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.

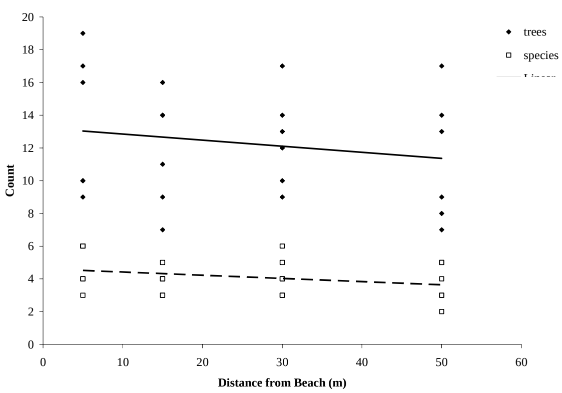

Figure 1. Tree and species counts with distance from the beach.

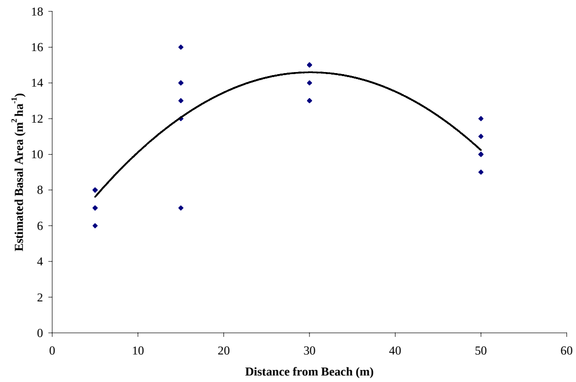

Figure 2. Estimated basal area with distance from the beach ($y = -0.011x^2 + 0.6654x + 4.5646$).

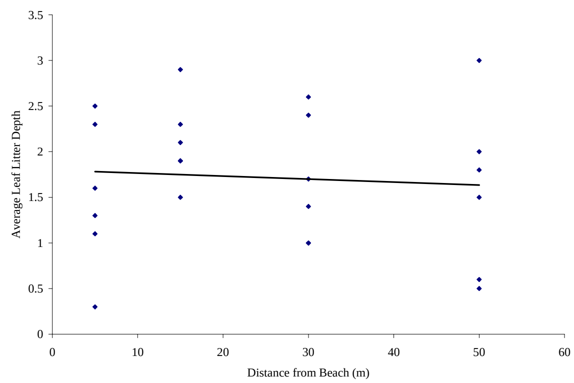

Figure 3. Average leaf litter depth with distance from beach.

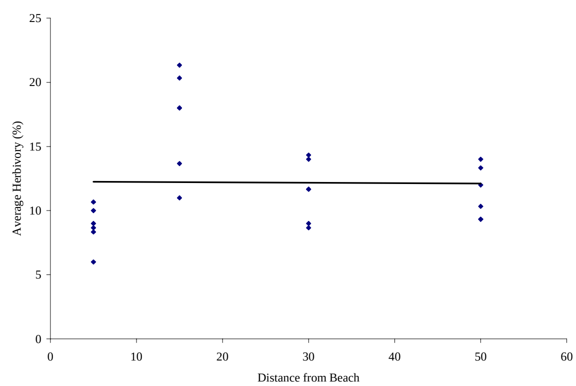

Figure 4. Average percent herbivory with distance from beach.

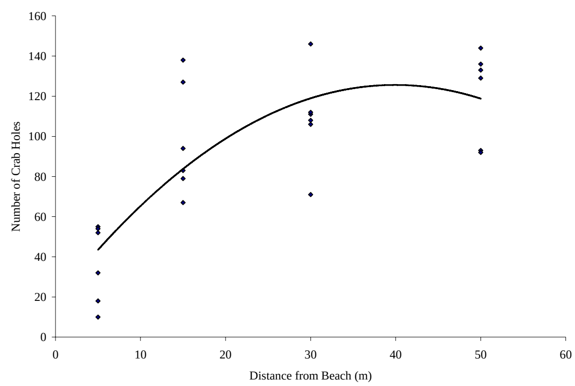

Figure 5. Number of crab holes with distance from the beach (y = -0.0673x2 + 5.3747x + 18.285).

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 ◎ diversity did not change with increasing distance from the beach. We could not estimate β 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.

LITERATURE CITED

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