PATTERNS OF COASTAL FOREST COMPOSITION, STRUCTURE, AND RECRUITMENT, COSTA RICA: FUNCTIONS OF AN ENVIRONMENTAL GRADIENT, SEED RAIN DISTRIBUTION, AND CRAB PREDATION PRESSURE

by

ERIN STEWART LINDQUIST

(Under the Direction of C. Ronald Carroll)

ABSTRACT

Ecologists have debated for more than a century in the theoretical literature over the predominant mechanisms that structure plant communities over a gradient. However, there have been few empirical comparative studies that investigate the relative importance of these proposed hypotheses. In this dissertation, I described the present composition and structure of a 40-year old secondary coastal tropical forest in Costa Rica. I assessed and tested the importance of seed rain distribution, environmental microhabitat along a coastal gradient, and seed and seedling predation by land crabs on tree recruitment.

Forest composition shifted with distance from shore: density and species richness of tree seedlings, saplings, and adults increased with distance. From a non-metric multidimensional scaling gradient analysis, compositional differences among the coastal and inland forest zones were apparent. Soil texture and fertility, topography, and land crab densities all changed with the coastal gradient. By overlaying the environmental variables on the forest compositional differences, I found that soil characters, topography, and canopy cover did not correlate with the spatial variation in forest composition, but distance from shore and crab burrow density did.

Over a two-year seed rain study, I found that seed rain density and species richness varied in space (related to adult distributions with long-distance dispersal surpassing adult distributions) and time (related to rainfall seasonality but no inter-annual variation). Seed dispersal does not appear to limit the recruitment of tree species in the coastal area.

To determine the importance of seed and seedling predation by the land crabs relative to canopy cover on seedling establishment, I conducted seed removal and seedling establishment experiments over a two-year period. I found: (1) crab predation affected seed and seedling survival rates, (2) crabs differentially preferred seeds and younger seedlings over older seedlings but showed no species preferences; and (4) canopy cover affected seedling survival. My results show that crab predation pressure has an important role as a limiting factor in tree recruitment in coastal forest ecosystems.

INDEX WORDS: Coastal tropical forest, Forest structure, Land crab, Seedling establishment, Seed predation, Tree recruitment

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B.S., Cornell University, 1997

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2003

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August 2003

DEDICATION

This dissertation and my current and future career in education are dedicated to the memory of my father Dr. John ("Jack") David Lindquist. Dad devoted his life to the advancement of undergraduate education, and in his later years to the personal and academic development of his only daughter. He's passed the reins over to me, but he'll always be my guide.

ACKNOWLEDGEMENTS

From the first Little Crooked Lyndon House party, through the numerous mid-day shell searches on the beach in Cabo Blanco, to the last Ecology First-Friday and post-social feast at Caliente Cab, I have fully celebrated my graduate days in Athens and Costa Rica. None of it would have been enjoyable however without the amazing support group of students, staff, and faculty of the Institute of Ecology, and the plethora of research assistants who worked with me in Cabo Blanco.

Firstly, I'd like to thank my graduate committee for all their encouragement, support, and advice: Drs. Carl Ronald Carroll, Robert Cooper, Mark D. Hunter, Diana Lieberman, Albert Parker, and Chris Peterson. I owe special thanks to my two major professors: Ron for his relentless zeal for tropical biology and conservation and continual support of my project, and Diana for her generous knowledge of forest ecology and experimental design.

Without the support of the Cabo Blanco Absolute Nature Reserve none of this dissertation would have been possible. I therefore give my sincerest gratitude to the administrators and park-guards of MINAE, ACT, and Cabo Blanco. I send a “gracias especial” to Don Carlos Castrillo, the first official park-guard of Costa Rica and Cabo Blanco, for the generous support and historical conservation perspective he gave me throughout my project at San Miguel. Without Carlos’ dedication to the station and the reserve, my project my not have been possible.

This dissertation depended on the generosity and selfless hard work of many student research assistants. My assistants came from numerous countries and institutions, and I must thank each one with an acknowledgement: Marcelo Ardón Sayaõ (UGA), Kerry Brewster (UGA), Chrissy Case (UGA), Wilfredo Castrillo Zamora (Malpais), José Castro (UGA), Mónica Castro (UNA), Minor Cedeño and Rosi (UNA), Fabricio C. Céspedes (UNA), Stephanie Conrad (UGA), Priyanka Gill (UGA), Solomon Graf (Brandeis), Rachel Holcomb-Gurley (UGA), Katie Jones (Ecolodge), Leah Katz (Colorado College), Shane Keebaugh (UGA), Anita Logotheti (Greece), Juan Luis

(UNA), David Mena (UCR), Jessica Metcalf (UGA), Jill Parsell (UCSanta Cruz), Nicole Penka (GSt), Lucas Ramirez (Ecolodge), Roger Alberto Rodriguez Cortes (Malpais), Kate Semon (UGA), Kim Shultz, Andrés Vaughn (UCR), Laura Wainer (UGA), and Tamara Zelikova (UGA).

Kerry Brewster deserves more thanks than I can give here or in my lifetime. She unselfishly dedicated the majority of 3 years in Costa Rica to my dissertation assisting me with every facet of my research from transect establishment through the endless sea of *Arrabidaea* and thorns of the bloody bromeliads…to the collection of thousands of those little “wing bastards”…to the pounding of our enemies heads into the unbearable hard earth…to her tender loving care of all the seedlings. Her seedlings were as proud of their mom, as Kerry was of her seedling kids.

I must thank Deedra McClearn, my mentor for life, for introducing me to Costa Rica, and encouraging me to reach the tropical stars.

I thank my mother, Shari Stewart, for her relentless encouragement of my career goals even when they take me to remote places far away from her. I also thank the entire Lindquist and Stewart families for cheering me through the process (with particular gratitude to my cool Tia).

I thank my best friend and companion throughout the second half of my graduate program, Marcelo Luiz Ardón Sayaõ, for my sanity. He provided me with immeasurable amounts of patience and encouragement, and devoted his precious time and clever mind to me for editing and problem-solving during the last demanding months of my dissertation madness. I also thank his parents, Doña Edith Sayaõ and Don José Ardón, and brother, José Ardón, for their hospitality and support during a week of frenzied dissertation analysis and writing in their beautiful home in Costa Rica. Muchísimas gracias por todo!

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INTRODUCTION

Tropical forests are diverse. Much of this diversity is assimilated in the trees, and this richness has been noted for centuries. Some of the first biogeography and ecology notes of Latin American trees were taken by the German naturalist Alexander von Humboldt. In 1799 with a Frenchman Aimé Bonpland he wrote:

> "What trees! Coconut trees 50-60 feet high.. . .pisang and a host of trees with enormous leaves and scented flowers, as big as the palm of a hand, of which we knew nothing. . . We rush around like the demented; in the first three days we were unable to classify anything; we pick up on object to throw it away for the next. Bonpland keeps telling me he will go mad if the wonders do not cease." (Whitmore 1990)

Humboltd's sentiments mirror my own and many temperate-zone reared students and researchers during our days in a tropical forest. I recall fondly times when I thought I'd lose my mind looking at one more tree, seedling, or seed voucher in hopes of identifying it. Yet, this feeling of taxonomic inadequacy is addictive. With every gratifying identification, comes a search for another species and the appreciation that there will always be one out there that you haven't come across yet. For me, this search wasn't just about the tree identification no matter how satisfying it was. It enabled me to investigate the patterns of forest structure, seed rain, and seedling establishment. In doing so, I hoped to better explain the factors influencing forest recruitment in a coastal tropical forest, and determine if certain life stages of recruitment were more limiting than others.

Tropical Tree Recruitment: A literature review

The factors that influence forest recruitment, and potentially limit population growth, in tropical regions remain unclear. Studies of tree recruitment are many, but the role of recruitment limitation on population dynamics is ambiguous, especially in tropical habitats. Recruitment limitation occurs when an abiotic or biotic variable decreases the transitional probabilities between one or more stages of plant recruitment, thereby causing a bottleneck in juvenile recruitment (Ribbens et al. 1994, Clark et al. 1999a; Figure 1). At each stage, environmental and biotic factors cause mortality of individuals but a certain proportion succeeds and advances to the next stage of recruitment. Locations and frequencies of recruitment will be determined by both probabilities of arrival and survival in the habitat mosaic of a tropical forest (Schupp et al. 1989). Probability of arrival is determined by dispersal factors, while the probability of survival is dependent on dormancy, physiological response to environmental conditions at colonization site, and the interactions of species with pathogens and predators. These combined factors will determine the relative probabilities that an individual plant will reach reproductive adulthood.

In temperate deciduous forests, Clark et al. (1999a) summarized the literature, with a temperate focus, into support for two views of forest recruitment limitation. The first view is that plant populations are limited by low fecundity and/or low dispersal. Arrows on the right-hand side of Figure 1 labeled "Recruitment Limited" represent these transitions. Seeds may not arrive at all sites suitable for germination and establishment. With low and variable seed supply and dispersal, populations may be rare or absent. The second view, represented on the left-hand side of Figure 1 ("Establishment Limited"), states that plant populations are limited by mortality factors at the site of establishment (environmental conditions, herbivory, pathogens, and competition). Once seeds arrive at a site, they may fail to germinate and establish successfully as seedlings. The distribution and quality of microsites and biotic factors affecting growth and mortality in seed bank and seedling stages may have large impacts on tree population dynamics. Clark et al. (1999a) found no apparent pattern in the results of the reviewed tree recruitment studies predominantly from temperate deciduous forests. Most studies of seed production, seed dispersal, and seedling establishment and growth have focused only on one or possibly two stages of recruitment, and one variable, and are therefore inconclusive. The relative effect of limiting factors on the population dynamics of a particular species was not investigated in these studies.

Likewise, the majority of tropical investigators have focused their efforts on only one or two phases of tree recruitment and one or two variables (e.g., Sork 1987). When the individual results are summarized together, however, new trends in forest dynamics may be discovered. Although there are a few tropical studies that quantified the relative effects of transitions shown in Figure 1 (Alvarez-Buylla and Garcia-Barrios 1991, Schupp and Fuentes 1995, Herrera et al. 1994), there is still little insight to which view of forest recruitment limitation (recruitment versus microsite) may be more influential to population dynamics. Results from previous tropical studies may be sufficient to allow for general conclusions of the importance of recruitment limitation to population dynamics and the stages upon which it operates most.

Recruitment variability among tree populations is expected; it allows for high diversity of species and stem sizes in tropical forests. Species-specific differences in seed production, dispersal, dormancy, microsite utilization, availability to predators and pathogens, and potential growth rates allow species to coexist by limiting interspecific competition (Grubb 1977). Species-specific responses to environmental fluctuations can cause large fluctuations in population growth. While this variability in recruitment is known, how it limits population growth is not. For example, limitation patterns may vary with the type and age of forest, and tree life history strategy. Review papers of Clark et al. (1999a) and Clark et al. (1999b) found large differences in recruitment patterns across different stand types. In another review that models plant recruitment, Hurtt and Pacala (1995) suggest that diverse communities, and therefore old-growth tropical forests, are more recruitment-limited than microsite-limited.

Much work has been done to investigate tropical tree recruitment patterns but has not been summarized in a review like that of Clark et al. (1999a) of temperate forest recruitment studies. I therefore conducted a literature review to answer the following questions: (1) Which stages of tropical forest recruitment have been found to be most limiting? (2) Which factors cause these limitations? and (3) How do the relative impacts of these factors differ across forest and species categories? This review will help scientists and land managers better understand how environmental conditions and biotic interactions influence tropical forest regeneration. For example, if any stage is known to limit tropical forest recruitment, forest managers may want to remove the bottleneck through manipulations of the limiting factor(s) to increase survival of threatened populations.

