

# FORAGING BEHAVIORS IN FISH-EATING BATS (*NOCTILIO LEPORINUS*)

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*Abstract:* Predator-prey interactions are largely affected by prey availability, which can be influenced by many abiotic and biotic factors. We studied the fish-eating bats, *Noctilio leporinus*, in Corcovado National Park, Costa Rica. Using model selection, we assessed the relative importance of four factors (tide, time, location, and number of fish jumps) on bat foraging and abundance. The best predictors of bat abundance were location, time of night, and the interaction of these two factors. These also were the best predictors of bat fishing frequency, although few fishing attempts were observed. Contrary to conclusions from previous studies in the same lagoon, tide and fish activity were not significant predictors of bat abundance or foraging. Circling behavior, which was most common near the roost, may facilitate defense of roost or assembly of small groups that aid in foraging. Bats upstream often flew in a straight line past our observers possibly searching for more optimal foraging locations. These bats probably forage at a range greater than our sample area.

*Key words:* bat foraging behavior, coastal systems, greater bulldog bat, predator-prey interactions, Río Sirena

## INTRODUCTION

Prey density may be the most important factor influencing foraging behavior among carnivorous animals. Prey density may also affect feeding success, particularly when prey are difficult to find or hunt, or when abundant refugia from predation are available.

In aquatic systems, both marine and aerial piscivores prey on fish, and fish density determines the success of these predators. Suitable prey fish below some threshold depth may be out of reach to all but the most effective diving terrestrial piscivores. In coastal systems, tidal fluctuations may interact with

bottom topography to determine the abundance and distribution of habitats that subject fish to aerial predation. In addition, tide likely influences marine predatory fish density, which could drive prey from deep water refugia into shallower water where they are vulnerable to aerial attack. Thus, the presence and activity of aquatic predators may benefit terrestrial piscivores by increasing prey accessibility. Alternatively, the prey fish distribution and position in the water column may be unrelated to predation or tide.

Fish-eating bats (*Noctilio leporinus*) have been reportedly observed every year since at least

1994 in a large lagoon at the mouth of the Río Sirena in Corcovado National Park. Since 1998, the bats have been the subject of four other Dartmouth FSP projects (Yale et al. 1998, Veysey et al. 2000, Leslie et al. 2001, Valderrama and Madigan 2005). Previous work suggested that bats may focus their hunting effort on times and places where large aquatic predators including bull sharks (*Carcharhinus leucas*) and crocodiles (*Crocodylus acutus*) are feeding most actively, driving smaller fish to shallower water (Leslie et al. 2001, Veysey et al. 2000). Bat foraging may also vary with tide, which simultaneously alters the total volume of water in the lagoon, the proportion of shallow water, and perhaps the density of marine predatory fish. Yale et al. (1998), Veysey et al. (2000) and Leslie et al. (2001) all found that bat fishing attempts peaked at high tide, most likely due to an increase in small fish density.

We found a colony of *N. leporinus* living in a large, common mangrove tree (*Mora oleifera* : Fabaceae) ~200 m northeast of the mouth of the Río Sirena (within 5 m of the present boat landing). We observed bats foraging in the lagoon at night. Preliminary daytime observations suggested that fish activity varied systematically by tide and/or time of day and roughly correlated with hunting activity by herons and shorebirds.

If bat foraging depends on prey density, then factors that determine prey availability should also influence foraging behavior. In Río Sirena lagoon, tide, time of night, location of observation, and fish activity (as measured by fish jump frequency) are likely to influence prey availability and subsequently bat abundance and fishing behavior. Specifically, we predicted that bats would forage more at high tide downstream of their nest, where a broad shelf with shallow water may act as a refuge for prey fish from aquatic predators but make them highly susceptible to bat attack.

## METHODS

Starting at dusk on 8 and 9 February 2008, we sampled a *N. leporinus* colony at the Río Sirena Lagoon ca. 1.5 km northwest of Estación Biología Sirena, Corcovado National Park, Costa Rica. We observed bats at 3 locations along the river: at the roost, 50 m downstream from the roost, and 50 m upstream from the roost. Beginning at 1800, 2200, and 0430, which roughly corresponded to the peaks of high, low and then a second high tide [Feb 8-9 high: 15:59, low: 22:02, high: 04:14; Feb 9-10 high: 16:37, low: 22:42, high: 04:52], we conducted 5 10-min observations (separated by 2 minutes) of all visible individuals. We used a flashlight to illuminate bats, following individuals for as long as

possible, and recording their fishing attempts (contact with the water), locations (0-2, 2-4, or 4+ m from either bank), and flight patterns (circular or straight). We also recorded the maximum number of bats observed during that time period, and counted the number of audible fish jumps (large or small fish), as Leslie et al. did to quantify large fish activity in 2001.

We created a depth map of the lagoon and upstream region to

evaluate a potential correlation between lagoon depth variation and fish and bat activity. We used 80 GPS and depth measurements at ca. 5 m intervals at or near high tide on 8 February. We also remeasured a point in the center of the river at low tide to calculate local tidal flux.

## RESULTS

TABLE 1. Comparison of alternative models predicting bat abundance in Río Sirena Lagoon, Costa Rica. Each row represents one theoretical driver of bat abundance and behavior. The three righthand columns indicate the best linear statistical model (minimum AIC with all parameters being statistically significant at  $P < 0.05$ ) that includes this theoretical driver;  $\Delta AIC$  values are reported relative to the best model overall.

Variable	Biological Reason	Best Model	$r^2$	$\Delta AIC$
Location (L)	Proximity to nest may affect number of flying bats	$Y=f(T, L, T*L)$	0.902	0
Time (T)	More bats fly at certain times of night	$Y=f(T, L, T*L)$	0.902	0
Tide (TD)	Bat activity may vary with water depth	$Y=f(TD, L)$	0.709	9.3
Fish Jumps (F)	Fish jumping indicates marine predator activity which may influence bat activity	$Y=f(L, F, T*L)$	0.913	-0.42

On each of two nights, we observed 44 bats emerge from their roost on the Río Sirena Lagoon beginning at dusk (~18:15) and returning at dawn (~05:30). Generally, bat density and behavior differed as a function of time of observation (dawn, dusk or night) and by location of observation.

Circular flight patterns were significantly more common near the bat roost. We observed more than 3 times as many bats flying in circular pattern in this location than at the upstream or downstream sampling points ( $F = 37.4$ ,  $df = 2,7$ ,  $P = 0.0002$ ; Fig. 1c). None of the other main effects or interactions were significant predictors of flight pattern. Bats flying in a circular path sometimes fished, often landed briefly near the nest entrance, and occasionally entered the nest. Many of the straight-flying bats at the sites away from the roost flew well out of sight, frequently in an upstream direction.

Although few fishing attacks were observed overall, the proportion of bats fishing reached a maximum of 23% ( $\pm 1 \text{ SE} = 18.3 - 83.2\%$ ) at dawn at the downstream site (Fig 1e). The model predicting proportion of bats fishing included location, time, and a time\*location interaction ( $F = 7.29$ ,  $df = 8,8$ ,  $P = 0.0055$ ). However, only the location\*time interaction was a significant predictor of bat fishing proportion ( $F = 12.82$ ,  $df = 4,8$ ,  $P =$

0.0015; Fig. 1e). Downstream, a greater proportion of bats foraged at dawn ( $P=0.0004$ ), while at the roost, fishing behavior didn't vary much over time ( $P = 0.49$ ), with the greatest proportion of bats fishing at dusk. Upstream, no bats foraged at dawn, and more foraged at dusk than at night (Fig 1e).

When time and location were held constant, the two nights of observation were very similar with respect to bat abundance counts and the proportion of circular flight. Note that the paired observations tend to fall on the line of equality in Fig. 1b and 1d. In contrast, the regression line for bat feeding proportion had a slope that was significantly different from 1 ( $F = 18.3$ ,  $df = 1,5$ ,  $P = 0.008$ ; Fig. 1f). This regression was strongly driven by one observation period dawn on the first night at the downstream site), in which 6 of 18 bats fished (a proportion of 0.33). Also shown in Fig. 1f is the regression line excluding this high fishing proportion, which falls very close to the line of equality. Because all three variables were similar on different nights, we elected to use date of observation as a replicate measure for all analyses.

Location, time, and the interaction between location and time were the best predictors of bat abundance according to AIC model selection (ANOVA,  $F = 10.4$ ;  $df = 8,9$ ;  $P = 0.001$ ; Table 1). The model

containing fish jumps was essentially equivalent ( $\Delta AIC < 2$ ) so we preferred the simpler model. Location (roost, upstream, or downstream) was a significant predictor of bat abundance ( $F = 28.8$ ;  $df = 2,9$ ;  $P = 0.0001$ ), as was observation time (dusk, night, or dawn) ( $F = 7.4$ ;  $df = 2,9$ ;  $P = 0.014$ ). The interaction of location and time was a non-significant predictor of bat abundance ( $F = 2.7$ ;  $df = 4,9$ ;  $P = 0.10$ ).

## DISCUSSION

Our results differed from previous studies, which found evidence of strong interactions between bat foraging behavior and tidal cycles, time of night, (Yale et al. 1998, Veysey et al. 2000), prey location, and lagoon morphology (Leslie et al. 2001). We found no evidence that bat foraging behavior was related to tide, water depth, and fish activity at the surface of the lagoon. Likewise, we did not detect indirect interactions between aquatic predators and bats influencing prey location and availability. Surprisingly, we also observed few fishing attempts, which suggests that changing environmental pressures may have caused a shift in *N. leporinus* foraging behavior. *N. leporinus* can be insectivorous (LaVal and Rodríguez-H. 2002), and a shift of main prey type from fish to insects may explain the reduced interaction of bat foraging behavior

with abiotic factors correlated to fish availability.

