A DANGER IN DENSITY: THE EFFECTS OF HOST DISTRIBUTION ON LEAF EPIPHYTE ABUNDANCE

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Abstract: Natural enemies of plants can influence plant distribution and abundance. Epiphylls are generally regarded as structural parasites of plants, a kind of natural enemy. I studied epiphylls of *Geonoma cuneata* to test if the local density of this understory palm affects the density of epiphylls as plant density can affect herbivore density. This extension of the Janzen-Connell model predicted that aggregated plants would have a greater epiphyll density. Epiphyll density was higher in aggregations of *G. cuneata*, which could produce a feedback in which plant density affects epiphylls, which in turn affects plant density.

Key Words: phyllosphere, foliicolous epiphytes, fishtail palm

INTRODUCTION

One reason cited for the apparent imperative of wide dispersal in plants is to escape natural enemies. The theory is that if seeds are dispersed close to the parent tree, herbivores, parasites and other natural enemies of that species of plant will more easily locate or spread to the vulnerable young plants, preying on them, reducing their chance to survive and grow, and reducing their fitness. This force is especially strong in tropical rainforests, and has been invoked as a reason why the local diversity of tropical trees is so high (Queensborough et al. 2007). It follows that if plant natural enemies are important, the risks for adult plants, as well as seedlings, may be higher when the plants occur in high density.

The phyllosphere is of broad importance because most of terrestrial photosynthesis occurs on the surface of leaves. In tropical forests with high moisture, foliicolous epiphytes are conspicuously abundant on the surface of lichens. While the knowledge of their ecology is limited, the leaf surface they occupy has clear detrimental effects on the host plant (Pinokiyo et al. 2006). I studied the fungal, lichen and bryophyte epiphylls of *Geonoma cuneata*, a common understory palm, at the La Selva biological preserve in Costa Rica. I compared epiphyll density on *G. cuneata* leaves of plants in high and low density patches, as well as plants within both types of patches with and without immediate neighbor plants of the same.

I hypothesized that high density would facilitate the spread of epiphylls that can grow on *G. cuneata* from one plant to another, and that density at the scale of the local patch would be more important in the spread of foliicolous epiphytes than the presence of immediate neighbors. From these hypotheses, I predicted that I would find greater epiphyll density for plants in dense patches than for isolated plants and that I would find little or no difference in epiphyll density between plants with and without immediate conspecific neighbors.

METHODS

On the 18 – 20 February 2008, I collected leaf samples from the Camino Circular Cercano and Camino Experimental Sur trails of the La Selva biological preserve, Costa Rica. I walked a random number of strides (1 – 60) on the trail, and five meters off the trail to opportunistically look for two *Geonoma cuneata* plants to measure. I sampled plants in high density stands, defined as fifteen or more other *G. cuneata* within a five meter radius, and plants in low density areas, defined as less than four plants within a five meter radius. For each plant I recorded if it had any neighboring *G. cuneata* within a one-meter radius.

For each plant I measured stem length and ranked available light on a scale from one to five. I measured epiphyte density on a random leaf of each sample plant, with the restriction that it be on the fourth growth ring to control for leaf age. On each leaf, I ran two 25-cm transects, measuring at each cm the presence or absence of fungus, lichen or bryophytes. I added these values together to estimate total epiphyte density for the leaf. I applied a square root transformation to normalize the data for statistical analysis.

RESULTS

There was a greater density of total epiphytes on the leaves of plants in dense patches than in isolated patches ($t = 8.56$, $df = 46$, $p < 0.0001$). of the same pattern applied for all three ephiphyte taxa: fungus ($t = 3.86$, $df = 46$, $p = 0.0004$), lichen ($t = 7.30$, $df = 46$, $p < 0.0001$) and moss (Kruskal-Wallis $S = 690$, $df = 22$, $p = 0.0058$).

There was no significant difference in total epiphyll density in isolated patches between plants that had close neighbors vs. those that did not ($t = 0.14$, $df = 22$, $p = 0.89$), nor was there any significant difference for fungus, lichen or moss density. In dense patches there was greater epiphyll density for plant with close neighbors ($t = 2.72$, $df = 22$, $p = 0.0125$). This difference was largely driven by a greater lichen density for plants with close neighbors ($t = 4.19$, $df = 22$, $p = 0.0004$). Fungal abundance varied in the same direction ($t = 1.74$, $df = 22$, $p= 0.096$), and moss density did not vary (Kruskal-Wallis $S = 162.5$, $df = 22$, $p = 0.44$).