In my review, I found a total of 32 studies that concluded at least one of the stages of juvenile recruitment was limiting in the investigated tree populations (Lindquist 2000; Table 1). I reviewed five additional studies that found no stage or factor to be limiting recruitment (Saulei and Swaine 1988, Kitajima and Augspurger 1989, Willson and Crome 1989, Fleming and Williams 1990, Butler and Chazdon 1998). Two of these studies found dispersal (seed rain) not limiting (Willson and Crome 1989, Fleming and Williams 1990), two found seed bank not limiting (Saulei and Swaine 1988, Butler and Chazdon 1998), and one concluded that light (microsite condition) was not limiting juvenile recruitment (Kitajima and Augspurger 1989). The majority of the tree recruitment studies (87%), therefore, found that at least one stage in juvenile development was limiting tree recruitment.

The reviewed studies found juvenile recruitment limitations in all four limitation categories (dispersal, dormancy, seed and seedling predation, and seedling establishment and growth). Within a given tree population, four studies found that more than one limiting factor affected population growth (Janzen 1985, Sork 1987, Schupp 1990, Alvarez-Buylla and Garcia-Barrios 1991). Within a community, four additional studies found that more than one limiting factor affected population growth (Swaine et al. 1990, Martinez-Ramos and Alvarez-Buylla 1995, Dalling et al. 1998a, Dupuy and Chazdon 1998). Likewise, each recruitment stage had its unique set of limitation agents. Except for seed dormancy (high pathogen attack), no single factor dominated each recruitment stage. In both the seed dispersal and seed dormancy stages, the limiting agent appears to vary with forest age, mode of dispersal, and species life history.

Limitation at Dispersal Stage

Limitation factors in the dispersal stage include: (1) high species diversity and short dispersal distances (Martinez-Ramos and Alvarez-Buylla 1995, Loiselle et al. 1996, Dalling et al. 1998a and 1998b, Hubbell 1999), and (2) lack of animal seed dispersers in fragmented successional forests (Janzen 1985, DaSilva et al. 1996, Holl 1999) and forest understory (Augspurger and Franson 1988). Contrary to findings from Augspurger and Franson (1988) where only four percent of the stand's animal-dispersed species were represented in forest understory seed rain but 33 percent of the species were present in gap seed rain, Loiselle et al. (1996) found that animal-dispersed seed rain was more abundant in forest understory than forest gaps, but wind-dispersed seed rain displayed the reverse pattern.

Limitation in Seed Bank

Seed banks also were found to be limiting stages in seven studies (Table 1). Pathogen attack was the limiting agent in all studies and caused rapid germination rates and high mortality rates on dormant seeds. Dupuy & Chazdon (1998) found that seed bank composition is variable within secondary forest stands but not limited in abundance, whereas it is homogenous but low in abundance in old-growth stands. Dalling et al. (1998b) and Martinez-Ramos and Alvarez-Buylla (1995) found that two pioneer species, *Cecropia sp.* and *Miconia sp.*, with abundant seed rain were limited by a minimal seed bank because of a high pathogen predation. To the contrary, Dalling and Denslow (1998) found that *Miconia sp*. was abundant in the seed bank, but shade tolerant species were not. Pioneer species appear to be more abundant in the soil seed bank than shade-tolerant species (Schupp et al. 1989, Martinez-Ramos and Alvarez-Buylla 1995, Dalling et al. 1998b). Long-term accumulation of dormant seeds allows species that depend on gaps (pioneer species) to survive until a gap-opening event occurs at the seed's colonization site. Seed bank limitation in pioneer species (Dalling and Denslow 1998), thus, is not due to seed rain limitation but more probably the result of high pathogen predation rates.

Limitations at Mircrosite: Seed and seedling

Microsite conditions also limited seedling survival and growth at the site of germination in 16 studies. Light was a common limiting agent (Augspurger 1984, Sork 1987, Molofsky and Augspurger 1992, Vennendaal et al. 1996b, Kyereh et al. 1999), along with drought and dessication (Lieberman and Li 1992, Schupp 1990, Swaine et al. 1990, Veenendall et al. 1996a), fire (Janzen 1985), interspecific competition (Chapman and Chapman 1997, Sarmiento 1997), and unknown abiotic factors (Kennedy and Swaine 1992, Martinez-Ramos and Soto-Castro 1993, Dalling et al. 1998a, Dupuy and Chazdon 1998). Drought, dessication, and fire were limiting agents only in dry forest. Seed predation by ants (Levey and Byrne 1993), bruchid beetles (Janzen 1985), mammals (Sork 1987, Schupp 1990, Augspurger and Kitajima 1992), and unknown animal vectors (Alvarez-Buylla and Garcia-Barrios 1991) were discovered to limit seedling germination and establishment. Seedling survival and growth were limited by several herbivorous agents: insects (Clark and Clark 1985), small mammals (Sork 1987, Augspurger and Kitajima 1992), elephants (Chapman and Chapman 1997), and unidentified herbivores (Swaine et al. 1990, Nuñez-Farfan and Dirzo 1991).

In summary, the factors causing microsite limitations varied with the focus of each reviewed study. The abiotic (microsite) and biotic (seed and seedling predation) agents of limitation in the seedling establishment, growth, and survival stages were many in the reviewed literature because each study focused on a small set of variables. It is therefore difficult to conclude which factors in the seedling phase limit juvenile recruitment more than others. The taxonomic group of plant frugivores and herbivores which had the largest impact on seedling establishment, growth, and survival depended on the specific forest stand and its respective animal inhabitants. Microsite conditions indeed vary from site to site, and it is difficult therefore to make a clear simple conclusion about the most recruitment limiting microsite factors. In addition to microsite variability, the results of the microsite limitation search may be influenced by the investigators' interests. Finally, not all potential limiting agents have been studied previously.

Overall Recruitment Patterns

Although establishment limitations were found to be more influential than recruitment limitations in dry forest studies, as a whole I did not find that any recruitment stage was more limiting in the reviewed literature. This deduction may have resulted for two reasons: (1) limitation agents in fact affect juvenile recruitment at all stages equally, or (2) previous literature has focused on each stage equally and found limitations in the majority of factors investigated. The literature on seedling establishment, growth, and survival rates is known to be larger than on the earlier stages of juvenile recruitment (Clark et al. 1999a). I also found more studies on the seedling establishment and growth stage, but the differences in limitation agents were not significant. I therefore dismiss the latter explanation for my results on limitation frequency among recruitment stages, and accept the former reason.

It is clear from this literature review that a better understanding of forest recruitment limitation is needed. In particular, studies that assess the relative importance of multiple abiotic and biotic factors over several stages of plant life history are critical. Not only will these tree recruitment studies further our scientific knowledge of the natural limitations to tropical forest regeneration, but they will also be of practical use in tropical and sub-tropical forest restoration efforts, sustainable forestry practices, and invasive tree eradication programs. From conclusions drawn from these scientific investigations, reserve and forestry managers will have the knowledge needed to encourage the regeneration of a highly diverse community of trees in the reserve, or the recruitment of preferable species in the managed timber stand. For example, if light was found to be a limiting factor, then forest managers may need to mimic light gaps. Or if a certain taxonomic group of seedling herbivores were found to have a significant effect on seedling establishment, growth, and survival, then managers would want to exclude these predators from planted seedlings.

Objectives of the Study

This dissertation focuses on patterns of tree recruitment and forest structure along a coastal gradient. Three ecological conditions or processes that may affect these patterns are assessed: environmental conditions, seed rain distribution, and crab predation pressure. I examine these processes at the seed and seedling stages of the forest's assemblage of tree species. The first step in accomplishing my research objectives is to answer the following questions: 1) How does the forest composition and structure change with distance from shore? and 2) How does the forest composition and structure relate to changes in environmental conditions along this coastal gradient? The next step is to determine if the distribution of seed rain in space and time potentially limits tree recruitment, by comparing its composition to that of the surrounding forest and to the environmental gradient. The last step is to incorporate a crab predation factor and an environmental factor, canopy cover, into a series of manipulative experiments to answer the questions: 1) How do crab predation and canopy cover affect seed and seedling survival and growth? and 2) How does crab predation pressure vary with distance from shore, tree species, and seedling age? By investigating the relative roles of these three processes—environmental gradient, seed rain, and predation pressure—at multiple stages of tree recruitment (Figure 1), I can better understand the mechanisms causing shifts in forest community composition and structure.

Crab Predation Pressure

The effect of predators on terrestrial community structure is a central question to our understanding of plant distributions, yet has been the topic of few studies (see Louda 1989 for a review). The majority of the work addressing the effect of predator pressure along environmental gradients has been conducted in intertidal (Hay 1981, Lubchenco 1980) and mangrove (Smith et al. 1989, Clarke and Myerscough 1993, McKee 1995, McGuinness 1997, Sousa and Mitchell 1999) communities. Smith et al.'s (1989) study was the first to document the effect of differential crab (Family Sesarminae) predation pressure on the distribution of mangrove species along a complex gradient. They found that seed predation rates negatively correlated with conspecific dominance of mangrove tree species along environmental gradients. Contrary to this "dominance-predation model", more recent studies discovered that high levels of seed predation by crabs did not correlate with conspecific dominance, and concluded that crab predation pressure is not the key mechanism causing the apparent zonation of mangrove communities (Clarke and Myerscough 1993, McKee 1995, McGuinness 1997, Sousa and Mitchell 1999). They suggest that physiological adaptation to variable abiotic conditions limit specific mangrove species distributions. Multiple processes may structure mangrove communities, but their relative importances are not resolved.

A few studies have concluded that differential predation pressure has the potential to cause spatial variation in plant abundances along terrestrial environmental gradients (Chapparal scrub, insect herbivore, Louda 1982; Subalpine Meadow talus, pika herbivore, Huntly 1987; Beach forbs and grasses, mice and vole herbivores, Boyd 1988; and Perrenial forb grasslands, insect herbivores, Reader 1992). No investigation, however, has assessed the potential for differential seed and seedling predation to influence terrestrial tree community structure.

Most crab predation studies have been conducted in mangrove communities (Smith et al. 1989, Clarke and Myerscough 1993, McKee 1995, McGuinness 1997, Sousa and Mitchell 1999), where high rates of propagule predation by mangrove crabs (Family Sesarminae) are common. In many coastal forests around the tropics, land crabs (Family Gecarcinidae) and hermit crabs (Family Pagaridae) are very abundant. Although these crabs are known to be omnivorous, they are assumed to forage predominantly on fruits, seeds, seedlings, and leaf litter. Yet researchers have only just begun to investigate the impacts of terrestrial land crab seed and seedling predation on plant recruitment (*Gecarcoidea natalis*, Christmas Island, Indian Ocean, O'Dowd and Lake 1990, 1991, Green et al. 1997; and *Gecarcinus quadratus*, Costa Rica, Pacific Ocean, Sherman 2002), while the impact of hermit crab predation pressure on seedling success has not been investigated.