We expected to see more bats downstream during high tide where a broad shelf with shallow water would drive fish seeking refuge from marine predators close to the surface, but more bats were observed upstream. Because bats echolocate prey better in calm water (Siemers 2001), it is possible that bats avoid areas with strong current or wave action close to the ocean. Additionally, if elevated frequency of fish jumps correlates with higher marine predator density, it is possible that predatory fish, sharks, and crocodiles may compete with *N. leporinus* for similar prey rather than facilitate bat fishing success.

Although a previous study (Valderrama and Madigan 2005) observed more circular flights at high tide when more bats foraged, we found that location, not tide or foraging behavior, influences flight pattern. Circular flight patterns of *N. leporinus* which were most common immediately around the roost may increase ability to protect the roost. Circling bats may also coordinate foraging through direct communication with scouts that return to the roosts after finding successful hunting grounds. *N. leporinus* are reported to forage in small groups that benefit from sharing information on prey location (Brooke 1994), so circling may facilitate the assembly of these

groups before leaving the roost area. In contrast, the straight flight patterns observed upstream and downstream may be more beneficial for locating and catching prey. Although we observed few fishing attempts, bats frequently moved beyond the range of our observers, particularly upstream. *N. leporinus* are strong fliers (Hayward and Davis 1964), and may prefer sites far upstream or in nearby rivers. This suggests that the foraging area is considerably greater than the 200-300 m visually assessed in this study. Further studies on *N. leporinus* foraging would benefit from broader sampling conducted over larger river sections.

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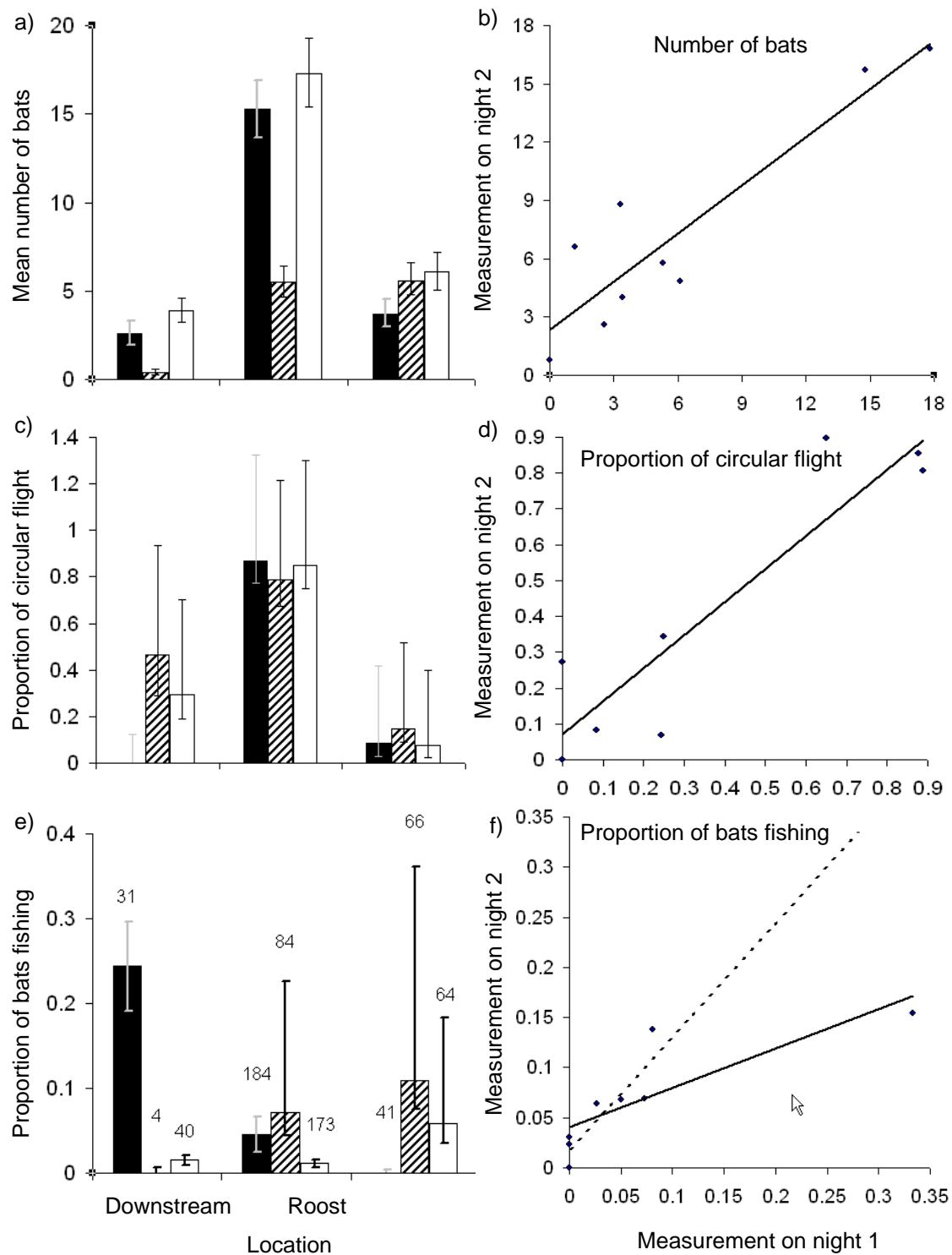


Figure 1. Left side: Mean ( $\pm 1$ SE) bat number, proportion of circular flight, and the proportion of bats fishing by location and time of day; dawn, dusk, and night = black bars, hatched bars, and white bars, respectively (back-transformed to original units). Numbers over the bars in (e) refer to the total bat count at each time and location. Right side: Comparisons of nights (paired for site and time).



Figure 2. Roost of *N. leporinus* in *Mora oleifera* (Fabaceae) along the Río Sirena, Corcovado, Costa Rica. White arrow indicates the entrance hole (oval opening 10 x 15 cm diameter). Note the guano at the base of the tree, just below the high tide line.



Figure 3. Close up of *N. leporinus* flying next to roost – 12 Feb 2008. Photo by Alex Spinoso.



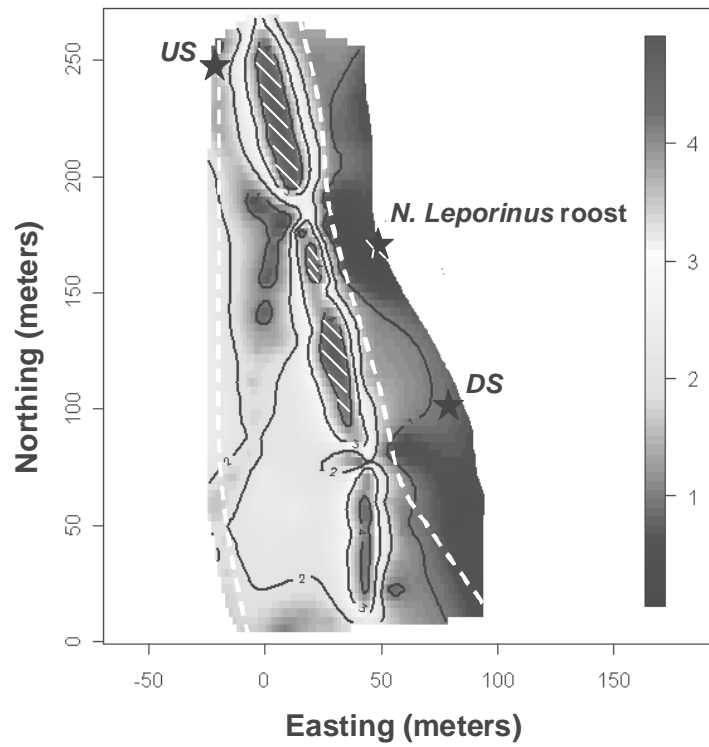


Figure 4. Contour map of depth in the Río Sirena lagoon. Stars show observations sites (Roost location near boat launch at N 8.48128 W 83.59694). Hatched area corresponds to the main canal; white dotted line corresponds to the approximate low tide line.

# SUN, SALT AND SAND: HOW THE COAST AFFECTS FOREST STRUCTURE

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*Abstract:* Oceans create edges to terrestrial ecosystems that generate unique environmental conditions in the adjacent terrestrial habitats. We investigated how tropical rainforest structure changed moving away from the beach edge. We hypothesized that tree density and diversity would increase with distance from the beach, along with leaf litter, herbivory and land crab density. Tree and land crab density varied significantly with distance, while other elements did not, and the factors we studied were generally intercorrelated, suggesting a large degree of biological interaction. Coastal forest structure is apparently shaped by both abiotic and biological factors.

*Key Words:* coastal edge, lowland rainforest, Corcovado

## INTRODUCTION

Edges are unique areas in forests for the conditions they provide and the species that colonize them. They present environments of dramatically increased light, which typically limits plant growth under the forest canopy. Many species can only thrive in the increased light and space provided at edges and in gaps. Oceanic coasts are a special example of forest edges. They are characterized by increased salinity, sandy soils that hold little water and few nutrients, wind and heat stress. Coastal edges may favor plants with specific adaptations to an environment that may not be found deeper in the forest. If so, the conditions of this coastal environment may have an influence beyond the beach edge that

gradually dissipates with depth into the forest.

Some of the physical conditions that could be affected by proximity to the ocean include moisture, soil character, salinity levels and light availability, all of which may have an effect on the tree community. Different soil types, based on organic content and particle size, retain varying amounts of water and dissolved nutrients. Also, structural stability of the soil is integral to a tree's growth potential, and would change with soil type. Soil salinity, influenced by tidal reach, could also change with distance from the coast, affecting plant communities. All these factors are critical in determining what tree species colonize certain habitats. Because trees are the foundation of forests, we expected that other forest species would be influenced by

changes in the tree community. Changes in these other species may in turn affect tree biology.

