was not different from that under the canopy (F=28.29; df=2,6; P=1.000; Fig. 2)

Tree seedling densities did not differ significantly between gap (5.9 ± 1.77) and edge (7.9 ± 1.16; F=1.694; df=2,6; P=1.000), gap and under canopy (4.31± 1.07; F=1.694; df=2,6; P=1.000), or edge and under intact canopy (F=1.694; df=2,6; P=1.000; Fig. 3)

DISCUSSION (JHB)

The high number of morphospecies unique to each of the three habitats supports our hypothesis that the variation in microhabitat in and around gaps contributes to higher species diversity. However, the significantly higher diversity and richness in the gap edge zones as opposed to other habitats and the lack of significant difference in density across the three zones did not substantiate our hypothesis that richness and diversity should be highest in the gap center. Higher diversity and richness in the gap edge area may have resulted from many species existing both in an intermediate environment, as well as in a gap center or canopy zone. However, because 81 of 88 morphospecies were unique to a particular zone, it does not seem to be the case that the edge zone is an "intermediate" environment in which species exist.

Furthermore, in the gap edge zone, where we expected to see a high number of shared species, or those that exist in at least two habitats, 46 of 51 species were found to be specific to that zone. Despite the greater diversity in the gap edge rather than the predicted gap center, the idea that variation in microhabitat from gap to canopy increase diversity and richness is supported by our data .

However, because so few species were shared among replicate treefalls within each habitat, the high number of species found in only one microhabitat type may not be representative. Our small sample size greatly limits the relevance of our statistical tests. To relate each species to a particular habitat, we would need a much larger sample to confirm that the high numbers of distinct species we found in each sampling area were in fact truly unique and not shared with other habitats. Further research is also needed to quantify life-history strategies of each plant species along the gradient from gap center to intact forest, and how these strategies affect their distribution.

In conclusion, our results show that microhabitat variation over the space of a few meters could have a profound impact on species composition and diversity of tree seedlings and saplings of tropical cloud forests. These results support the idea advanced by Connell (1978) that disturbance, as evidenced here by tree fall dynamics, is an important mechanism for the maintenance of diversity and richness. Without disturbance and the corresponding creation of new habitats, species diversity would have been lower.

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TERRITORIAL DEFENSE BY *COLIBRI THALASSINUS* : IMPACT ON OTHER HUMMINGBIRD VISITS

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Abstract. (SDK) We investigated the effects of patch defense on hummingbird behavior. Two patches of a shrub species of *Fuchsia* with equal flower densities, one defended by a territorial *Colibri thalssinus* and one undefended, were observed. As predicted, the total duration of foreign hummingbird visits was shorter in the defended patch. However, contrary to our predictions, the total number of foreign hummingbird visits was greater in the defended patch. The latter were mostly fly-bys while those to the undefended patch were feeding bouts. Our findings suggest that territorial vocalizations made by *Colibri* may not deter other hummingbirds from visiting a patch, but such defensive behaviors may inhibit vistors from feeding within that patch.

INTRODUCTION (JLM)

Many species of hummingbirds specialize on certain types of flowers which they aggressively defend. This defense can lead to both intra- and interspecific aggressive interactions among hummingbirds competing for a common nectar resource.

Colibri thalassinus, the green violet-ear hummingbird, is found during the dry season (December-March) at Cerro de la Muerte, Costa Rica. During this time, *Colibri* feeds almost exclusively on *Centropogon valerii* which it defends against both conspecifics and hummingbirds of other species (Colwell et al. 1974). *Colibri* defensive behavior consists of vocalizations, displays, and chases (Colwell et al. 1974).

We examined the effects of patch defense by a *Colibri* individual on other hummingbird visitations to that patch. We hypothesized that, in comparison to undefended patches of flowers, *Colibri*-defended patches would be visited by fewer other hummingbirds and the total duration of these visits would be reduced.

METHODS (CDW)

Our study sites were located at Cerro de la Muerte, near the Albergue Cuerici Biological Station in San Jose Province, Costa Rica, at an elevation of about 2700 m. At the time of this study, *C. valerii* was low in abundance and we often observed *Colibri* vocalizing near patches of an unknown species of *Fuchsia*, which was an abundant tall flowering shrub in our study area. *Colibri* is morphologically capable of exploiting nectar from *Fuchsia* flowers, but we did not know whether *Colibri* actually utilizes *Fuchsia* when *C. valerii* is scarce.