Both O'Dowd and Lake (1991) and Green et al. (1997) found that the red land crab, *Gecarcoidea natalis*, consumed seeds at extremely high rates. O'Dowd and Lake (1991) found that removal rates of the seeds positively correlated with their nitrogen concentration, and negatively correlated with their condensed tannin concentration. Green et al. (1997) concluded from their seed preference study, that crabs prefer species with "pulpy exocarps". Green et al. (1997) and O'Dowd and Lake (1990) also found that *G. natalis* predates significantly on seedlings by destroying the entire individual, but does not exhibit seedling species preferences. Using exclusion and control plots in and out of forest gaps, Green et al. (1997) found the highest seedling densities in the exclusion plots out of gaps than the other three treatments, and large differences in densities between exclusion and control plots (29-fold and 21-fold greater in the exclusion plots in the understory and gaps treatments respectively). Species richness of seedlings also was significantly higher (10-fold) in the exclusion plots than the controls.

A land crab species, *Gecarcinus quadratus*, also was found to significantly affect seedling densities in a Costa Rican coastal rain forest (Sherman 2002). From crab exclosure and enclosure studies, Sherman concluded that *G. quadratus* significantly limits the density and diversity of the seedling community in the coastal forest where crabs dominate by preferentially consuming large numbers of seedlings. Because Sherman's study is the first to document the effect of land crabs on seedling densities in a mainland forest, it is important to test his findings in a different system. Also, my study examines the combined and differential effect of seed and seedling predation by both land crabs (*G. quadratus*) and hermit crabs (*Coenobita compressus*) on the forest community in relation to tree community composition and structure, seed rain distribution, and plant response to environmental conditions.

Only one investigator (McGuinness 1997) has compared the relative effects of propagule predation, light availability, soil conditions, and seed rain distribution on the seedling success of one species of mangrove. From his clever study design, McGuinness concludes that a combination of limited dispersal, predation of propagules, and high soil temperatures limit the species spatial patterns. Like McGuinness' study, several other crab predation studies in mangrove communities (Osborne and Smith 1990, Sousa and Mitchell 1999), and a maritime forest community (Green et al. 1997) have compared seedling recruitment relative to canopy cover and crab predation pressure. Both Green et al. and McGuinness found that seedling survival and growth were higher in shadier habitats than in gaps. There is evidence from McGuinness' study suggesting that in light gaps the negative impact of increases in soil temperature and evapotranspiration rates is larger than the positive impact of an increase in light availability. There is also some evidence that canopy cover may affect crab foraging patterns, thereby indirectly affecting seedling success. Osborne and Smith (1990) found that crab predation rates were negatively correlated with gap size in an Australian mangrove, whereas Sousa and Mitchell (1999) found that canopy cover (gap or non gap) did not affect crab predation rates on mangrove propagules. It is apparent from these studies that there is no consensus as to how canopy cover directly and indirectly affects community spatial patterns.

Coastal Gradient

Besides canopy cover, other environmental factors may vary along a gradient in a coastal forest and affect tree species composition differentially including soil texture (e.g., Clark and Clark 2000), soil nutrient levels (e.g., Swaine 1996), soil salinity (e.g., Williams et al. 1998), and others. This ecologically important gradient encompassing the boundaries of the marine and terrestrial ecosystems may influence species distributions and abundances (see Louda 1989, Smith 1992, Polis et al. 1997 for reviews). Environmental gradients are prevalent in coastal ecosystems such as salt marshes (e.g., Hacker and Bertness 1999), mangroves (e.g., Jiménez 1991), coastal scrub vegetation (e.g., Louda 1982), and temperate maritime forests (e.g., Wimberly and Spies 2001). In many cases they have been found to influence zonation of plant species in these vegetative communities (Jiménez 1991, Hacker and Bertness 1999, Sousa and Mitchell 1999). Often in coastal systems, plant species are found to be adapted to specific ranges along the environmental gradients, and experience differential competitive (e.g., Emery et al. 2001), facilitative (e.g., Hacker and Bertness 1999), and predatory (e.g., Smith et al. 1989) interspecific interactions in relation to the gradient.

With few empirical comparative studies, it is unknown if these environmental variables working independently, and/or interacting with the biotic processes of predation, dispersal, and interspecific competition, are more important in structuring plant communities than differential seed predation. This study will describe the environmental gradient in the coastal forest, and relate any changes in abiotic conditions to the surrounding forest composition through ordination analyses.

Regional Context

I conducted this study in the coastal terrestrial forest surrounding the Estación Biológica San Miguel (EBSM) of the Reserva Absoluta Cabo Blanco on the Pacific Coast of the Nicoya Peninsula, Puntarenas Province, Costa Rica (9˚ 35' N, 85˚ 08.5' W). The study area is bordered on the southwest by the Pacific Ocean, on the northwest by a private reserve and buffer area, the Refugio de Vida Silvestre Cueva los Murciélagos, and on the north by a patchwork of privately owned forest and cattle pasture.

Cabo Blanco Absolute Nature Reserve was established as the first protected area in Costa Rica on 21 October 1963 through the conservation foresight and initiative of Nicolas Wessberg and Karen Mogensen (Timm et al. unpublished). The reserve is considered by many in the Costa Rican park service to be the prototype of the country's commitment to conservation. The original protected terrestrial area of 1272 ha was increased in 1982 to include the first one km from the shore, protecting 1700 ha of ocean. When the reserve was established, the majority of the area, approximately 85 percent, was previously cleared for agriculture. Small subsistence farmers planted corn and beans on the relatively level terrain nearest the coast, while cattle ranchers used the inland areas with slightly higher elevation (C. Castrillo pers.com.). The remaining undisturbed 15 percent consisted of forest found in the upland slopes of the reserve and a few patches within the secondary forest on steep slopes and in riparian areas.

For the first 22 years of the reserve's history, the public did not have access, and only park guards were present to protect the reserve against fire, logging, and poaching. In 1985 a government decree opened the Cabuya (eastern) sector to the public for day visits on a system of nature trails and access to educational services. The San Miguel (western) sector has remained closed to the general public, but in 1997 the Estación Biológica San Miguel opened to students and researchers.

In 1998, the University of Georgia signed a "convenio", or covenant, with the Costa Rican government to encourage education, research, and conservation at EBSM and the surrounding areas. In exchange for receiving permission to bring student groups into the station and researchers to conduct approved investigations, the University of Georgia supports the station financially and logistically under the direction of EBSM's Directors, Drs Milton and Diana Lieberman. This provided an opportunistic setting for my dissertation research of tree recruitment and forest structure in the reserve. Because of the new relationship, this study is the first long-term study to be conducted at EBSM. This investigation, thus, is critical to the future understanding of regeneration patterns in the area; it creates base-line descriptions of the forest structure and composition at its current stage of regeneration (approximately 40 years after agricultural abandonment). To aid future assessment of the forest's regeneration path, I established long-term vegetative plots for monitoring of survival, growth, and compositional changes through time.

The information I present here will be most helpful to future studies in the reserve and surrounding areas. The Area de Conservación Tempisque, MINAE (in effect the Costa Rican national park service), will have the knowledge needed to encourage the regeneration of a diverse and natural community of trees within the reserve and beyond. Currently, the conservation area's management is obtaining deforested areas to the north of the reserve to restore biological corridors between Cabo Blanco and other existing public and private reserves. In addition, my collaboration with the professors and students of the Universidad Nacional Autonoma (UNA) initiates an essential working research relationship among native Costa Ricans and the reserve.

Seasonally Dry Tropical Forests

This study describes a seasonally dry, or transitional dry-moist tropical forest (Holdridge 1967), on the Pacific slope of Costa Rica. This forest is in the most disturbed and ecologically threatened ecosystem of the tropics: tropical dry forests (Janzen 1988). Due to this intense human land use, less than 1% of Latin America's tropical dry forests remain today (Gillespie et al. 2000). Throughout tropical America, human population and agricultural centers have been and still are concentrated in the dry forest regions—approximately 79% of the current Central American human population lives in the dry forest regions (Murphy and Lugo 1995). The majority of current dry forest vegetation exists in habitat fragments and degraded patches surrounded by cattle ranches and agricultural farms.

Fortunately, there is great potential for dry forest regeneration and re-establishment in abandoned farmland (Janzen 1988). However, as a result of rapid deforestation detailed descriptions of dry tropical forest structure and composition are lacking compared to tropical humid forest and savanna (Bullock et al. 1995). Previous studies that assessed forest recovery following abandonment of pasture and agricultural lands have focused on the early stages of regeneration within the first 20 year of growth (Uhl et al. 1988, Nepsted et al. 1990, Sabogal 1992, Aide et al. 1995). Few have studied the long-term result of natural forest recovery (but see Gillespie et al. 2000, Aide et al. 1996). Long-term information is critical for many public and private organizations in Latin America that now are striving to restore and manage these dry forest ecosystems. This study, thus, will provide essential information on the current state of a 40-year old secondary forest and assist future work that will examine the forest in later stages of regeneration.

Outline of the Thesis

This thesis moves from more descriptive (Chapter 2 - 3) to more experimental studies (Chapter 4).

In Chapter 2, the study site forest is described in terms of changes in forest structure and composition relative to distance from shore. Three tree life stages are described and quantified: seedling, sapling, and adult. Various environmental variables that make up the complex coastal gradient are then described relative to the shore. Finally, the structure and composition of the forest is then compared to the environmental changes through NMS ordination analyses.

In Chapter 3, the seed rain composition and distribution is examined in the study site over a two-year period. Both spatial (relative to the shore) and temporal (seasonal) seed rain patterns are described and quantified with NMS ordination analyses. Phenological observations are also mentioned. Seed rain composition is compared to the forest neighborhood with regression analyses of the axes scores of the seed rain, juvenile, and adult ordination analyses.

In Chapter 4, the effects of land crab predation of seeds and seedlings on tree seedling establishment are investigated. Through a series of manipulative exclosure experiments with transplanted seeds and seedlings, and natural light-gap and understory microhabitats, the relative influence of crab predation pressure and canopy cover on seedling survival and growth is determined.

The survival and growth rates of marked seedling, sapling, and tree individuals also were studied, but the results will be presented later when more long-term data have been collected. In addition, I am co-authoring a field guide to the woody plants (primarily trees, with a few shrubs and lianas included) of Cabo Blanco Absolute Reserve that will be published in the next year by the National Institute of Biodiversity (INBio) of Costa Rica.

The early stages of the book were initiated when the co-author, Fabricio C. Céspesdes, was assisting me in this study's vegetation analyses.