In Corcovado National Park in southwestern Costa Rica, we studied the elements of tropical rainforest structure that change with distance from the coast. We sought to distinguish the driving forces behind this change, to determine whether biological or physical conditions were more influential. We predicted that if abiotic factors were the main drivers of structural variation, changes in the elements we measured would be staggered. In this individualistic response model, different species respond to abiotic factors independent of each other, since the specific requirements and preferences of each differ. Dominance of biological factors would show up in clustered variation of individual elements. Change in one species' abundance would drive change in others, due to the tight interactions that exist between species.

## METHODS

We ran six 55-m transects perpendicular to the coast, starting at the beach edge of the forest and moving inland. We divided a roughly 350 m-long stretch of beach into 60 m sections. Within each section we randomly chose a point to commence each transect. Each transect contained 4 circular plots of

radius 5 m, with centers at 5, 15, 30 and 50 m from the beach. We chose this quasi-logarithmic spacing of plots based on the assumption that changes would occur faster closer to the beach. In each plot, we measured number of trees with a DBH greater than 3 cm, number of tree species by morphotype, basal area, average leaf litter coverage, average percent herbivory, and soil type (sand or silt) in 15 cm core samples. As a further measure of change in community structure with distance from the beach, we measured the number of land-crab holes. These forest dwelling crabs feed on leaf litter, carrying fallen leaves into their burrows, contributing to the nutrient cycle of the soil. To evaluate inter-relations among these elements of forest structure we analyzed the correlation structure and conducted a principle components analysis.

In preliminary analyses of soil samples, we found no change in pH or salinity with distance from the beach. Given this, we dropped further measurements of pH and salinity because it seemed unlikely that either would have an effect on the structure of this coastal community.

## RESULTS

Number of species did not change with distance from the beach (Figure 1;  $r^2 = 0.09$ ,  $df = 1,22$ ,  $P =$

0.16), nor did the number of trees ( $r^2 = 0.03$ ,  $df = 1,22$ ,  $P = 0.4$ ). There was a nonlinear change in basal area with distance from the beach, which we fit with a second order polynomial function (Figure 2,  $r^2 = 0.71$ ,  $df = 2$ ,  $21$ ,  $P < 0.0001$ ), showing an initial increase and subsequent decrease in basal area as we moved inland. Leaf litter did not change with distance from the beach (Figure 3,  $r^2 = 0.01$ ,  $df = 1,22$ ,  $P = 0.72$ ), nor did percent herbivory (Figure 4,  $r^2 = 0.00$ ,  $df = 1,22$ ,  $P = 0.95$ ). The number of crab holes was significantly related to distance from the beach (Figure 5,  $r^2 = 0.63$ ,  $df = 2,21$ ,  $P < 0.0001$ ), in a nonlinear fashion similar to the pattern observed with basal area.

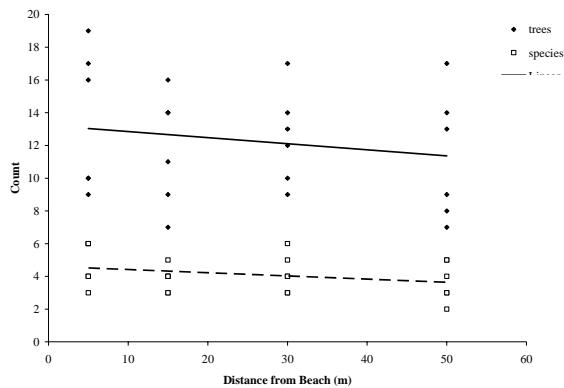


Figure 1. Tree and species counts with distance from the beach.

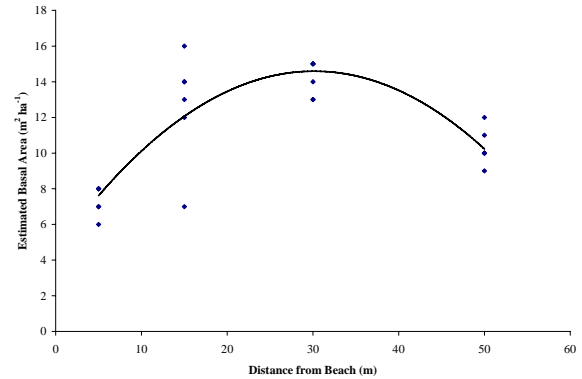


Figure 2. Estimated basal area with distance from the beach ( $y = -0.011x^2 + 0.6654x + 4.5646$ ).

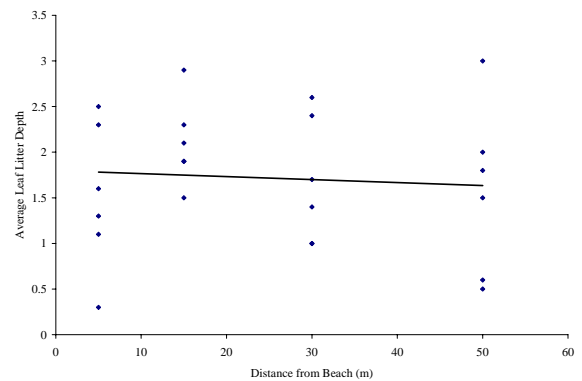


Figure 3. Average leaf litter depth with distance from beach.

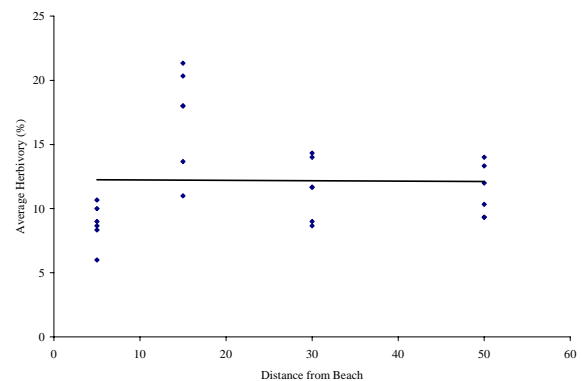


Figure 4. Average percent herbivory with distance from beach.

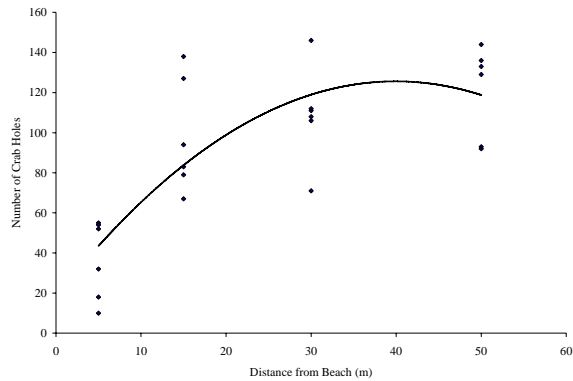


Figure 5. Number of crab holes with distance from the beach ( $y = -0.0673x^2 + 5.3747x + 18.285$ ).

All soil cores revealed a silty soil of uniform particle size and appearance, except for cores taken from four of the six plots 5 m from the beach, which were almost entirely sand. Thus, the soil quickly changed from sand to silt within the first 15 m of the beach. We did not encounter clay soil in any of our 15 cm deep soil cores.

A correlation analysis revealed positive relationships between basal area and herbivory ( $r = 0.45$ ), basal area and crab holes ( $r = 0.51$ ) and crab holes and herbivory ( $r = 0.43$ ). PC1 explained 32% of variance in the elements of forest structure we measured. PC1 had positive loadings for basal area, herbivory and crab holes of 0.46, 0.43 and 0.46, respectively. There were also strong negative loadings for number of hibiscus (*Hibiscus pernambucensis*) and number of species: -0.45 and -0.33, respectively. PC2 explained another 21% of the variance in forest structure and had

positive loadings for number of trees, number of lianas and number of *Simaba cedron* trees of 0.59, 0.43 and 0.65. Together, the first two axes of the principle component analyses explained 53% of the variance in eight measures of forest structure.

## DISCUSSION

Our sampling of the number of trees and tree species contradicted our initial impressions, and showed that  $\alpha$  diversity did not change with increasing distance from the beach. We could not estimate  $\beta$  diversity for our study area because we could not identify most species. However, our sense was that the beach margin had a more uniform plant community across plots, while plant composition seemed to differ more among inland plots.

Though the number of trees was consistent, the relationship between basal area and distance from the beach suggested a change in tree biomass. Within 30 m of the beach, the increase in BA could have resulted from improved soil conditions such as higher nutrient content and better structural support. Additionally, plants in this zone may have had improved access to light from the short stature of the trees closer to the beach edge, whilst suffering less from the wind and heat stress present at the beach edge. Soil conditions after 15 m were constant, so the decrease in BA after

30 m was possibly caused by reduced edge benefits.

Abiotic conditions may not be the only, or even the strongest influences on forest structure. If abiotic factors were paramount, one might expect change in components of the forest community to be staggered, as species requirements differ. However if there are strong biological interactions that drive forest structure one would expect many factors to correlate and change together due to the influence they exert on each other.

The strong positive relationships between crab holes, basal area and herbivory along PC1 indicates that these three aspects of forest structure are biologically linked. We assumed that the crab holes belonged to the forest-dwelling land crabs, *Gecarcinus quadratus* (Griffiths *et al.* 2007), which are known to feed on leaf litter, relocating litter underground in the process. The correlated increases in tree density and levels of herbivory could be indicators of higher primary productivity at intermediate distances from the edge, possibly because of higher resource availability, or reduced investment in plant defense. Crabs may facilitate nutrient cycling of the coastal system (Sherman 2003), and improve soil condition. Such changes in soil nutrient content, depth and cohesion may enhance the growth and persistence of trees.

This is an example of how biotic and abiotic mechanisms interact to influence forest structure. In this study we attempted to distinguish the influence of these two driving processes and found evidence that they are tightly linked. Abiotic conditions drive tree assembly, which is foundational to the community, and biological interactions in turn cause spatial clustering of associated elements of the forest. What is more, biota can influence abiotic conditions, through nutrient fixation and cycling, further linking physical and biological processes.

