulvus* and *Aphytis lingnanensis*. Competitive exclusion of the parasitoids by the voracious predator may partly explain why the parasitoid introductions were unsuccessful.

The onset of mortality of the in situ *C. micronesica* population was rapid following the scale invasion[2,3] and mortality has been sustained to date. To inform management decisions, we have attempted to determine why predator control of the scale infestation has been ineffective. We first noticed that mortality of seedlings and small juvenile plants occurred prior to the onset of mortality of mature trees.[2] This population-level response to the pest invasion may have been due to a greater susceptibility of the small plants to the scale infestations and/or ineffective biological control at these lowest strata of the vertical range in available prey. More recently we determined that the size differential between scale and predator allows the pest to infest *Cycas* plants in locations that are inaccessible to the predator.[4] Following removal of the physical obstructions that protect the hidden scale insects, the *R. lophanthae* predation level reaches that of scale insects located on fully exposed plant surfaces in only one week.[5]

Interesting aspects of arthropod spatial heterogeneity have emerged from this case study. For example, when the scale insect immigrated into a new *Cycas* habitat, the initial trees that were infested became fully covered by scale insects before the adjacent trees became infested (**Fig. 1**, top). Now that all seedlings and juveniles have been killed, the only *Cycas* leaves located near the ground are on side stems of some mature trees. In these individuals, often there is a scale outbreak on the ground-level leaves on trees that have minimal scale insects on the upper leaves of the same tree (**Fig. 1**, bottom).

Our latest efforts in trying to understand the three-way interactions among the host plant, herbivore, and predator followed predation of scale insects on container-grown *C. micronesica* seedlings that were at ground level or suspended at 75- or 150-cm height. A significant increase in predation of scale insects occurred by

Figure 1. Spatial heterogeneity of *Aulacaspis yasumatsui* infestations on *Cycas* trees occurs after the initial invasion of a habitat whereby the initially infested tree becomes heavily infested before the scale crawlers migrate to surrounding trees (top). Vertical stratification of *A. yasumatsui* infestations on *Cycas* trees occurs whereby the ground-level leaves become infested, because *Rhyzobius lophanthae* predators preferentially attack scale on mature leaves at greater heights (bottom).

artificially elevating the seedlings to the height of mature tree leaves.[6] This latest addition to our understanding of the interplay between the scale pest and beetle predator contributes to the study of spatial heterogeneity and biological control efforts.

Spatial Heterogeneity

Arthropods dominate in forest ecosystems in terms of species abundance and are related to many ecological processes. Accurate assessment of arthropod incidence can clarify various roles in ecosystem function and inform plans for conservation.[7] Considerable variation in arthropod abundance across landscapes and from tree to tree is universally considered in design of arthropod abundance studies. However, spatial heterogeneity within individual host trees is often overlooked in survey methods, possibly due to the logistical difficulty of accessing various components of host plants. In surveys of scale insects, for example, methods have often treated within-tree variation as homogeneous,[8] or have attempted to estimate population sizes based on measurements on the tree trunk near the ground level.[9]

Biological control programs. Knowledge of the spatial distribution and abundance of a target arthropod within each sampling site is essential to accurately estimate the potential impact of herbivorous insects on host trees or biological control success. Surveys of the predator, parasitoid, or target herbivore are therefore mandatory components of validating success or failure in biological control efforts of arthropod pests. In these sampling schemes, distributions of the arthropods are known to vary in distance from release sites, but are generally assumed to be uniformly or randomly distributed within individual host trees surveyed. For example, when we released the *R. lophanthae* to control *A. yasumatsui* in Guam, we did not consider the influence of elevation on predator behavior. Therefore, our initial surveys were at one fixed height.[1] Similarly, when *C. fulvus* was released to control *A. yasumatsui* in Florida the subsequent survey locations were random.[10]

Our study indicates that reliance on either of these survey approaches may generate inaccurate results. Because of the high degree of within-tree heterogeneity in population density, the total population size of herbivorous insects on an individual tree cannot be predicted from measurements that ignore the full height range of the prey.

Increments. When elevation is considered in an arthropod sampling scheme, gross increments are typically employed, for example ground layer, bole and large limb layer, and upper canopy layer. This approach may indeed reveal that elevation influences arthropod abundance, but it does little to understand the incremental changes with elevation. Our study corroborates that of Beaulieu et al.,[11] by underscoring that sub-meter vertical increments may significantly influence arthropod abundance. Therefore, a full understanding of the influence of vertical stratification on arthropods will require greater emphasis on precision that can only be achieved with the use of small height increments in sampling protocols.

Determinants of vertical heterogeneity. Variation in abiotic factors, tree architecture, resource availability, and arthropod behavior are some of the proposed mechanisms that lead to the vertical stratification of arthropod abundance.[12,13] However, when vertical stratification of arthropod abundance has been studied, a descriptive approach is often employed. This approach allows speculation on causes of the observed patterns, but does not enable the validation of mechanisms that generate the observed variation.

Our study presents a case where influence of elevation within a host plant on arthropod herbivore incidence is indirect, and the influence of vertical stratification on the behavior of a third organism determines the herbivore spatial patterns. Wardhaugh et al.,[14] reported greater scale abundance in elevated side branches of *Nothofagus* forests and briefly discussed possible determinants. However, they did not directly assess the role of biological control. Schal and Bell[15] used trapping methods to reveal a vertical migration of some cockroach species in patterns that infer predator avoidance. They also did not directly measure predation. Our case study is the first to my knowledge that directly measured the role of vertical stratification of biological control on incidence of a scale herbivore during its immobile life stage.

The third organism in our example was a predator. However, plant–insect–microbe[16] and specifically plant–insect–pathogen[17] interactions can determine insect abundance and distribution, and these three-way interactions may indeed define vertical stratification of arthropods in some systems. I conclude that while studies of interactions among coexisting species are more difficult, a simplistic single species approach to studying vertical stratification of arthropods is inadequate. Researchers should be careful not to overlook the role of interacting organisms in defining the variation in phytophagous arthropod abundance throughout the height range of host trees.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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