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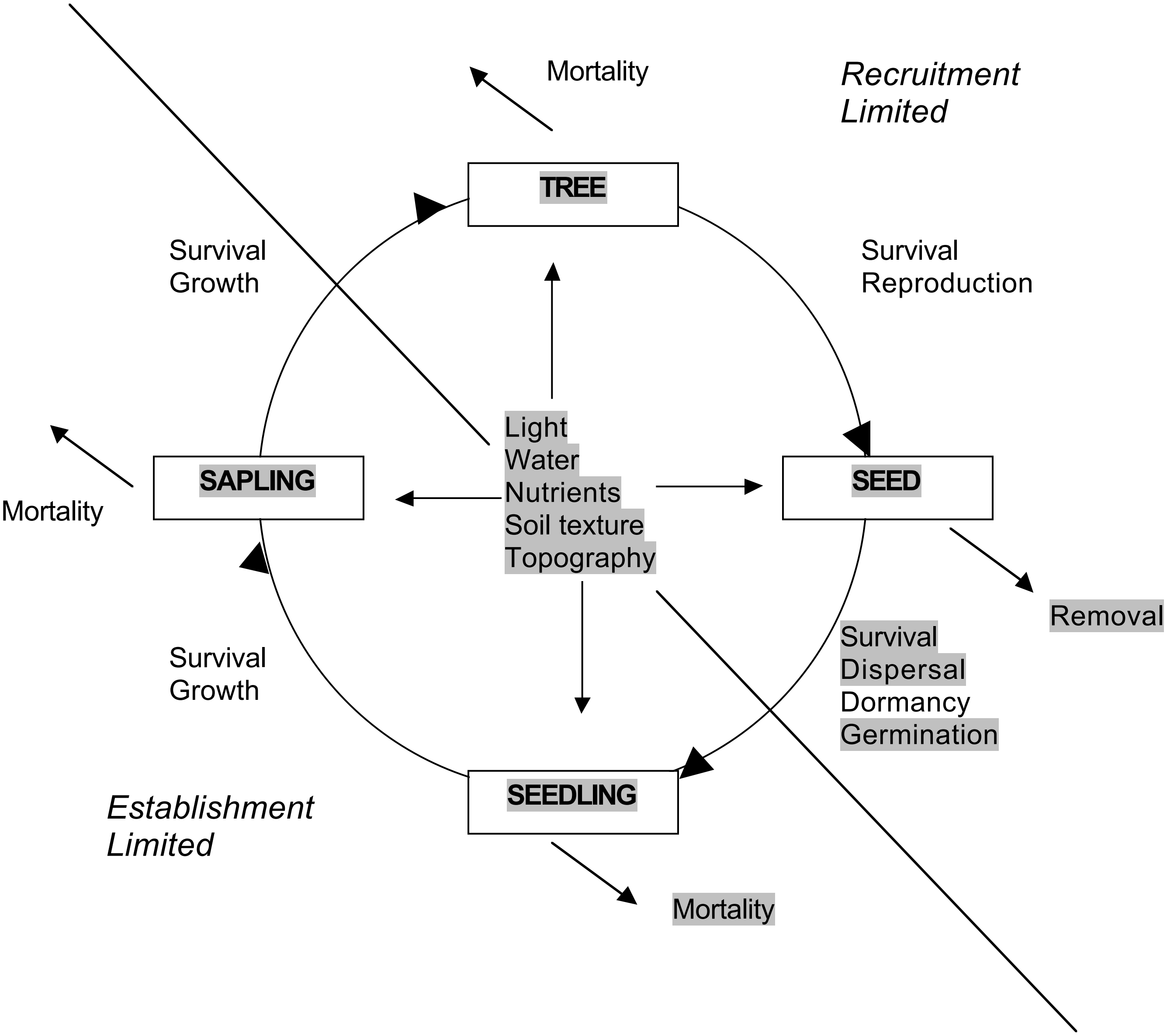
Table 1. A summarized list of reviewed tropical literature that found recruitment limitations in least one of the limitation categories: dispersal, dormancy, predation at seed and seedling stage, and microsite at seedling stage.

Dispersal	**Dormancy**	**Predation**	**Microsite**
•Augspurger & Franson 1988	•Alvarez-Buylla & Garcia-Barrios 1991	•Alvarez-Buylla & Garcia-Barrios 1991	•Augspurger 1984
•Dalling et al. 1998a	•Augspurger 1983	•Augspurger & Kitajima 1992	•Chapman & Chapman 1997
•Dalling et al. 1998b	•Augspurger & Kelly 1984	•Chapman & Chapman 1997	•Dalling et al. 1998a
•DaSilva et al. 1996	•Dalling & Denslow 1998	•Clark & Clark 1985	•Dupuy & Chazdon 1998
•Holl 1999	•Dalling et al. 1998b	•Janzen 1985	•Janzen 1985
•Hubbell 1999	•Dupuy & Chazdon 1998	•Levey & Byrne 1993	•Kennedy & Swaine 1992
•Janzen 1985	•Kennedy & Swaine 1992	•Nuñez-Farfan & Dirzo. 1991	•Kyereh et al. 1999
•Loiselle et al. 1996	•Martinez-Ramos, & Alvarez-Buylla 1995	•Schupp 1990	•Lieberman & Li 1992
•Martinez-Ramos & Alvarez-Buylla 1995		•Sork 1987	•Martinez-Ramos & Soto-Castro 1993
		•Swaine et al. 1990	•Molofsky & Augspurger 1992
			•Sarmiento 1997
			•Schupp 1990
			•Sork 1987
			•Swaine et al. 1990
			•Vennendaal et al. 1996a
			•Vennendaal et al. 1996b

Figure 1. The life cycle of a tree. Different life stages are shown in boxes. Processes that affect the transitions between stages are in italic. Shaded stages or processes are covered in this study. The environmental conditions of the area that may affect the different life cycle stages and processes are included in the center of the life cycle, with those I investigated shaded.

Fig 1, Chap I
Lindquist



COMPOSITION AND STRUCTURE OF A SEASONALLY DRY TROPICAL FOREST ALONG A COASTAL GRADIENT, COSTA RICA[1]

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[1] Lindquist, E.S., and D. Lieberman. To be submitted to Journal of Tropical Ecology

Abstract

Seasonally dry forests are the most threatened tropical ecosystems, and their long-term regeneration patterns are not well known. Coastal forests are an exceptionally endangered and understudied subset of seasonally dry forests, and are well-suited for investigating how complex environmental gradients can influence forest structure and composition. In this study we examined the environmental conditions in a coastal secondary forest in Costa Rica, and assessed their potential effects on tree distribution, abundance, and frequency at three stages of recruitment (seedling, sapling, and adult). We found differences in the forest structure and composition between the coastal and inland areas. There were higher adult and sapling densities, canopy height, and species richness of all stages in the inland area (250-350m from coastline) relative to the coastal area (0-100m from coastline). Seedling densities did not differ between the two zones, but were low throughout the study area. The coastal zone lacked recruitment in the sapling and small adult stem size-classes of all species (2.5 cm<dbh≤5cm), whereas the interior zone lacked only small stems of several light-demanding canopy species. Several environmental and biotic variables changed with distance from shore: altitude (+), soil texture (sand to clay), soil phosphorus content (-), soil pH (-), and land crab density (-). Conversely other soil characteristics (e.g., soil salinity), slope, and canopy cover did not. A nonmetric multidimensional scaling (NMS) ordination showed some segregation of adult plots by topographical and substrate categories. In the ordination, distance to shore was the only variable that explained at least 20 percent of the compositional differences among adult plots. The findings I present here provide a quantitative description of the changes in forest structure and composition along a coastal gradient, and how these patterns relate to environmental differences.

Key words: coastal gradient, dry forest, forest structure, non-metric multidimensional scaling ordination, regeneration

Introduction

Dry deciduous forests are one of the key forest types in the tropics (Bullock et al.1995), and are globally the most threatened tropical ecosystem (Janzen 1988). Yet in comparison to tropical humid forest and savanna, detailed descriptions of dry tropical forest structure and composition are lacking (Bullock et al. 1995). This paucity of information on dry forests is partially due to the scant distribution of dry forests today after four centuries of human settlement (Janzen 1986) and recent decades of rapid deforestation for cattle ranching. Throughout tropical America, human population and agricultural centers have been and still are concentrated in the dry forest regions– approximately 79% of the current Central American human population lives in the dry forest regions (Murphy and Lugo 1995). Due to this intense land use, less than 1% of Latin America's intact tropical dry forests remain today (Gillespie et al. 2000). The majority of current dry forest vegetation exists in habitat fragments and degraded patches surrounded by cattle pasture and farms.

Fortunately, in some of these disturbed regions such as the dry forests of Costa Rica, there is potential for dry forest regeneration and re-establishment on abandoned agricultural lands (Janzen 1988). However, because there is a lack of original dry forest, and subsequent lack of literature documenting original and secondary forest composition and regeneration patterns, it is uncertain with what success the forests will grow back, and to what state. Previous studies that assessed forest recovery following abandonment of pasture and agricultural lands have focused on the early stages (≤ 20 yr) of regeneration (Uhl et al. 1988, Nepstad et al. 1990, Sabogal 1992, Aide et al. 1995, Nepstad et al. 1996, Guariguata et al. 1997). Few have studied the long-term result of natural forest recovery (but see Aide et al. 1996, Finegan 1996, Rivera and Aide 1998, Gillespie et al. 2000, Gauriguata and Ostertag 2001). Long-term information is critical for many public and private organizations in Latin America that now are striving to restore and manage these dry forest ecosystems.

Because the Neotropical dry forest regions are mostly found along the Pacific Coast and slopes of Latin America, a significant portion of dry forest ecosystems lie within a few kilometers or even meters of the Pacific Ocean.   This coastal forest interface with the ocean has not been described or investigated in any detail (Chapman 1976), with the exception of one study that loosely described the remnant coastal dry forests of Northwest Costa Rica before most of the study area was lost to development (Sauer 1975).

The boundary between marine and terrestrial ecosystems is ecologically important because of its environmental, productivity, and species interactive gradients that can influence species distributions and abundances (see Louda 1989, Smith 1992, Polis et al. 1997 for reviews).   Environmental gradients are prevalent in coastal ecosystems such as salt marshes (e.g., Hacker and Bertness 1999), mangroves (e.g., Jiménez 1991), coastal scrub vegetation (e.g., Louda 1982), and temperate maritime forests (e.g., Wimberly and Spies 2001). In many cases they have been found to influence zonation of plant species in these vegetative communities (Jiménez 1991, Hacker and Bertness 1999, Sousa and Mitchell 1999). Often in coastal systems, plant species are adapted to specific ranges along environmental gradients, and experience differential competitive (e.g., Emery et al. 2001), facilitative (e.g., Hacker and Bertness 1999), and predatory (e.g., Smith et al. 1989) interspecific interactions in relation to the gradient.

Here we describe a coastal terrestrial forest in Costa Rica and its environmental gradient in relation to distance from the ocean-forest interface. We examine the environmental conditions in the forest to assess their potential effects on tree distribution, abundance, and frequency along the gradient at three stages of recruitment: seedling, sapling, and adult. Because the forest has regenerated from pasture and farmland in the past 39 years, we also considered the previous land use as a potential factor affecting current forest structure, composition, and recruitment, and examined the size-class distribution of the trees to describe the forest dynamics. This study provides base-line information to better understand the regeneration patterns of coastal forests. It will also prove helpful to Reserve managers and regional conservationists interested in understanding and protecting seasonally dry tropical forest, especially the areas near the coast.

Study site

We conducted the study in the coastal terrestrial forest surrounding the Estación Biológica San Miguel (EBSM) of the Reserva Absoluta Cabo Blanco on the Pacific Coast of the Nicoya Peninsula, Puntarenas Province, Costa Rica (9˚ 35’ N, 85˚ 08.5’ W). The study area is bordered on the southwest by the Pacific Ocean, on the northwest by a private reserve and buffer area, the Refugio de Vida Silvestre Cueva los Murciélagos, and on the north by a patchwork of privately owned forest and cattle pasture.

Cabo Blanco Absolute Nature Reserve was established as the first protected area in Costa Rica on 21 October 1963 through the conservation foresight and initiative of Nicolas Wessberg and Karen Mogensen (Timm et al. unpublished). The original protected terrestrial area of 1272 ha was increased in 1982 to include the first one km from the shore, protecting 1700 ha of ocean. When the reserve was established, the majority of the area, approximately 85 percent, was previously cleared for agriculture. Small subsistence farmers planted corn and beans on the relatively level terrain nearest the coast, while cattle ranchers used the inland areas with slightly higher elevation (C. Castrillo pers.com.). The remaining 15 percent consisted of forest found in the upland slopes of the reserve and a few patches on steep slopes and in riparian areas.