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# WHAT'S IN A FIG? THE INTERACTIONS BETWEEN FIGS, FIG WASPS, AND FIG WASP PARASITIDS

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*Abstract:* Many plants provide consistent and predictable fruit rewards to obtain reliable services from seed dispersers. Fig fruit production, however, is unpredictable in time and space. This behavior creates a scramble for resources in the fruit foraging community. I evaluated one hypothesis that could explain this fruiting behavior. Parasitoids of the obligate fig pollinator wasp (Hymenoptera: Agaonidae) can exert selection pressure on fig fruiting period by increasing the rate of parasitism on late-developing fruits. I sampled sequentially ripening fig fruits from one tree (probably *Ficus obtusifolia*) over 48 hours near the Sirena Biological Station in Corcovado National Park, Costa Rica. I assessed parasitism levels by counting parasitoids directly (Hymenoptera: Torymidae) and also by examining ovules for irregularly shaped exit holes presumably made by parasitoids. The probability of fruits containing parasitoids increased by 3-times over time (although the number of parasitoids within parasitized fruits remained constant at ~ 120 per fruit). This suggests that fig wasps in later figs are more likely to be parasitized, which presumably decreases the fitness of the fig tree. Therefore, increased parasitism may have contributed to selection for the strikingly synchronous fruiting behavior of neotropical fig trees.

*Keywords:* Figs, *Ficus obtusifolia*, *fig wasp*, *fig wasp parasitism*, *fruiting synchrony*

## INTRODUCTION

Many plants provide consistent and predictable fruit rewards that promote the development of specialist seed dispersers. These dispersers in turn increase plant fitness by supplying reliable dispersal. One such example is the interaction between *Piper* species (Piperaceae) and bats in a tropical dry forest (Fleming, 1985). Most individual *Piper* plants produce new flowers continuously for 3-4 months and therefore tend to have flowers and fruits of all developmental stages at all times. This continuous supply of food attracts bats to the same plant every

day, which ensures the continued service of bats to plants and avoids the problem of disperser satiety. Although many other plants also utilize this fruiting strategy, it is not universal. Fig trees are conspicuous fruit producers in tropical forests that behave very differently. Individual fig trees occasionally produce large quantities of flowers that develop synchronously, leading to fruiting events that are localized (a single tree), unpredictable, and highly ephemeral (Janzen 1983). This results in associations with frugivores that lack recognizable community structure (Alexander et al. 2002). Arboreal and ground animals ranging

from spider monkey to red brocket deer, crested guan to white-nosed coati, and scarlet macaw to tapir, have been seen feeding simultaneously and unpredictably at fruiting fig trees.

Synchronous fruiting in figs may be adaptive with respect to seed dispersal. Because food resources are limited, large concentrations of high quality fruits are more likely to attract diverse dispersers than smaller concentrations. Fruiting synchrony may also be an adaptation to selectively attract generalist seed dispersers. Because figs are themselves generalists (Janzen 1983), they may generally benefit from being dispersed into diverse environments by an assortment of animals with varied behaviors.

However, it is also possible that synchronous fruiting behavior in figs is suboptimal and reflects constraints arising from other community interactions. For example, fruiting synchrony could be an evolutionary response to minimize the deleterious effects of fig wasp parasitoids. Every fig species has a species-specific obligate mutualism with a fig wasp species. These wasps are the sole pollinators of fig trees, and fig trees are the only host plants of fig wasp larvae. One problem for the fig wasps, and therefore the fig trees, is the deleterious effect of fig wasp larvae parasitoids. These insect parasitoids are often as abundant as fig wasps (Janzen 1983), and have the potential to exert strong selection

pressure on fig wasps and their fig mutualists. Assuming that female fig wasps are more attracted to higher concentration of fig flowers, and that fig flower abundance increases over the flowering period, fig wasp oviposition and larval abundance should increase over time. And if parasitoids are more likely to aggregate in fig trees containing more fig larvae (possibly identified by stronger chemical signals), parasitism should also increase over fruiting period. If so, fig wasp reproduction, and therefore fig tree fitness, should decrease over time, selecting for a shorter flowering and fruiting period in figs.

#### *Natural history of figs*

Fig flowers are pollinated by fig wasps in the family Agaonidae. Bearing pollen grains from another fig tree, a female wasp enters a very small, developing fig (known as a synconium) through a natural opening (ostiole). The insides of the fig are lined with hundreds of fully developed and receptive female flowers. Once inside, the female wasp moves from stigma to stigma and pollinates each floret while probing down the style with her ovipositor. If the style is short, she contacts the single ovule and lays an egg. If the style is too long, she cannot reach the ovule and lays no egg. Wasp eggs subsequently develop inside their fig ovule, feeding on and killing the seed. At the same time, parasitoid wasps



(Hymenoptera: Torymidae) may locate the fig synconia and oviposit through the synconium wall, parasitizing the developing fig wasp larvae. As the male fig wasps emerge from fig ovules, they copulate with the females within the fig (chiefly sisters) and die. When the newly mated females emerge within the synconia, they collect pollen from the recently matured male fig florets and exit to pollinate another fig tree, completing the fig wasp life cycle (Janzen 1983).

## METHODS

I located a fruiting fig tree ~ 80 m inland from the coastal end of the Rio Claro trail. It was 25 – 30 m tall with a dbh of 1.5 – 2 m and was probably *Ficus obtusifolia*, based on the size of the fruit, the size of the fruit sepals, and the lack of white spots on the skin (Quesada et al. 1997). I collected freshly fallen fig fruits from this tree on 5 occasions: 08:00 and 17:00 on 8 and 9 February, 2008, and again at 08:00 on 10 February.

I chose 10 - 15 freshly fallen undamaged green figs from each of the five samples and opened the fruits with an exactor knife in the laboratory. If adult parasitoids were present (black with an extremely long ovipositor), I waited for them to leave the fruit (seconds) and counted them on the lab bench. I then examined the inside of each fruit under a dissecting scope and counted developing

parasitoids (ones that were still inside the ovules), and fig wasps (brown with a slim body and lacking a conspicuous ovipositor). To study the fate of ovules and fig wasps within fruits, I randomly chose two subsets of 10 adjacent ovules within each fig, and classified each into one of the three following categories: seed, ovule with circular exit holes presumably made by a fig wasp (Janzen 1983), or ovule with irregular exit holes presumably made by a parasitoid. I also selected five figs representing a range of sizes to look for effects of fruit size on flower provisioning (number of flowers and proportion intended for fig wasps). I measured the two diameters of these fruits, and divided each fruit into 4 - 16 equal-sized sections. For one randomly selected section in each fruit, I counted the total number of male flowers, female flowers, and female flowers with exit holes. I then multiplied these numbers by the number of sections to estimate the totals for each fruit.

## RESULTS

Diameters of fig fruits ranged from 2 - 4 cm. Of the 64 study fruits, 15 had fig wasps and 32 had fig wasp parasitoids. When fruits were opened, fig wasps stayed inside and appeared to continue collecting pollen from male florets. In contrast, parasitoids quickly hopped out and away from the fig fruit (Figure 1).

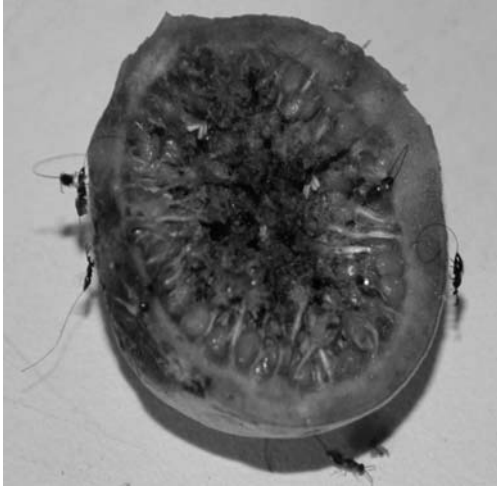


Figure 1. Fig wasp parasitoids hopping out of a *Ficus obtusifolia* fig fruit near Sirena Biological Station in Corcovado National Park, Costa Rica.

Within figs, I observed developing and mature seeds, ovules with circular exit holes (presumably made by fig wasps), ovules with irregular exit holes (presumably made by fig wasp parasitoids), and male florets (Figure 2). Most mature seeds seemed to have shorter styles than ovules with exit holes, and appeared to be non-randomly concentrated near the synconia wall.

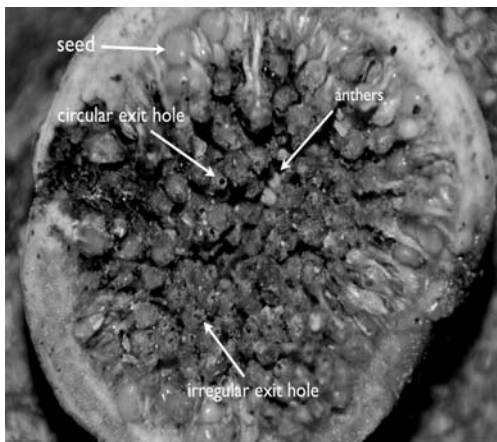


Figure 2. Inside of a *Ficus obtusifolia* fruit near Sirena Biological Station in Corcovado National Park, Costa Rica.

Fruits that ripened later were about 3-times more likely to be parasitized than fruits that ripened earlier (Figure 3). The probability of any fig fruit containing visible parasitoids increased over 48 hours from about 30% to about 90% ( $\chi^2 = 11.61$ ,  $df = 1$ ,  $P = 0.0007$ ). However, among the figs that were parasitized, the number of parasitoids per fig did not vary over time ( $F = 0.44$ ,  $df = 1, 33$ ,  $P = 0.51$ ,  $r^2 = 0.013$ , Figure 4). This suggests that the numbers of parasitic females and eggs were similar between fruits.