There was no change in total epiphyll density with height of plant stem ($r^2 =0.01$, $df= 1,46$, $p= 0.57$). There was a nearly significant trend of decreasing total epiphyll density with increased sunlight ($r^2 = 0.07$, $df = 1,46$, $p = 0.08$). This trend was driven by a decrease in lichen density with increased light intensity ($r^2 =0.10$, $df= 1,46$, $p= 0.0001$). There was no significant change in fungus density($r^2 = 0.00$, $df = 1,46$, $p = 0.77$), or moss density ($r^2 = 0.00$, $df = 1,46$, $p = 0.64$) with light intensity.

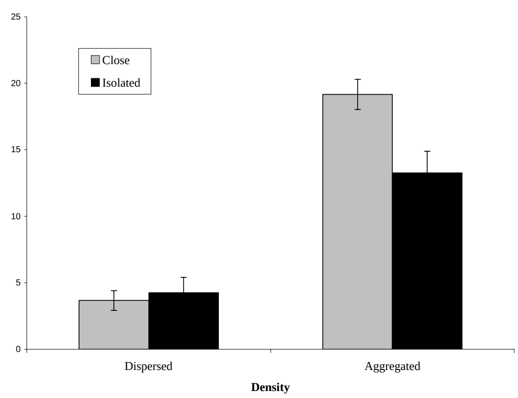

Figure 1. Estimated epiphyll density by *G. cuneata* density at five-meter (dispersed vs aggregated) and one-meter radius (close vs. isolated).

DISCUSSION

The number of *Geonoma cuneata* within a five-meter radius was related to the abundance of epiphylls. Presumably foliicolous epiphytes can disperse from plant to plant more easily when their host is aggregated. This explanation requires that epiphylls be in some part dispersal limited, which seems likely since the surface of the leaf is never fully covered. The greater epiphyll density for plants with close neighbors in aggregations may reflect that higher *G. cuneata* density at the scale of one-meter radius intensifies the effects created by the five-meter scale aggregation, further facilitating the spread of epiphylls from plant to plant. Notably, local abundance did not produce the same effect. Apparently density at the five-meter scale is more important in the spread of epiphylls. This might be a clue about the mode and tempo by which epiphyll propagules move from plant to plant.

Because epiphyll density did not change with stem length, I inferred that variation in plant size (presumably related to age) did not influence the effect of host plant aggregation on epiphyte density. Similarly, light had little effect, except for lichens, which were negatively related to light, perhaps due to the effects of desiccation or heat stress.

Fungal, lichen and bryophyte densities all increased similarly with aggregation, suggesting similarities in their ecology. Moss was only found on leaves of aggregated plants, and of these relatively few. Yet moss tended to occur at high density when present on a leaf. This may indicate that relative to the other epiphylls they are competitively dominant and especially dispersal limited. Lichens were the most abundant epiphylls in *G. cuneata* and showed the greatest response to changes in density. Fungus was affected to a lesser degree by changes in host density, and this may be due to its higher density on dispersed and isolated host plants. Foliicolous fungi may be better dispersers than lichens or bryophytes.

One problem with the application of the natural enemies theory is that it is unclear if epiphytes are truly structural parasites, or in fact commensalists The epiphytic cover of many *G. cuneata* leaves was enough that it seems probable that they reduce photosynthesis, and these understory plants are probably generally light limited. While epiphylls are often thought of as having a parasitic relationship with their host plant, other research has pointed to possible benefits of epiphylls for host plants, complicating the relationship. There is some evidence that foliicolous epiphytes may reduce leaf herbivory or provide extra nutrients (from nitrogen fixing lichens) that compensate for, or even outweigh, their detrimental effects (Pinokiyo et al. 2006). It seems clear that plant dispersion influences the epiphylls. If the epiphylls are ecological antagonists or protagonists of the plants, then the epiphylls may produce a feedback system in which the effect of plant density on epiphylls may in turn determine the distribution of host plants.

LITERATURE CITED

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