For the first 22 years of the reserve's history, the public did not have access, and only park guards were present to protect the reserve against fire, logging, and poaching. In 1985 a government decree opened the Cabuya (eastern) sector to the public for day visits on a system of nature trails and access to educational services. The San Miguel (western) sector has remained closed to the general public, but in 1997 the Estación Biológica San Miguel opened to students and researchers.

The forest of Cabo Blanco is classified as a transitional dry to wet tropical forest. Annual precipitation ranges from 2500 to 3200 mm year^{-1} (mean of 3000 mm year^{-1} with little interannual variation in total amount), which lies in the wet tropical forest precipitation range. But because almost all the annual rain (95 to 100%) falls during the wet season (May -November), the seasonality of precipitation classifies the forest as a seasonally dry tropical forest (Figure 1). Average annual temperature is 27˚C, with average low and high temperatures of 24˚C and 32˚C respectively. The soils within the study area were primarily formed from weathered marine limestone and turbidite (Timm et al. unpublished).

Methods

Our study area, contained entirely within secondary forest, is situated along a 1 km stretch of coastline and extends 350 meters away from the coastline (Figure 2). For sampling methodology, the study area was divided into two sub-study areas, or forest zones, separated by a steep limestone rock outcropping located at approximately 90 to 150 meters away (varying with topography) from the start of the vegetation along the coastline: (1) the "coastal" zone is contained within the first 100 meters (100 m X 1000 m, or 100,000 m^2 = 10 ha) of the coastline, and (2) the "inland" zone extends inward after the rock shelf; approximately 150 to 350 m from the coastline (200 m X 500 m, or 100,000 m^2 = 10 ha, Figure 2).

To sample with respect to distance from the coastline, in February 2000 we established 18 permanent 100 m-long belt transects, 9 in each forest zone, running perpendicular to the shoreline. The inland zone was restricted in its length dimension by deep stream gorges and rock-falls on its edge; yet the sampling area of both zones was kept equal by doubling the depth dimension of the inland zone.

Forest structure and composition

We conducted the vegetation analyses of adults and saplings in the late dry seasons (February-March) of 2000 and 2001, and the seedling analyses in the wet season

(July) of 2000. One set of concentric circular quadrats was located randomly on the permanent transects within every 25 meters. We measured species composition and densities of tree seedlings (stem height above ground < 0.50 m for dicots and non-separated leafed palms), saplings (2.5 m $\geq$ stem height $\geq$ 0.50 m for dicots, and palms with well-separated frond leaflets), and adult stems (diameter at breast height > 2.5 cm for dicots, palms with above-ground meristems) (Gentry 1995). Quadrat sizes for each life stage were: (1) seedling: radius (r) = 2m, area (A) = 12.57 m^2, (2) sapling: r = 3m, A = 28.27 m^2, and (3) adult stem: r = 5m, A = 78.54 m^2. For the adult quadrats, we constructed a species accumulation curve to assess sampling effort efficiency. Only tree species were included in the vegetation analyses; other woody species such as shrubs and lianas were excluded from the study. For those adult tree individuals with multiple stems that bifurcated above ground, we grouped their multiple stem measurements together as one individual.

All seedlings (to the nearest 1 cm), saplings (to the nearest 10 cm), and adults (to the nearest meter) of all woody tree and palm species were measured for above ground stem height, and for adults diameter at breast height (1.3 m dbh) was also measured. For adult stems less than 6 m tall, we used a pole to measure the height above ground. For adult stems with heights greater than 6 m tall, we used both a Leitz optical range-finder, and the naked eye if the ground was not sufficiently level to use the clinometer, to estimate height to the nearest five meters. We measured main stem height from ground level to the top-most leaf node. For juvenile (seedling and sapling) palm individuals that lacked an above-ground stem, we measured the length of the longest palm frond from plant center to tip of frond as an estimate of relative height.

We identified individuals to species in the field when possible using field guides (Gentry 1993, Holdridge et al. 1997, Quesada et al. 1997, Poveda and Sánchez-Vindas 1999, Zamora et al. 2000). If the species was unknown in the field for saplings and trees, we took a voucher specimen, and identified the species later with the assistance of expert taxonomists. Collections of the voucher specimens have been deposited in herbariums at San Miguel Biological Station, Universidad Nacional Autonoma (UNA), and National Institute of Biodiversity (INBio) all in Costa Rica. For seedlings, we differentiated individuals into morpho-species and, if possible, identified species later with the assistance of expert taxonomists and seedlings grown in the greenhouse from collected seeds of known species.

Forest stand density, total basal area, and species richness (S) were calculated for each of the forest zones. Species richness (R) was also calculated as: (S-1)/ln(n), where S is the number of species in each zone, and n is the number of individuals sampled in each zone. Species relative densities, relative frequencies, and stem size-class distributions for the most common species were also determined.

Environmental Gradient

In February 2003 we measured the slope, aspect, and altitude of each vegetation quadrat along each transect. Along the axis of steepest slope, we extended a meter tape 5 m above and below the center of the quadrat, and measured its aspect with a compass. We measured the slope to the nearest degree with a Sokkia clinometer at the two 5 m intervals and averaged the two values for one slope reading. Altitude was recorded at the center of each quadrat with a dial altimeter to the nearest 5 m.

Soil samples were collected from within the vegetation quadrats near the end of the dry season in 2001 (March 1 to 3 2001); we randomly selected one quadrat within every 50 m of transect for a total of 36 random samples (18 in coastal zone and 18 in inland zone). After removing the litter layer, we collected a 1000 cm^3 sample of soil after removing large rocks and organic material. Samples were placed in Polyethylene lined soil sample bags and dried at 50ºC in an oven until no condensation formed on plastic storage bags. Once dry, samples were stored at room temperature (27ºC) and approximately 60% humidity until we transported them to the Soil Laboratory at the Universidad Nacional Autonoma in Heredia, Costa Rica for analysis. A total analysis was done on all samples to measure: soil texture (Bouyoucos hydrometric method), soil pH (Potentiometric method relation 1:2.5), soil organic matter (Walkely-Black method), soil primary nutrient levels (% N, P, K; Micro- Kjeldahl method modified, Colorimetric methods assay PO_4, and Spectrophotometry Atomic Absorption respectively), soil secondary nutrient levels (Ca, Mg; Spectrophotometry Atomic Absorption), soil trace metals (Cu, Fe, Zn; Spectrophotometry Atomic Absorption), and aluminum (Al^{+3}; Titulation).

In the dry season 2002 (March 22 to 25 2002), we collected 20 additional soil samples in the same manner as 2001 to test the precision of the 2001 soil analysis. The samples were taken from 8 random quadrat locations and sifted for rocks and organic matter. Each sample was mixed thoroughly, and then divided into two replicates. The samples were analyzed in the same laboratory and methods as those from 2001 (UNA, Heredia) for the same soil characteristics. We found no significant differences between the total soil analyses results of the 8 replicate samples and their paired samples (paired *t*-test, $t_{1,40}$= 0.601, P= .28), and conclude that the analyses findings are precise.

From a subset of the soil samples taken in 2001 (6 coast 0 to 50 m from coastline, 6 coast 51 to 100 m, 6 interior 0 to 50 m, and 6 interior 51 to 100 m), we assessed soil salinity by measuring the conductivity (Oakton WD-35615-75 conductivity meter) of a 1:5 soil and water solution as a surrogate for soil salinity (water ratio of 20% was recommended by Baize, 1993). We mixed 20 ml (or approx. 20.5 g) of distilled water (conductivity of 0.75 µS) with 4 g of soil from each sample in sterile cell culture vials, and measured the conductivity of the solution until constant (48 hr after mixing).

We also assessed salt spray deposition into the first 50 meters of forest, along 5 of the transects. On 6 February 2000 between 13:30 and 14:30, we placed semicircular pieces of filter paper (Fisher's Qualitative; diameter= 15 cm) at 0.4 m and 1.4 m above the ground, at intervals of 0, 10, 20, and 50 m away from the forest-beach interface. On 8 February 2000 between 14:30 and 15:45 we collected all the filter papers, and placed them in 100 mL distilled water. On 10 February 2000 at 14:00, water conductivity readings for the samples had reached stability and were recorded with a Oakton WD-35615-75 conductivity meter. Five controls consisted of untreated filter papers and distilled water. Differences in conductivity responses among the distance and height treatments were analyzed with a nonparametric general linear model (JMP 4.0).

To estimate percent canopy cover we used a densiometer at the center of each vegetative quadrat along all permanent transects while collecting the vegetative data (February 2000, 2001). We held the densiometer level with the ground at elbow height and determined the percent of grid intersections covered by vegetation reflected in the densiometer's mirror. At each point we took 4 densiometer readings while facing each cardinal direction, and averaged the four readings to determine percent canopy cover of each quadrat.

Finally, we estimated densities of the Harlequin land crab, *Gecarcinus quadratus*, which have an effect on seedling establishment through considerable predation of seeds and seedlings (Lindquist and Carroll 2003). Land crab densities were assessed during the onset of the wet season of 2001 (June) when crabs were actively foraging outside their holes. We assumed one hole per crab and one entrance per hole. We counted only visibly active holes (crabs continually clean their holes and accumulate clay soil pellets at the entrance of the hole) in continuous 2 m x 2 m quadrats along the length of the study’s permanent transects.

To assess the relationship of the environmental and biotic variables to distance from shore, Pair-wise Pearson product-moment correlations were found independently for each variable (JMP 4.0).

Gradient Analyses

Variation in the forest community composition was spatially described with nonmetric multidimensional scaling (NMS) ordination analyses using PC-ORD software (Kruskal 1964, Mather 1976, McCune and Mefford 1999, McCune and Grace 2002). We conducted two NMS ordinations: one with the abundance data for species of seedlings and saplings combined (stem dbh ≤ 2.5 cm), and one for the tree abundance data. The advantage of NMS over other ordination techniques is that it is based on ranked distances, and does not assume linear relationships among variables (McCune and Grace 2002). The ranked distances linearize the relationship between distances measured in species and environmental space. Before the analyses, Beals smoothing was used to transform the heterogeneous compositional data for the adult and juvenile plots because of the high frequency of zeros (McCune and Grace 2002). Plots with no individuals of any species (all 0 frequencies), and outliers that were at least 2.3 standard deviations from the average ordination distances between plots, were excluded from the analyses after preliminary runs with the entire data set (McCune and Grace 2002).

For the analysis, we used the Sorenson distance measure recommended by McCune and Grace (2002) for NMS analysis of community data. We started each analysis with a random configuration, and conducted 15 runs with the real data. The number of dimensions was selected by PC-ORD; it found the best solution for each dimensionality (lowest stress or the inverse measure of fit to the data), and added additional dimensions only if they reduced the final stress 95% of the time or more ($p \leq 0.05$ for the Monte Carlo test). We examined the stability of the solution with a plot of stress versus iteration number, to verify that the solution reached stability before the final iterations (200 iterations maximum) (McCune and Grace 2002). The environmental variables' values for the vegetation quadrats were overlaid on both the juvenile and adult ordinations as a second matrix to assess potential correlations between the environmental conditions and the variation in forest composition. Plots were grouped into coastal and inland zone categories for the NMS ordinations.