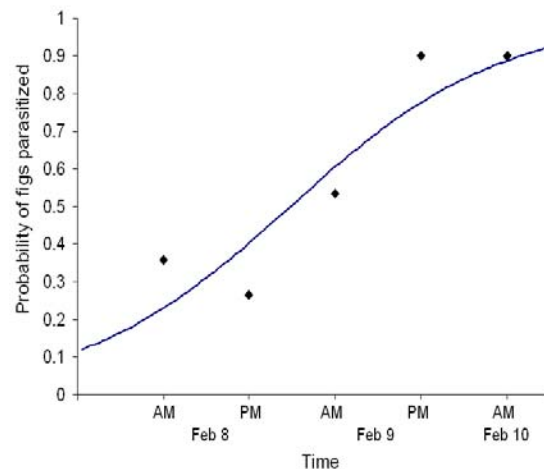


Figure 3. Proportion of figs that contained fig wasp parasitoids as a function of the time ripened fruit dropped to the ground. Data from a single *Ficus obtusifolia* tree near Sirena Biological Station in Corcovado National Park, Costa Rica:  $y = 1 - 1 / (1 + e^{-2.023 + 0.817x})$ .

Contrary to the direct counts of parasitoids, examination of exit holes in ovules revealed no relationship with time: number with irregular exit holes (putative parasitoids) vs. time ( $F = 1.96$ ,  $df = 1, 62$ ,  $P = 0.17$ ); number with regular exit holes (putative fig

wasps) vs. time ( $F = 3.26$ ,  $df = 1, 62$ ,  $P = 0.076$ ); and number of seeds per fig vs. time ( $F = 0.11$ ,  $df = 1, 62$ ,  $P = 0.74$ ; Figure 5). It was not easy to classify exit holes as made by fig wasps vs. parasitoids. Since the exit hole data was not at all consistent with the direct counts of parasitoids, I don't believe that the exit hole data can be reliably interpreted as measures of parasitoid abundance.

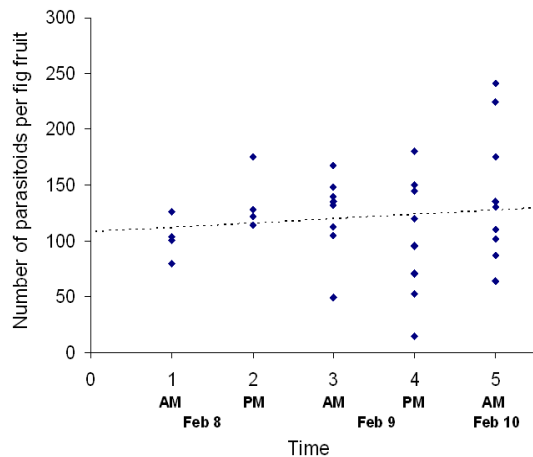


Figure 4. Number of parasitoids per parasitized fig fruit over time of a *Ficus obtusifolia* tree near Sirena Biological Station in Corcovado National Park, Costa Rica.

Individual fig fruits contained about 400 to 1000 flowers, depending on size. But regardless of size, there were ~10 times more female flowers than male flowers (Figure 6, upper). About 40-50% of female flowers had short styles (Figure 6, lower), presumably allocated by the plant to feed fig wasps.

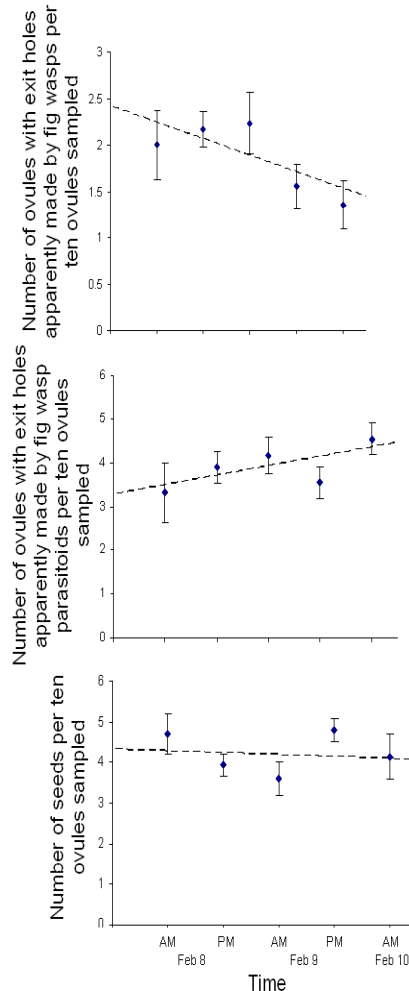


Figure 5. Number of ovules with exit holes apparently made by fig wasps (top), ovules with exit holes apparently made by parasitoids (middle), and seeds (bottom) per subsample of ten ovules over time of *Ficus obtusifolia* fruits near Sirena Biological Station in Corcovado National Park, Costa Rica. Mean  $\pm$  SE; dashed lines indicate insignificant linear regression models.

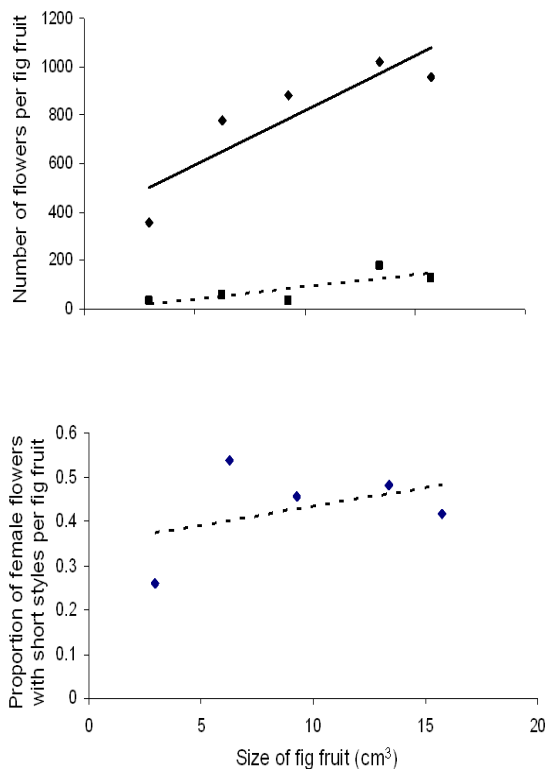


Figure 6. Number of male (top) and female (middle) flowers and proportion of female flowers with wasp exit holes (bottom) inside *Ficus obtusifolia* fruits near Sirena Biological Station in Corcovado National Park, Costa Rica. Solid vs. dashed lines indicate respective significant vs. insignificant regression models ( $\alpha = 0.05$ ).

## DISCUSSION

The surprisingly strong increase in fig wasp parasitism within fruits that matured 48 hours later than other fruits on the same tree was consistent with the hypothesis that fig wasp parasitoids could select for synchronous fruiting in figs. Because fig wasps are the sole pollinators of figs, the fitness of fig trees must be influenced by figs' success in producing female fig wasps that disperse pollen. If it is general that

late developing figs are more heavily parasitized, natural selection for increasing within-tree fruiting synchrony could be quite strong. However, because I only sampled one fig tree over a single fruiting period, further studies are needed to justify generalizing this pattern.

The skew sex ratio of flowers may result from fact that a female flower can produce only one seed where as a male flower can produce thousands of pollen grains. It could also be that investment in female fitness is more important because it is more certain than male fitness. Once pollinated, a female flower can develop immediately into a seed. In contrast, pollen has to travel long distances to a flowering plant of the same species before a seed can be produced.

Janzen suggested that the number of flowers intended for fig wasp larvae is optimized at 30-80% (1983), which is consistent with the 40-50% that we observed. However, Janzen did not seem to consider potential effects of fig wasp parasitoids on this optimum. In addition to selecting for increased within-tree fruiting synchrony, fig wasp parasitism may also affect the optimum proportion of female flowers allocated to fig wasp larvae. It may be that the optimum proportion would change from the earliest developing flowers to the latest developing flowers (even if fruiting is only over 2-3 days). Since higher

parasitism risk decreases fig wasp reproductive success, perhaps there would be selection for less female flowers to be allocated to fig wasps towards the end of the fruiting period.

Fruit size could also affect the optimal proportion of female flowers intended for fig wasps. It may be that figs can provide only as many ovules as the average number of eggs a female fig wasp lays. If so, the proportion of female flowers with short styles should decrease with increasing fruit size because larger fruits have more flowers. Alternatively, the ratio of short to long styled female flowers is genetically fixed and does not change with fruit size.

I was surprised to observe that most flowers that produced mature seeds had shorter styles than those with exit holes from fig wasps or fig wasp parasitoids. The conventional wisdom is that fig wasps oviposit in fig ovules with short styles (Janzen 1983). One possibility is that parasitism risk decreases towards the center of the fig, where fig wasp larvae are least accessible to female adult parasitoids that oviposit from outside the syconium wall. This gradient in larvae survival is likely to select for pollinator avoidance of outer ovules during oviposition, ensuring that some fig ovules will produce seeds (Dunn et al. 2008).

Fig wasp parasitism could be a significant selective force on the fruiting biology of fig trees. Because

synchronous fruiting in tropical trees is also evident in some non-figs, such as members of the Lauraceae family and *Dipteryx panamensis*, fig wasp parasitism cannot be the only ecological factor that favors this fruiting syndrome. However, selection from fig wasp parasitoids on pollination may be a partial explanation for the fleeting tumults of frugivory that accompany fig fruiting events in tropical forests (Alexander et al. 2002).