On the morning of 26 January 1995, we made one-hour observations of hummingbird visitors to two patches of understory *Fuchsia* flowers. The patches contained a roughly equal density of *Fuchsia* inflorescences. Using percent of time each patch was occupied by a *Colibri* individual to determine defense, we decided that one patch was defended by a *Colibri* individual and the other patch was undefended. The territorial *Colibri* was present in the first patch approximately 90% of the observation period, whereas there was a *Colibri* in the undefended patch only about 30% of the observation period. The defending individual made high-pitched vocalizations constantly, whereas there was no persistent singing in the undefended patch.

For each observation period, we noted the presence of any hummingbird, including brief visits (<5 seconds) which we called fly-bys. Visits of >5 seconds were timed and classified as either feeding or resting, and the duration of each visit was

recorded. We also tracked and recorded the movements of the focal *Colibri* within each floral patch.

RESULTS (CDW)

We observed more total visits, but fewer feeding and perching visits, to the area defended by the *Colibri* than to the undefended area (Fig. 1). The total duration of visits to the undefended area was greater than to the defended area (Fig. 2).

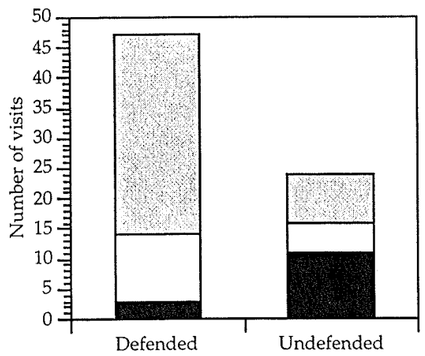

FIG. 1. Number of visits by foreign hummingbirds in areas defended and not defended by *Colibri thalassinus* (black=feeding, white=perching, gray=fly-bys).

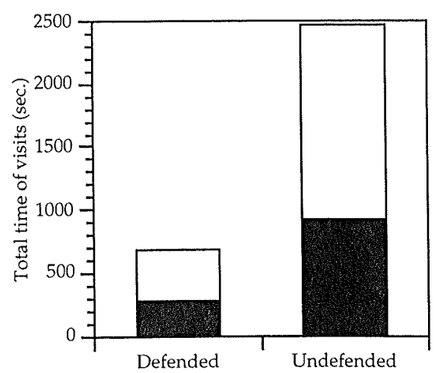

FIG. 2. Total duration of non-flyby visits to areas defended and not defended by *Colibri thalassinus* (black =feeding, white=perching).

Behavior of the territorial *Colibri* included repeated and consistent vocalizations from a high perch within the defended floral patch. We also observed the focal hummingbird leave one tree and perch in another when following the movement of foreign hummingbird patch visitors.

DISCUSSION (SDK)

Our first hypothesis that the number of hummingbird visitors should be fewer in a defended floral patch was not supported. Indeed, there were more visits to the defended patch, suggesting that vocalizations by a territorial *Colibri* do not deter visitors before arrival at a patch. However, we did find important differences in the types of visits in the defended and undefended patches. The majority of hummingbird visits in the defended patch were flyby encounters, indicating the reluctance of visitors to settle in a defended area. In contrast, the majority of visitors to the undefended patch remained for more than five seconds and a greater proportion of visitors also fed. Thus, it is the proportion of different types of hummingbird visits that more accurately differentiates between a defended and undefended floral patch.

The second hypothesis, however, that the total duration of hummingbird visits will be shorter in a defended floral patch, however was supported. Continued vocalizations by the territorial *Colibri* probably alerted other visitors of its presence, and deterred them from staying and feeding in the patch. In addition, we observed the territorial *Colibri* change locations from one tree to another, following the movements of visiting birds. This following behavior, while not an obvious chasing encounter, suggests an aggressive response by the defending *Colibri* to deter the foreign hummingbird. Thus, threat of an aggressive reaction from the territorial *Colibri* seems to account for a shorter duration of hummingbird visits.

While there has been extensive documentation of *Colibri* territorial

behavior in patches of *Centropogon valerii* (Colwell et al. 1974), we are unaware of studies of *Colibri* defensive behaviors on other floral species patches. Although we did find three plants of *C. valerii* within the defended floral patch, it appears that the territorial *Colibri* guard the surrounding *Fuchsia* plants as well. We were unable to find *C. valerii* flowers in the undefended patch. *Fuchsia* defense suggests that the *Colibri* utilizes additional flower species as a nectar resource when preferred *C. valerii* are scarce. The generality of our conclusions, however, is limited by our small sample size.

Additional studies should examine the significance of territorial *Colibri*'s effects on hummingbird visits to a defended floral patch. It would also be important to differentiate between territorial, defensive behaviors and mating behaviors of *Colibri*. It is possible that *Colibri* vocalizations from high perches may serve dual purposes for defense and mating. It remains to be seen, however, if mating vocalizations of *Colibri* would deter hummingbird visitors from an occupied floral patch.

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