Results

Forest structure and composition

Sixty-two species of trees were present in the 36 adult plots (total sample area= 0.56 ha) of the permanent transects (Table 1), representing 55 genera and 32 families. Eighteen of the species were found in the coastal plots, and of these 18, three were not present in the inland zone– *Sterculia apetala*, *Terminalia catappa*, and *Triplaris melaenodeudron* (Table 2). Fifteen species were shared among the two zones (Table 1). Total species richness (R) for the study area was 10.3, with an R of 3.6 in the coastal zone and 9.6 in the inland zone. The species accumulation curves for both the coastal and inland zones level out well before the end of the sampling effort (Figure 3), with the possibility that only a few rare species were missed, particularly for the inland zone.

Total stand adult density differed between the two zones ($t_{1,70}$= -7.79, P<.0001), as did canopy height ($t_{1,70}$= -3.57, P=.0007, Table 1). The inland forest was much more closed both in the understory and canopy with a relatively high tree density of 1710 individuals ha^{-1}, but the stem density was quite variable. Total stand basal area did not differ between the two zones ($t_{1,70}$= 0.159, P=.87, Table 1) and was 27 and 26 m^2 ha^{-1} in the coastal and inland zones respectively.

Of all species, *Bombacopsis quinata* (Bombacaeae) had the highest basal area with 11 m^2 ha^{-1} in the coastal zone and 3.3 m^2 ha^{-1} in the inland zone (Table 2). *Luehea seemannii* (Tiliaceae) had the highest basal area in the inland zone at 7.3 m^2 ha^{-1}, followed by *Calycophyllum candidissimum* (Rubiaceae) at 4.0 m^2 ha^{-1} (Table 2). *C. candidissimum* also had the 2nd highest basal area in the coastal zone (6.9 m^2 ha^{-1}, Table 2). The largest tree in the forest was an emergent *Sterculia apetala* (Sterculiaceae) located 50 m from the coast with a dbh of 110 cm and a height of 35 m.

C. candidissimum was the most common species throughout the study area, with plot frequencies of 67% and 97% and densities of 166 and 272 stems ha^{-1} in the coastal and inland zones respectively (Table 2). The next most common species was *Trichilia* *martiana* (Meliaceae); it was present in 50% of the inland plots with an average density of 191 stems ha^{-1}, but absent in the coastal plots. Other species had densities of greater than 100 stems ha^{-1}: *Cordia collococca* (Boraginaceae) in the coastal plots, and *Picramina latifolia* (Simaroubaceae) in the inland plots. *P. latifolia, Tabebuia ochracea* (Bignoniaceae), *Luehea seemannii* (Tiliaceae), *Trichilia pleeana* (Meliaceae), and *Piper tuberculatum* (Piperaceae) were all found in at least 1/3 of the inland plots (Table 2). In the coastal zone, only *C. candidissimum* was found in more than 1/3 of the plots, but both *Bombacopisis quinata* (Bombacaceae) and *Hyperbaena tonduzii* (Menispermaceae) were present in at least 1/5 of the coastal plots.

Similar to the structure and compositional patterns for trees among the two sampling zones, densities and species richness of seedlings and saplings varied with distance from shore. Thirty-six species of tree saplings were identified, representing 34 genera and 22 families (Table 1). Thirty of these species were present in the inland zone, and 11 in the coastal zone, with 5 species shared among the two. There were higher sapling densities in the interior zone ($t_{1,42}$= -3.88, *P*=.0002, Table 1). Seedling densities, however, did not differ between the two zones ($t_{1,42}$= -1.79, *P*=.081, Table 1); they were low throughout the study area. Of the 15 seedling species identified, 10 were present in the inland zone, 9 in the coastal zone, and 4 species in both (Table 1,3).

No seedling species was abundant due to the very low densities of seedlings throughout the study area, and a clumped distribution of some species. *Attalea butyracea* (Arecaceae) and *Spondias mombin* (Anacardiaceae) were found in 1/5 of the coastal plots and *Inga vera* was found in 1/3 of the inland plots (Table 3). The species with the highest average density, *Plumeria rubra* (Apocynaceae), was found in only 10% of the plots, but had high densities in those two plots (1.6 and 1.0 stems m^{-2}, Table 3). *A. butyracea* also had high sapling frequencies of 33% and 61% in both the coastal and inland zones respectively (Table 3). Three other species were common in the inland zone: *T. martiana* (56%), *P. latifolia* (14%), and *Manilkara chicle* (Sapotaceae, 22%;

Table 3). *Bactris major* (Arecaceae), a clonal palm, had high densities in some plots in both the coastal and inland zones (Table 3). Also in the inland zone, *Chrysophyllum cainito* (Sapotaceae) had relatively high sapling densities (0.32 stems m^{-2}, Table 3).

The size-class distributions for all species in the two zones differed (Figure 4). In the inland zone, the majority of stems were in the smaller size-classes (Figure 4), but in the coastal zone the curve was more bell-shaped with the mid-size stem class (dbh= 2.5 to 5.0 cm) contributing the most individuals (38%). The size-class distribution curve for the most common species in both zones, *C. candidissimum*, was similar to the combined curve (Figure 4). Size-class 1 was deficient in stems, however, for both zones. Two common species showed skewed size-class distributions: *B. quinata* had no stems in size classes 1,2, or 3; and *Luehea seemannii* had few individuals in the first three size-classes (Figure 4). Several species, especially in the inland zone, had high small size-class abundances but had few to no larger individuals. *C. collococca* and *T. martiana* had considerable numbers of individuals in the first four and three size-classes respectively (Figure 4).

Environmental Gradient

Altitude increased with distance from shore along the permanent transects with a maximum altitude of 75 m above sea level at approximately 350 meters from the coastline (r = 0.95, df=1,72, *P*<.0001), Figure 5). Slope varied among the study quadrats, with a minimum and maximum slope of 0º and 38º respectively (x = 11.6º ± 9.77º) and positively correlated with distance from shore (r = 0.55, df=1,72, *P*<.0001, Figure 5). Aspect also varied (min = 116º, max = 329º, x = 230º ± 45.3º) but not relative to shore (r = -0.023, df=1,72, *P*=0.85, Figure 5).

We found a gradient in soil texture from 97% sand in one sample taken near the shore to clay (40 to 50%) for a few samples taken approximately 300 to 350 meters away from the shore. The majority of samples were classified in the loam, sandy clay loam, and clay loam of the USDA textural classes. As the clay content of the samples increased, the sand content decreased (Figure 6). Phosphorous, aluminum, iron, zinc, and pH H_2O all correlated with distance from shore, whereas percent organic matter, percent nitrogen, potassium, calcium, copper, magnesium, and pH KCl did not (Table 4). Aluminum, iron, and zinc increased with distance from shore (Figure 6). Percent sand, phosphorous and pH water decreased with distance from shore (Figure 6). There was no relationship between soil conductivity (salinity) and distance from shore (Table 4), although the samples within the first 50 meters of the coastline did have higher conductivities in general (Figure 6).

We found high levels of salt deposition at the 0 m marine-forest interface at both ground (0.4 m above ground) and breast-height (1.4 m above ground) levels, some salt deposition at 10 m from shore, but little to no salt deposition at the 20 and 50 m intervals (Figure 7). Distance from the shore explained some of the variation observed in salt deposition ($F_{3,33}$= 3.44, P= .028), but height above ground did not ($F_{3,33}$= 0.45, P=.51).

Canopy cover did not vary with distance from shore (Figure 8). It was high (x = 96% ± 4.0) throughout, with the exception of one outlier, a light-gap, with a canopy cover of 81% (Table 4). Active crab hole densities along the transects decreased with distance from shore (Figure 8), from a maximum of 6.5 crab holes m^{-2} at 60 m from shore to 0 crab holes m^{-2} at approximately 200 and 275 m (Table 4).

Gradient Analyses

For both the juvenile and adult non-metric multidimensional scaling (NMS) analyses, two major gradients captured most of the variance in the adult and juvenile plot compositions with no additional stress reduction with additional dimensions. With 30 randomized runs for the adult and juvenile analyses, there were not significant reductions of stress with the addition of the third (*P*= 0.968) or fourth dimensions (*P*= 0.968). The final stresses for the adult and juvenile solutions were 14.1 and 17.9 respectively, after 30-40 iterations (of 200 total). The NMS analysis for the adult plots explained 88.2% of the total variation between the ordination distances and the original plot compositional space, with 34.0% loaded on the axis 1 and 54.2% on axis 2 (Table 5). The juvenile NMS analysis explained 80.4% of the variation, with 43.9% explained by the first dimension, and 36.5% on the second axis (Table5).

When plotted on the NMS ordination's two axes (Figure 9), the 62 adult plots separate out into the coastal and inland zones. The coastal plots are aggregated in the upper-right hand corner (positive correlations with axis 1 and 2), and the upland flat and slope plots are found predominantly in the lower-left hand corner (negative correlations with the two axes) (Figure 9). Of all the environmental variables, only distance and altitude explained approximately 20% of the plot compositional variation in species space (Table 5, Figure 9). Crab hole density explained the next largest proportion of the ordination-explained variation (6.5%, Table 5).

Unlike the adult ordination, the juvenile (seedling and sapling) plots did not separate out into the zone categories as well as the adult tree plots (Figure 9). Furthermore, no environmental variables explained more than 20% of this variation (Table 5). Distance from shore (12%), altitude (11%), and percent organic matter (12%) were the three best explanatory variables (Table 5). Between-juvenile-plot variation was large, and any differences relative to environmental variables that existed for the adults were possibly obscured in the juvenile plot ordination.

Discussion

In the coastal forest of EBSM, we found a change in the forest structure and composition along an environmental gradient from the marine-terrestrial interface inland. Adult species richness and stem density increased sharply with distance from shore. Of the 62 total tree species, 44 species were only found further than 150 m from shore, and 18 species were present only in the coastal zone (Table 1). Sapling density and species richness also increased with distance from shore (Table 1). Although seedling densities were very low throughout, with a few patches of higher densities, the inland zone was characterized with high densities of saplings and small-stemmed adults. Species composition of the tree plots also varied between the coastal and inland plots (Figure 9). This evident zonation in coastal forest composition and structure is similar to that found in mangrove ecosystems (Jiménez 1991, Smith 1992), but with a larger number of tree species involved making the shift in forest composition more complex.

As a whole, after approximately 40 years of regeneration from pasture and small agricultural fields, the forest has regained much of its presumed original structure and species richness. When compared to the small remnant patches of primary forest in Cabo Blanco Absolute Reserve the inland secondary forest is very similar in species composition (Bocanegra et al. 1999), basal area (Panuncio 2000), and stem density (Panuncio 2000). Although there are no comparable intact primary forests outside the reserve, the size-class distribution of trees found here is characteristic of other secondary tropical forests, where the canopies are dominated by light demanding species, like *L. seemannii* and *B. quinata* (Finegan 1996, Peña-Claros 2001). These species should continue to dominate the canopy through the later stages of succession (50 to 100 years), as the more shade-tolerant species like *T. martiana* and rare species like *Alchorneopsis floribunda* continually establish and grow. The EBSM forest, classified as a transitional dry-humid forest, lies well within the typical ranges for species number, canopy height, and basal area of dry forests, and in the lower ranges of those properties in wet forests (Bullock et al. 1995, Table 6). Differences among dry forest types are expected due to variation in the amount and seasonality of precipitation, and soil fertility (Killeen et al. 1998, Murphy and Lugo 1995).