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# LEAF ORIENTATION IN HELIOTROPIC *CALATHEA* (MARANTACEAE)

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Faculty editor: Matthew P. Ayres

*Abstract:* Leaf movement in response to light, or heliotropism, should benefit plants where light intensity is a limiting factor. Heliotropic Marantaceae *Calathea* should exhibit one of three movement patterns. 1) Leaves could be perpendicular to the sun (diaheliotropic) to maximize light absorption and photosynthesis, 2) Leaves could be parallel to the sun (paraheliotropic) to minimize radiation and thermal damage, or 3) Leaves could move either diaheliotropically or paraheliotropically to optimize for changing light intensities. We found that at low light levels, plants had perpendicular leaf orientation to the sun, while at high light intensities; leaf orientation was parallel to the sun's rays. This movement suggests that *Calathea* tends to maximize photosynthesis when light is limiting, and minimize thermal damage when light is excessive. This ability to optimize at various light intensities could explain why *Calathea* can thrive in high-light gaps, and low-light understory.

*Key Words:* diaheliotropism, paraheliotropism

## INTRODUCTION

Light availability in the tropical forest is a common limiting factor in plant distributions (Chazdon & Fletcher 1984). Consequently, plants have evolved various ways to optimize light exposure. One such adaptation is heliotropism, or the ability to orient leaves in response to the sun. Heliotropic plants specialize in one of three different movement patterns. 1) Leaves are perpendicular to the sun (diaheliotropic) to maximize light absorption and photosynthesis, 2) Leaves are parallel to the sun (paraheliotropic) to minimize radiation and thermal damage, or 3) Leaves move either diaheliotropic or paraheliotropic to

optimize changing low and high light intensities (James & Forseth 1980, Cronlund & Forseth 1990). A plant's ability to optimize light intensity may affect distribution ranges. We focused on the heliotropic genus *Calathea*, of the Marantaceae family, which occurred along forest edges and in light gaps in Corcovado National Park, Costa Rica. To determine the extent and nature of heliotropism in *Calathea*, we measured the vertical, rotational, and cupping angles of three plants over time, noting sun and shade.

## METHODS

We surveyed two *Calathea* plants on either side of the airstrip 200 m south of the Estación

Biológica, Corcovado, Costa Rica (Plant 1, 2). On 8 Feb 2008 from 13:00 – 19:00, 9 Feb from 05:00 – 19:00, and 10 Feb from 05:00 to 11:00, we measured each plant every other hour. On 8 Feb 2008 from 05:00 – 19:00, we measured a 3<sup>rd</sup> plant in the same habitat that we artificially shaded with a sheet.

For each plant, we measured the topmost leaf representatives of each cardinal direction, for a total of four leaves per plant. For each individual leaf we took five measurements; leaf face's vertical angle ( $\alpha$ ) from horizontal (Fig. 1a), leaf face's vertical angle to the sun ( $\beta$ ) (Fig. 1a), leaf face's rotation relative to horizontal (angle  $\theta$ ) (Fig. 1b), and the 'cupping' angle of a leaf face ( $\gamma$ ) (Fig. 1c).

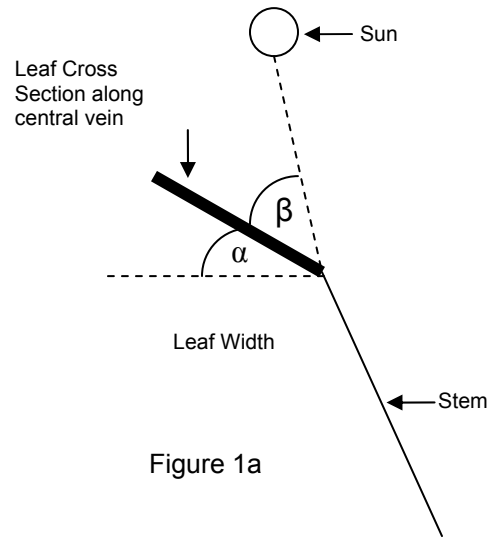


Figure 1a

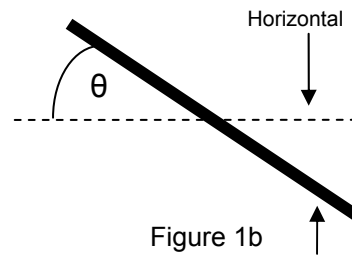


Figure 1b

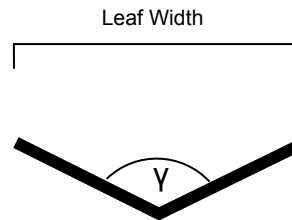


Figure 1c

Figure 1. A-C are diagrams of various angular measurements. A) Picture of a leaf cross-section taken along the central vein. The vertical angle between the leaf face and horizontal is pictured by alpha ( $\alpha$ ), while Beta ( $\beta$ ) refers to the vertical angle between the leaf face and the sun. B) Graphical representation of leaf cross section (perpendicular to central vein). Theta ( $\theta$ ) refers to the rotational leaf angle relative to horizontal, in degrees. C) Gamma ( $\gamma$ ) represents the angle of 'cupping' of each leaf. The smaller the  $\gamma$  value, the more 'cupped' a leaf is, and the less photosynthetic surface there is exposed.



We graphed  $\alpha$ ,  $\theta$ , and  $\gamma$  angles over time (Figure 2) to show absolute motion for Plants 1 & 2. We determined how many degrees ( $\theta$ ) off of horizontal the leaf face was, and attributed a +/- value to right or left rotation respectively. We also noted whether the plant was in shade, sunlight, or darkness.

From the theory of diaheliotropism, we inferred that maximal absorption for a leaf would be at a perpendicular vertical angle to the sun ( $\beta=90^\circ$ ) and open flat (uncupped;  $\gamma=180^\circ$ ). We calculated the difference from maximal absorption for each leaf by taking the

difference from  $\beta$  angles and  $90^\circ$  (Figure 3).

## RESULTS

*Calathea* leaves showed a wide range of motion in vertical, rotational, and horizontal angles (Figure 2). Their similar ranges suggested more than just random motion throughout the day (Table 1). For both vertical and cupping angles we fit a general linear model including day (1 or 2), hour (0500-1900), Plant (1 or 2), all interactions, and leaf (nested within plant).

	Plant 1	Plant 2	Plant 3 (Shade Treatment)
<b>Vertical</b>			
Mean Vertical Angle $\pm$ SE	37.3 $\pm$ 2.6	56.4 $\pm$ 2.5	42.8 $\pm$ 4.17
Min. Vertical Angle	-25	4	0
Max. Vertical Angle	70	90	85
<b>Rotational</b>			
Mean Rotational Angle $\pm$ SE	.83 $\pm$ 1.2	.92 $\pm$ 1.6	-.68 $\pm$ 1.6
Min. Rotational Angle	-25	-25	-30
Max. Rotational Angle	70	90	85
<b>Cupping</b>			
Mean Cupping Angle $\pm$ SE	148.2 $\pm$ 5.4	154.3 $\pm$ 4.5	156.2 $\pm$ 7.2
Min. Cupping Angle	45	55	70
Max. Cupping Angle	180	180	180

Table 1: Means and ranges of motion for the three angle vectors (vertical, rotational, & cupping) for each of the 3 plants.

Plants 1 and 2 showed similar repeating patterns; leaves stood up straight at midday (higher  $\beta$ ) and were folded at the central-vein (smaller  $\gamma$ ), while they flattened out during the morning and afternoon (Figure 2). Vertical angles were more parallel to the sun at midday (large difference from 90 degrees), and

more perpendicular to the sun during the morning and afternoon (small difference from 90 degrees; Figure 2). This daily pattern was reflected in highly significant effects on vertical and cupping angles of hour ( $F > 17$ ,  $df = 7,90$ ,  $p < 0.0001$ ) and hour\*plant interactions ( $F > 12$ ,  $df = 7,90$ ,  $p < 0.0001$ ) (Figure 2). In

contrast, leaf rotation to horizontal was invariant with respect to hour and hour\*plant ( $F < 1.36$ ,  $df = 7,90$ ,  $p > 0.22$ ).

Whether Plant 1 or 2 was in direct sunlight or shade had little effect on the overall pattern of vertical movement (Figure 2a). However, Plant 1 had lower vertical

angles when shaded than Plant 2 did in the sun. The shaded treatment (Plant 3) showed similar patterns of vertical and horizontal movements, with the highest vertical angles, and lowest cupping angles occurring at midday (Figure 2a, 2b).