It is evident that recruitment of tree juveniles is minimal, however, particularly in the coastal zone. Only 36 tree species were found in the sapling stage (R= 5.9) and only 15 in the seedling stage (R= 2.6; Table 1). Of the species present in the juvenile stages, most had very low and heterogeneous densities among the study plots. Past land use of these coastal flats may still be affecting patterns of succession in this area. A native liana, *Adenocalymna inundatum* (Bignoniaceae), is known to be a common weed in the cornfields (C. Castrillo pers. comm.), and has persisted in the coastal area through sexual and vegetative propagation as the forest has regenerated around it. Currently, its shrub-stage dominates the understory in the coastal flat areas as a large dense monoculture of 1 to 2 m tall shrubs, and is also found in the canopy. Few to no seedlings or saplings are found underneath *A. inundatum*, and it most likely limits recruitment of any species where it is most dense. The liana is present in the inland areas, but not in high abundance.

Another factor affecting juvenile recruitment in the area is the Harlequin land crab, *Gecarcinus quadratus*. In a series of manipulative experiments in a previous study, we found that crab predation and secondarily canopy cover affected seedling establishment of various tree species in the coastal forest (Lindquist and Carroll 2003). Crab predation caused high levels of mortality of seeds and young seedlings regardless of species, and was at significantly higher levels in the coastal zone than in the interior zone. Here, distance from shore negatively correlated with land crab density and, presumably, the intensity of crab predation pressure. Differential predation pressure of seeds and seedlings by crabs, therefore, could be an important factor influencing coastal forest zonation, as it has been reported in mangrove and island coastal systems (Smith et al. 1989, Green et al. 1997).

Along with the shift in species distributions, forest structure, and land crab predation pressure, we found an apparent environmental gradient in the coastal forest (Table 4). There was a slight increase in altitude (a change of only 75 m over 350 m of horizontal distance), as one might expect when starting at sea level, but although slope and its direction varied throughout the study area, they did not relate to distance from shore. These topographical findings are ecologically interesting because of their interaction with wind direction and intensity. Winds could have significant effects on the growth and distribution of plant species through the deposition of salt and high evapotranspiration rates particularly in the dry season (Ceron et al. 2002) and during storm events (Gustafsson 1997, Kerr 2000). Although there is often a slight breeze coming off the ocean, only on occasion does the coast experience a large storm and intense onshore winds (Sauer 1975, C. Castrillo pers. com.). Our results from the salt spray experiment showed that significant salt aerosols are only deposited within the first 10 meters of the coastline (Figure 7). A similar experiment conducted in 2002 during a 30+- year storm event also found that salt was only deposited in the first 10 meters of the coastal forest (Allen et al. 2002). We conclude therefore that because there was no relation of aspect and soil salinity with distance and the variation in the vegetative composition of the forest, and because of minimal salt deposition, wind and salt interception alone are not the decisive factors causing shifts in forest composition.

Variability in soil characteristics is known to affect species distribution (Swaine 1996), and soil fertility to affect growth rates (Veenendaal et al. 1996, see Turner 2001a,b for a review). It remains unclear, however, how species richness and tree density are directly influenced by a gradient in soil composition. We found a soil texture and fertility gradient with respect to the shore. Clay content increased while the sand content of the soil decreased with distance from shore (Table 4). There was a slight decrease in soil fertility with distance from shore as both phosphorous and pH decreased (Table 4). This may be due to the difference in historical land use of the area. The soils may be more leached of nutrients where the cattle grazing occurred in the inland areas. Aluminum, which often increases in concentration with leaching, was higher in the inland zone (Table 4). However, aluminum is typically abundant in tropical soils due to acidic soils (Turner 2001b).

Irrespective of the gradient, the ranges of soil texture and fertility lied well-within typical ranges for Central American tropical forests (Young 1976, CITATION). Low silt content (less than 15%) and high clay content are expected in the tropics (Young 1976), and soils derived from basic rocks, like the marine limestone, are high in clay and organic matter content. The organic matter contents were higher than those typically found in the tropics, by an order of 2 or 3 (Young 1976), but this result may be partially explained by the failure to remove all fine root material from the soil samples before analysis. Although texture and organic matter content influence soil water availability, nutrient availability, and root densities (Martinez-Yrizar 1995), none of the observed values suggest that these variables have a large limiting influence on species distribution in the study area. The primary plant nutrients– nitrogen (N), phosphorous (P), and potassium (K)– were also high compared to other tropical undisturbed soils (Young 1976) and disturbed dry forests (Maass 1995). Finally, the very high concentration of calcium originating from the limestone parent material serves as a basic buffer for potentially acidic soils that are prevalent in the humid tropics (Turner 2001a), improving the cation exchange capacity of the soil (Young 1976).

The non-metric multidimensional scaling (NMS) analysis for the adult plot compositional data found a satisfactory solution with only two major gradients. The solution for the composition variation in the juvenile plots fit the data more poorly due to low species frequencies, but did lie in the acceptable range for ecological data. Although the measured environmental variables did not explain the variation in juvenile composition, we can not assume that the environmental gradient has no effect on juvenile tree distribution and abundance. The mere absence of juveniles along the gradient, suggests there is severe juvenile recruitment caused by harsh environmental and biotic conditions.

From the NMS solution for adult tree compositional variation, however, it is clear that distance (with its correlate altitude) alone captures a large proportion of the compositional variation (24%). Minimal additional variation was explained by any of the other variables. Although crab hole densities varied with distance from shore, it only explained 6.5% of the ordination variation. The distance gradient incorporates a lot of the environmental variation into one factor, and represents the complex environmental gradient. Because no other variable was as conclusive as distance from shore, it appears there is a complex environmental gradient associated with change in the distribution and abundance of tree species in the coastal forest.

The findings we present here provide a better understanding of the forest structure and composition of a secondary coastal tropical forest. Our results should assist local, national, and international efforts in conserving and restoring these threatened and ecologically important ecosystems. For example, there is interest from the Tempisque Conservation Area (ACT, MINAE) of the Tempisque River Basin and Nicoya Peninsula to restore forested corridors between already protected areas such as Cabo Blanco. The information we provide here can be used to better comprehend the natural regeneration processes of the region's forests, and how proximity to the coastline may change the forest structure and composition. Finally, and very importantly, researchers and students can use our findings as base-line data for future monitoring of the forest regeneration around Estación Biológica San Miguel.

Acknowledgements

The NSF Dissertation Improvement Grant (DEB-0104791), Sigma Xi, and various field and travel award grants from the University of Georgia given to E. Lindquist supported this work. We are grateful to the Costa Rica MINAE administration of San Miguel Biological Station, Cabo Blanco Absolute Nature Reserve for allowing this study to be conducted in such a restricted area, and expressing interest in the study's findings. This study wouldn't be possible without the unselfish field help of numerous field assistants, with particular thanks to Kerry Brewster for her painstaking dedication to every detail of the study. Finally, we thank Marcelo Ardón, C. Ronald Carroll, Bob Cooper, Mark Hunter, Al Parker, and Chris Peterson for their comments on earlier versions of the manuscript.

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Table 1. Total stand values for tree, sapling, and seedling quadrats in coastal and interior zone.

			Inland		
Total stand variables	**n**	**avg ± sd**	**n**	**avg ± sd**	**Total**
Trees					
Basal Area (m^2 ha^{-1})	36	27.3 ± 40.5	36	26.0 ± 26.6	
Canopy height (m)	36	17 ± 8.7	36	24 ± 8.0	
Density (stems ha^{-1})	36	509 ± 348	36	1710 ± 856	
Total number of species		18		59	62
Species richness		3.6		9.6	10.3
Total number of genera		17		53	55
Total number of families		13		31	32
Saplings					
Total Density of Saplings	36	0.096 ±0.18	36	0.29 ± 0.26	
Total Number of Species		11		30	36
Species Richness (R)		2.2		5.1	5.9
Total Number of Genera		11		29	34
Total Number of Families		13		31	32
Seedlings					
Total Density of Seedlings	20	0.23 ± 0.56	24	0.80 ± 1.35	
Total Number of Species		9		10	15
Species richness (R)		1.9		1.8	2.6
Total Number of Genera		9		10	15
Total Number of Families		8		7	11

Table 2. Densities, basal area, and frequencies of species in adult plots (stems > 2.5 cm dbh). Relative densities and basal areas are for all plots. The number of plots frequented by a particular species is given in parentheses.

	Coast			**Inland**		
Species	**BA (m^2 ha^{-1})**	**Density (stems ha^{-1})**	**Frequency (plots)**	**BA (m^2 ha^{-1})**	**Density (stems ha^{-1})**	**Frequency (plots)**
Alchorneopsis floribunda	-	-	-	0.002	3.54	0.028 (1)
Alibertia edulis	-	-	-	0.026	10.6	0.083 (3)
Anacardium excelsum	0.062	3.54	0.028 (1)	0.66	14.1	0.11 (4)
Andira inermis	-	-	-	0.008	7.07	0.056 (2)
Attalea butyracea	0.000	10.6	0.083 (3)	0.00	7.07	0.028 (1)
Bactris major	-	-	-	-	28.3	0.083 (3)
Brosimum alicastrum	-	-	-	0.15	63.7	0.28 (10)
Bombacopisis quinata	11	42.4	0.22 (8)	3.3	7.07	0.056 (2)
Bursera simaruba				0.025	3.54	0.028 (1)
Calycophyllum candidissimum	6.9	166	0.67 (24)	4.0	272	0.97 (35)
Capparis amplissima	-	-	-	0.003	7.07	0.056 (2)
Capparis verrucosa	-	-	-	0.000	3.54	0.028 (1)
Casearia commersoniana	-	-	-	0.001	3.54	0.028 (1)
Cedrela odorata	-	-	-	0.69	3.54	0.028 (1)
Chrysophyllum cainito	-	-	-	1.4	28.3	0.11 (4)
Copaifera aromatica	0.036	3.54	0.028 (1)	0.001	3.54	0.028 (1)
Cordia collococca	1.2	106	0.19 (7)	0.021	3.54	0.028 (1)
Crescentia cujete	0.013	3.54	0.028 (1)	0.008	3.54	0.028 (1)
Diospyros digyna	-	-	-	0.030	7.07	0.056 (2)
Eugenia salamensis	-	-	-	0.002	3.54	0.028 (1)
Ficus trachelosyce	-	-	-	0.17	7.07	0.056 (2)
Guapira costaricana	-	-	-	0.002	3.54	0.028 (1)
Guarea glabra	-	-	-	0.003	10.6	0.083 (3)
Guazuma ulmifolia	0.073	7.07	0.056 (2)	0.82	14.1	0.083 (3)
Heteropterus laurifolia	-	-	-	0.020	3.54	0.028 (1)
Hyperbaena tonduzii	0.022	31.8	0.22 (8)	0.006	7.07	0.056 (2)
Inga sp	-	-	-	0.71	3.54	0.028 (1)
Inga vera	-	-	-	2.1	46.7	0.17 (6)
Lacistema aggregatum	-	-	-	0.048	28.3	0.14 (5)
Licania arborea	-	-	-	0.013	7.07	0.056 (2)
Lonchocarpus felipei	0.85	49.5	0.17 (6)	0.077	3.54	0.028 (1)
Lonchocarpus minimiflorus	0.096	3.54	0.028 (1)	0.28	21.2	0.11 (4)
Luehea seemannii	-	-	-	7.3	67.2	0.36 (13)
Macrocnemum roseum	-	-	-	1.5	38.9	0.22 (8)
Manilkara chicle	-	-	-	0.035	28.3	0.19 (7)