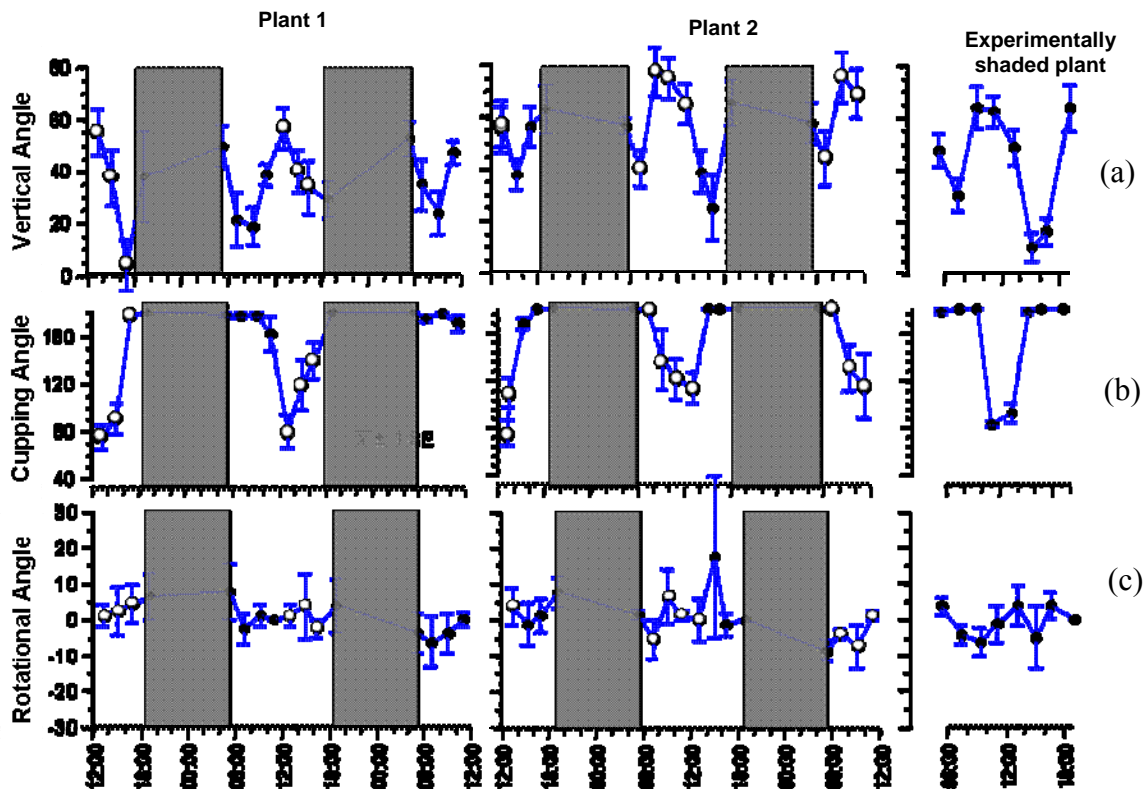


Figure 2 A-C: Temporal patterns in leaf angles (Vertical to horizontal, Cupping, and Rotation to horizontal respectively) over time for Plants 1, 2, & 3. Gray bars indicate nighttime, while filled and open circles represent times that plants were in the shade or sun respectively; Error bars show  $\pm 1$  SE based on leaves within plants.

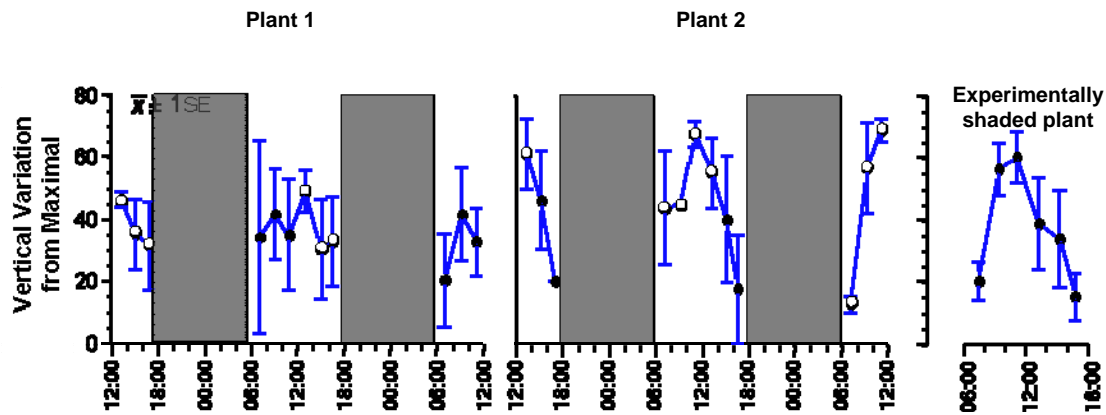


Figure 3: Graphs of vertical distance away from 'maximal' absorption angle for each plant over time. Gray bars indicate night, while filled and open circles represent times that plants were in the shade or sun respectively; Error bars show  $\pm 1$  SE based on leaves within plants.

## DISCUSSION

*Calathea* leaves moved significantly in response to direct sunlight. Leaf movement was both paraheliotropic and diaheliotropic. Paraheliotropic movement occurred at midday when the light intensity was greatest, suggesting that the plant was under light, heat, and desiccation stress. Because of the high solar flux at midday, it is likely that photosynthesis of *Calathea* was well above light saturation, and was physically responding to prevent light damage.

Conversely, diaheliotropic movement occurred in the morning and afternoon when light levels were low. During these times, the plants could maximize photosynthetic activity without reaching their maximum light saturation points. The ability of *Calathea* to act both paraheliotropically and

diaheliotropically depending on light levels could explain its distribution and success in both gap and understory habitats. Further studies could compare *Calathea* distribution and light capturing efficiency with a similar non-heliotropic plant, such as *Heliconia*, to evaluate if there is a quantifiable benefit to heliotropism in the tropics.

Interestingly, the pattern of vertical leaf movement in Plants 1 and 2 were not affected by time in the shade. This result was supported further by the similar vertical leaf patterns of Plant 3, despite being artificially shaded all day. Both of these results suggest the possibility of an established circadian clock in *Calathea*. If light and temperature stimuli establish a circadian clock, even after the stimulus is removed, the pattern of leaf movements will continue for a certain amount of time. Future studies could modify

light and shade treatments for longer periods of time, to quantify how new stimuli would affect this circadian clock. Abrupt light changes may occur in the tropics with the abundance of tree falls, and the *Calathea's* ability to respond could be noteworthy.

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# GOING BEYOND THE EXPLOITATION ECOSYSTEM HYPOTHESIS FOR ALGAE IN RÍO CLARO

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*Abstract:* Algae account for most of the primary production of some riparian systems. In the Río Claro of Corcovado, Costa Rica, most of the algal biomass is found in a filamentous and very fragile morphology in a small part of the intertidal zone. Previous studies suggested that trophic cascades limit the algae upstream, but have not examined the full spectrum of abiotic and biotic possibilities which could limit its distribution and abundance. Trophic cascades appeared to be affected by the tide as predicted by the Exploitation Ecosystem Hypothesis (EEH), but there was also evidence for abiotic effects, especially from depth and water velocity. Apparently, the standing biomass of primary producers in the Río Claro, chiefly one species of alga, depends on several factors, many of which are associated with the tide.

*Key Words:* *autochthonous, competition, conductance, salinity, substrate, transplants*

## INTRODUCTION

The energy flux within ecosystems is limited by the primary productivity, which in rivers is commonly based upon algae. However, the pool size of primary producers can be quite variable depending on a variety of local conditions that influence plant productivity and the rate at which plant matter is consumed by herbivores. In rivers of the Osa Peninsula, Costa Rica, there tends to be relatively little standing algal biomass (Winemiller 1983), but it is not clear why. The foodweb of the Río Claro, near Sirena Biological Station, is strongly based on algae (Winemiller 1983), chiefly a blue-green algae, which attains conspicuously high biomass (in a

filamentous morphology) within a band of the intertidal zone (Figure 1).

The lower reaches of the river change dramatically with ebbing tides because the river lacks an extensive floodplain or estuary. The factors that influence why algae are much less abundant near the mouth of the river and above the intertidal zone are poorly understood. Carreras et al. (2006) suggested the possibility that tidal-induced trophic shifts influence the intensity of herbivory on algae, and reported some results that were consistent with this hypothesis. However, they were unable to sample at high tide and only assessed the impact of one family (Gobiidae) of primary consumers.

In general, algal morphology and abundance may be limited by 1)

abiotic factors such as salinity, depth, current, and substrate; 2) biotic factors such as herbivory or interspecific competition; 3) a combination of biotic and abiotic factors, acting in conjunction or separately at either end of the tidal zone. To distinguish between these, we sampled water depth, conductance, substrate type, algal cover, and the bird and fish communities along the intertidal zone of Río Claro, and transplanted algae upriver and downriver.

## METHODS

We sampled the intertidal zone of Río Claro (river mouth: N 08.46417°, W 083.59298°; Table 1) in Playa Sirena, Corcovado National Park, Costa Rica from 8 - 10 Feb 2008. We divided our study area into eleven transects spaced approximately 60 m apart, each 2 m wide and spanning the width of the river. Within each transect, we randomly sampled four 2 x 2 m sites at low and high tide.

TABLE 1. GPS coordinates on the eleven study transects along the Río Claro of Corcovado, Costa Rica.

Transec	
t	UTM
1	17 P 214494 936565
2	17 P 214626 936676
3	17 P 214721 936669
4	17 P 214765 936693
5	17 P 214883 936802
6	17 P 214906 936821
7	17 P 214977 936816
8	17 P 215110 936761
9	17 P 215170 936843
10	17 P 215268 936809
11	17 P 215294 936793

For each plot, we estimated the depth, percent algal cover, and substrate composition: i.e., percentage of silt (fine particulate matter), sand, gravel (0-1 cm), cobble (1-10 cm), boulder (>10 cm), and leaves. We performed a principal components analysis to condense the six substrate types into two principal axes. We also measured the conductance ( $\mu$ Siemens / cm) of a water sample from each transect.

For six plots along the study area, we spent two minutes estimating the number and size of fish within the plot, and the number and species of birds within 100 m of the plot. We estimated fish biomass by calculating length\*number of fish.

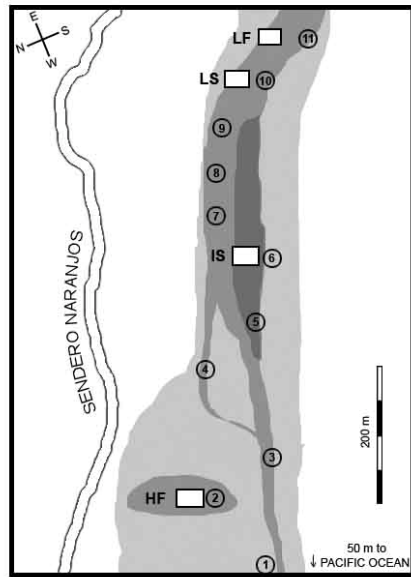


FIGURE 1. Map of the intertidal zone of the Río Claro, Corcovado National Park, Costa Rica. The river roughly doubles in width at high tide (light grey) from low tide levels (medium grey). Algae were present throughout, but the filamentous morphology was only abundant on the south side of the river along the central stretch of the intertidal zone (dark grey). Algae-covered rocks were transplanted from the site of Treatment IS to the other indicated treatments to assess the affect of water velocity, herbivory and salinity on algal survival. Numbers indicate location of transects.

We collected a total of 40 rocks covered by the long, filamentous algae from the middle of the river (Treatment IS, Fig. 1) and transplanted the rocks to four areas along the river: high salinity and fast water (HF), intermediate salinity and slow water velocity (IS), low salinity and high water velocity (LF) and low salinity and low water velocity (LL) at how tide. Rocks from Treatment IS were handled and replaced to serve as a control. Each treatment consisted of 10 transplanted rocks, five of which were bagged to protect

against herbivory and mechanical stress. After two days, we examined and photographed the rocks from each treatment.

## RESULTS

After the river depth peaked at high tide, the width of the river dramatically shrunk. Conductance at low tide decreased non-linearly with increasing distance upriver, with the greatest change occurring at the river mouth. For transects 3 and above, the water was relatively fresh (conductance < 500  $\mu\text{S}/\text{cm}$ , corresponding to salinities < 2 parts per thousand). We were unable to obtain conductances at high tide due to water damage to the conductance meter. Water turbidity and time constraints prevented accurate species identification and abundance estimation of fish at high tide.

Average algal cover was very low on the edge of the study area (Transects 1, 2, and 11) and was highest at transect 4 (Figure 3). The depth of the river at low tide did not significantly affect algal cover ( $F = 0.74$ ,  $df = 1, 42$ ,  $P = 0.39$ ). However, the difference in water depth between high and low tide was positively related to algal cover for upstream transects ( $r^2 = 0.25$ ,  $df = 26$ ,  $P = 0.0065$ , Figure 4).

Treatment IS (control) revealed that even slight handling of the algae significantly reduced its abundance and biomass. For all of

transplants, most of the long strands were broken, and only the algae that remained firmly attached to the rocks were compared (Figure 2).



FIGURE 2. Rocks from Río Claro, Corcovado, Costa Rica, covered in filamentous algae (top) from a bagged treatment and devoid of long filaments (bottom) from an unbagged treatment.

Bagging the treatments reduced the mechanical stress of fast currents. Unbagged algae in Treatments HF and LS both were subjected to fast currents and lost >90% of their long filaments, whereas bagged algae in both treatments were longer and more intact. Algae seemed to suffer in salty marine water, since algae in Treatment LS remained green while

algae in Treatment HF started to become brown within 48 h after being moved. In the slow water current transects (Treatments IS and LF), there were no clear physical differences between the bagged and unbagged treatments.

Unbagged algae in Treatment IS (fast current) was greatly reduced, while unbagged algae in Treatment LF (slow current) retained much of its long filaments, supporting the result that fast currents decrease algal biomass.

Most substrate types showed no clear relationship with algal cover. There was no linear relationship between algal cover and PC1 ( $F = 0.11$ ,  $df = 1, 42$ ,  $P = 0.11$ ; PC1 was positively correlated with sand and leaves ( $r = 0.60$  and  $0.44$ , respectively), and negatively related to cobble ( $r = -0.54$ ). Plots with abundant boulders were significantly more likely to have high algal cover, since PC2 (which was negatively correlated with gravel,  $r = -0.76$ ) was negatively related to algal cover ( $F = 28.1$ ,  $df = 1, 42$ ,  $P < 0.0001$ ). In contrast, the fish community was clearly affected by substrate. PC1 was positively and linearly related to fish biomass ( $F = 9.49$ ,  $df = 1, 22$ ,  $P = 0.0055$ ).

Small shrimp (Palaemonidae) were observed in most transects throughout the study area, but were most abundant in the dense, filamentous algae mats (transects 5 - 8). There was a positive, linear



relationship with depth at low tide ( $F = 8.98$ ,  $df = 1,4$ ,  $P = 0.04$ ). The distribution and abundance of fish are summarized in Table 2.

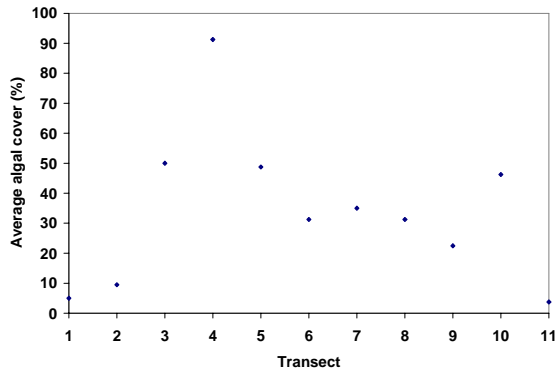


FIGURE 3. Average algal cover within eleven transects separated by 50 meters (transect 1 – 11 goes upriver) in the Río Claro of Corcovado National Park, Costa Rica

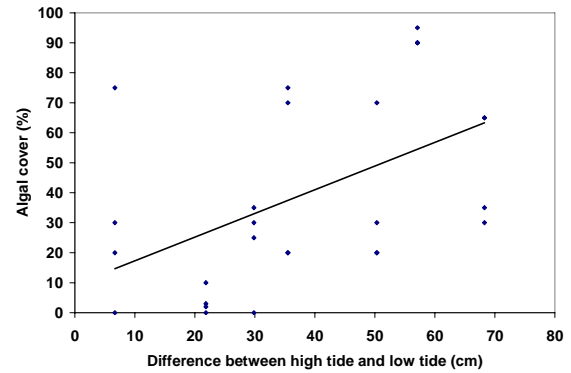


FIGURE 4. Relationship between tidal difference in depth between high tide and low tide (cm) and algal cover (%) in Río Claro, Costa Rica.

TABLE 2. Locality, abundance and description of each fish species sampled at low tide in the Río Claro of Corcovado National Park, 9 and 10 Feb, 2008.

Species	Common name	Description	Diet	Localities	Greatest # individual s observed among 3 sampled plots	Average length (cm)
<i>Eucinostomus currani</i>	Pacific flagfin mojarra	Black-tipped spinous dorsal fin, silvery coloration	Vegetable matter, microinvertebrates , detritus (Bussing 1998)	6, 10	15, 14	2
<i>Awaous transandeanus</i>	River goby	Tan coloration, dark dappling along body, fins transparent	Detritus, filamentous algae, chironomids, microbivalves (Bussing 1998)	8	5	5
<i>Lutjanus Colorado</i>	Colorado snapper	Red anal, caudal and pectoral fins, darker dorsal coloration	Fish, shrimp (Winemiller 1983)	8	5	25
<i>Lutjanus argentiventris</i>	Yellowtail snapper	Head pink, anterior half of body salmon color, posterior yellow-orange, fins yellow-orange	Fish, shrimp (Bussing 1998)	8	15	20
<i>Lutjanus novemfasciatus</i>	Pacific dog	Tan coloration with darker	Fish, shrimp (Winemiller 1983)	8	10	8

s	snapper	bands along body, reddish pectoral fins, dark ridge along edge of caudal and dorsal fins				
<i>Gobionellus sagittula</i>	Long tail goby	Tan-brown coloration, darker dappling along body and caudal fin	Benthic microalgae (personal observation)	10	1, 5	2.5
<i>Sphoeroides annulatus</i>	Bullseye Pufferfish, Cuchusapo	Grey dappling interrupted by yellow-tan oblong circles on dorsal half of body, unmistakable	Benthic crustaceans, snails (Winemiller 1983)	8	1	7
Unknown	-	Large minnow, sandy coloration, schooling	?	3, 10	1, 1	6
Unknown	-	Small minnow, sandy coloration, schooling	Hiding in algae	3, 4, 6, 8	50, 15, 1, 1	2

## DISCUSSION

Most of the algal biomass of Río Claro occurs in a filamentous form within a zone of relatively shallow, sunny, and calm water about 200 m upstream from the river mouth. Transplant studies showed that there was no suitable habitat for algae near the ocean (likely due to high salinity), nor upriver (likely due to herbivory), and that fast currents rapidly decreased algal biomass.

Algal abundance was not related to substrate, and substrate availability was not the factor limiting algae upstream. We also

doubt that interspecific competition influences algal abundance here because there appeared to be only one common species of algae in the system.

All the shallow, calm regions of the intertidal zone supported large algal biomass, thus it seemed that suitable algal habitat was largely determined by water velocity, depth, and the presence of piscivores. Our data supported the hypothesis that neither biotic nor abiotic factors alone, but rather a combination the two (high salinities downstream and lack of a third trophic level

upstream) determine the distribution of the algae.

Piscivorous fish come in with the tide, which might effectively add an additional trophic level to the system. Theory from community ecology predicts that changes from even to odd numbers of trophic levels will produce alternations in the abundance of plants due to alternations in the pattern of top-down effects (exploitation ecosystem hypothesis; Oksanen et al. 1981). Thus changes in the number of trophic levels from the incursions of marine fish at high tides could theoretically explain the high algal abundance in the middle reaches of the river. Presumably our study transects with the largest tidal fluxes also experience the most large fish at high tide, which could be why they contained more algae. We were unable to do a thorough sampling of the aquatic communities at each transect, but our results were consistent with the exploitation ecosystem hypothesis, in that we observed more algae where larger fish were found, and less algae and more herbivorous fish (gobies) above the intertidal zone. We also recorded the abundance of piscivorous birds (herons and kingfishers), but less than ten birds were observed feeding, so we doubt that birds significantly affect the lower trophic levels of this system. If the exploitation ecosystems hypothesis is at work, and herbivores are indeed

exhibiting top down control of algae upstream in Río Claro, then more complete surveys from the intertidal zone all up way upriver should confirm that algal abundances are highest in regions where there is an odd total number of trophic levels.

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