Miconia argentea	-	-	-	0.035	10.6	0.083 (3)
Nectandra sp	-	-	-	0.002	3.54	0.028 (1)
Neea sp	-	-	-	0.002	3.54	0.028 (1)
Ocotea veraguensis	-	-	-	0.034	14.1	0.11 (4)
Oxandra venezuelana	-	-	-	0.050	32.9	0.17 (6)
Picramnia latifolia	-	-	-	0.12	120.	0.44 (16)
Piper tuberculatum	-	-	-	0.14	104	0.33 (12)
Plumeria rubra	1.0	21.2	0.056 (2)	0.15	3.54	0.028 (1)
Posoqueria latifolia	-	-	-	0.083	31.8	0.17 (6)
Pouteria campechiana	-	-	-	0.011	14.1	0.083 (3)
Pouteria reticulata	-	-	-	0.039	38.9	0.22 (8)
Pseudobombax septanum	0.028	3.54	0.028 (1)	0.23	3.54	0.028 (1)
Randia monatha	-	-	-	0.012	7.07	0.056 (2)
Sloanea termiflora	-	-	-	0.017	7.07	0.056 (2)
Sorocea sp	-	-	-	0.021	7.07	0.056 (2)
Spondias mombin	0.64	10.6	0.056 (2)	0.33	10.6	0.056 (2)
Swartzia simplex	-	-	-	0.038	3.54	0.028 (1)
Sterculia apetala	3.4	3.54	0.028 (1)	-	-	-
Tabebuia ochracea	-	-	-	0.20	88.4	0.36 (13)
Tabebuia rosea	1.34	21.2	0.14 (5)	0.024	21.2	0.14 (5)
Terminalia catappa	0.025	7.07	0.056 (2)	-	-	-
Terminalia oblonga	-	-	-	0.013	3.54	0.028 (1)
Trichilia martiana	-	-	-	0.25	191	0.50 (18)
Trichilia pleeana	-	-	-	0.20	84.9	0.33 (12)
Triplaris melaenodeudron	0.008	3.54	0.028 (1)	-	-	-
Trophis racemosa	-	-	-	0.14	42.4	0.28 (10)
Zanthoxylum setulosum	-	-	-	0.18	7.07	0.056 (2)

Table 3. Densities and frequencies of species in seedling and sapling plots. Densities are averages of only those plots with the species present. The number of plots frequented by a particular species is given in parentheses. Total density of individuals includes all plots and unidentified individuals.

	Coast		**Inland**	
Species	**Density (stems m^{-2})**	**Frequency (prop. of plots)**	**Density (stems m^{-2})**	**Frequency (prop. of plots)**
Seedlings (ht < 0.50m)		**n= 20**		**n= 24**
Alibertia edulis	-	-	0.080	0.083 (2)
Attalea butyracea	0.10	0.20 (4)	0.080	0.042 (1)
Bombacopsis quinata	0.080	0.050 (1)	-	-
Calycophyllum candidissimum	0.080	0.10 (2)	0.080	0.083 (2)
Copaifera aromatica	-	-	0.080	0.042 (1)
Hyperbaena tonduzii	0.080	0.10 (2)	0.080	0.083 (2)
Inga vera	0.16	0.050 (2)	0.27	0.33 (8)
Luehea seemannii	-	-	0.16	0.042 (2)
Manilkara chicle	-	-	0.080	0.042 (1)
Picramnia latifolia	-	-	0.080	0.083 (2)
Plumeria rubra	1.3	0.10 (2)	-	-
Pouteria reticulata	-	-	0.080	0.083 (2)
Pseudobombax septenatum	0.20	0.050 (2)	-	-
Spondias mombin	0.080	0.20 (4)	-	-
Terminalia catappa	0.080	0.05 (1)	-	-
Saplings (ht ≥ 0.5m, dbh ≤ 2.5 cm)		**n= 36**		**n= 36**
Alchorneopsis floribunda	-	-	0.035	0.028 (1)
Alibertia edulis	-	-	0.062	0.11 (4)
Astronium graveolens	-	-	0.035	0.028 (1)
Attalea butyracea	0.10	0.33 (12)	0.13	0.61 (22)
Bactris major	1.0	0.028 (1)	0.48	0.11 (4)
Brosimum alicastrum	-	-	0.035	0.083 (3)
Calycophyllum candidissum	-	-	0.11	0.028 (1)
Capparis verrucosa	0.071	0.028 (1)	-	-
Cedrela odorata	-	-	0.035	0.028 (1)
Cesearia sylvestris	-	-	0.071	0.056 (2)
Chrysophyllum cainito	-	-	0.32	0.056 (2)
Copaifera aromatica	-	-	0.035	0.15 (4)
Cordia collococca	0.12	0.056 (2)	-	-
Eugenia salamensis	0.035	0.028 (1)	-	-
Guarea glabra	-	-	0.035	0.056 (2)
Hyperbaena tonduzii	0.086	0.19 (7)	0.053	0.11 (4)
Lacistema aggregatum	-	-	0.071	0.028 (1)

Lonchocarpus felipei	0.053	0.056 (2)	-	-
Lonchocarpus minimiflorus	-	-	0.035	0.028 (1)
Manilkara chicle	-	-	0.035	0.22 (8)
Miconia argentea	-	-	0.035	0.028 (1)
Nectandra sp.	-	-	0.053	0.056 (2)
Ocotea veraguensis	-	-	0.035	0.056 (2)
Oxandra venezuelana	-	-	0.071	0.14 (5)
Picramnia latifolia	-	-	0.086	0.39 (14)
Piper tuberculatum	-	-	0.11	0.14 (5)
Posoqueria latifolia	-	-	0.035	0.028 (1)
Pouteria campechiana	-	-	0.035	0.056 (2)
Pseudobombax septenatum	0.035	0.028 (1)	-	-
Sorocea sp.	-	-	0.035	0.028 (1)
Spondias mombin	0.035	0.028 (1)	-	-
Sterculia apetala	0.035	0.028 (1)	0.035	0.056 (2)
Tabebuia ochracea	-	-	0.035	0.083 (3)
Trichilia martiana	0.035	0.028 (1)	0.062	0.56 (20)
Trichilia pleeana	-	-	0.059	0.12 (3)
Trophis racemosa	-	-	0.035	0.028 (1)

Table 4. Pearson product-moment pairwise correlations of individual environmental variables with distance from shore.

Variable	**n**	**Mean**	**Stdev**	**Min**	**Max**	**r**	***P*-value**
% Clay	36	25.8	10.2	0.00	50.0	0.60	0.0001
%Sand	36	46.0	11.5	24.0	97.0	-0.48	0.0029
% Organic Matter	36	10.3	7.04	4.1	49.9	-0.18	0.28
% N	36	0.3	0.1	0.1	0.7	-0.058	0.74
P (ppm)	36	22.6	11.0	9.50	57.1	-0.51	0.0015
K (meq/100g)	36	3.7	1.7	0.7	7.1	-0.13	0.44
Al^{+3} (meq/100g)	36	0.3	0.2	0.1	0.8	0.37	0.026
Ca (meq/100g)	36	43.4	11.3	24.5	69.5	-0.031	0.86
Cu (ppm)	36	0.9	0.4	0.3	2	0.16	0.36
Fe (ppm)	36	114	118	16.0	526	0.41	0.012
Mg (meq/100g)	36	10.0	2.87	4.00	15.8	-0.13	0.45
Zn (ppm)	36	0.9	0.6	0.2	2	0.45	0.0057
pH H2O	36	6.8	0.51	5.7	7.6	-0.34	0.042
pH KCl	36	5.6	0.42	4.6	6.5	-0.27	0.11
Conductivity (µS)	23	35.6	15.4	10.5	77.4	-0.24	0.27
Canopy cover (%)	40	96	4.0	81	100	0.094	056
Crab density (m^{-2})	46	1.8	1.6	0	6.5	-0.65	<0.0001

Table 5. Correlation efficients for the relationships of the environmental variables to the two main ordination axes scores of the nonmetric multidimensional analysis for (a) the tree plots, and (b) the juvenile plots. Pearson's *r* correlation coefficient expresses the linear relationship between the individual variables and the ordination scores, which Kendall's tau expresses the rank relationship. R^2 expresses the proportion of variation on the ordination axis that is explained by the variable in question.

(a) Adult plots

Axis		**1**			**2**	
	r	**R^2**	**tau**	***r***	**R^2**	**tau**
Distance	-0.491	0.241	-0.313	-0.597	0.356	-0.371
Altitude	-0.473	0.224	-0.280	-0.506	0.256	-0.286
Slope^o	-0.098	0.010	-0.025	-0.119	0.014	-0.109
SlopeAzi	-0.029	0.001	-0.018	0.137	0.019	0.063
Canopy	0.107	0.011	0.077	0.030	0.001	0.062
Crab	0.255	0.065	0.158	0.359	0.129	0.213
%Clay	-0.124	0.015	-0.103	-0.127	0.016	-0.084
%OrgMat	0.197	0.039	0.051	0.269	0.072	0.116
%N	-0.015	0.000	-0.019	-0.001	0.000	0.009
P	0.174	0.030	0.080	0.160	0.025	0.085
K	0.114	0.013	0.057	0.061	0.004	0.059
Al^{+3}	-0.120	0.014	-0.70	-0.132	0.017	-0.024
Ca	0.069	0.005	0.039	0.046	0.002	0.034
pH-H_2O	0.052	0.003	0.069	0.013	0.000	0.052
		R^2			**R^2**	
Total		**0.340**			**0.542**	**= 0.882**

(b) Juvenile plots

Axis		**1**			**2**	
	r	**R^2**	**tau**	***r***	**R^2**	**tau**
Distance	-0.349	0.122	-0.205	0.167	0.028	0.128
Altitude	-0.329	0.109	-0.166	0.190	0.036	0.158
Slope^o	-0.137	0.019	-0.043	0.087	0.008	0.021
SlopeAzi	-0.057	0.003	-0.042	-0.184	0.034	-0.038
Canopy	-0.206	0.042	-0.069	-0.173	0.030	-0.011
Crab	0.148	0.022	0.066	0.016	0.000	0.045
%Clay	0.021	0.000	0.023	-0.046	0.002	-0.096
%OrgMat	0.339	0.115	0.197	-0.131	0.017	-0.185
%N	0.199	0.040	0.152	-0.126	0.016	-0.173
P	0.123	0.015	0.147	-0.195	0.038	-0.161
K	0.136	0.019	0.118	-0.096	0.009	-0.163
Al^{+3}	0.075	0.006	0.081	-0.105	0.011	-0.136
Ca	0.102	0.010	0.102	-0.123	0.015	-0.159
pH-H_2O	0.150	0.023	0.155	-0.134	0.018	-0.170
		R^2			**R^2**	
Total		**0.439**			**0.365**	**= 0.804**

Table 6. Comparison of forest properties of Cabo Blanco with other tropical dry and wet forests around the world.

Forest Property	Dry	Wet	Cabo Blanco
Tree species on 1-3 ha	33-90	50-200	62+
Canopy height (m)	10-40	20-84	20
Basal area of trees (m^2 ha^{-1})	17-40	20-75	26

Source: Murphy and Lugo (1986). Values are global ranges.

Figure 1. Annual monthly-accumulated rainfall at San Miguel Biological Station, Cabo Blanco Absolute Nature Reserve from June 1999 to July 2002. Annual totals are listed for 2000 and 2001, and for these same years monthly rainfalls for November and December are combined because of infrequent field recording of daily rainfall.

Fig. 1, Chap II
Lindquist

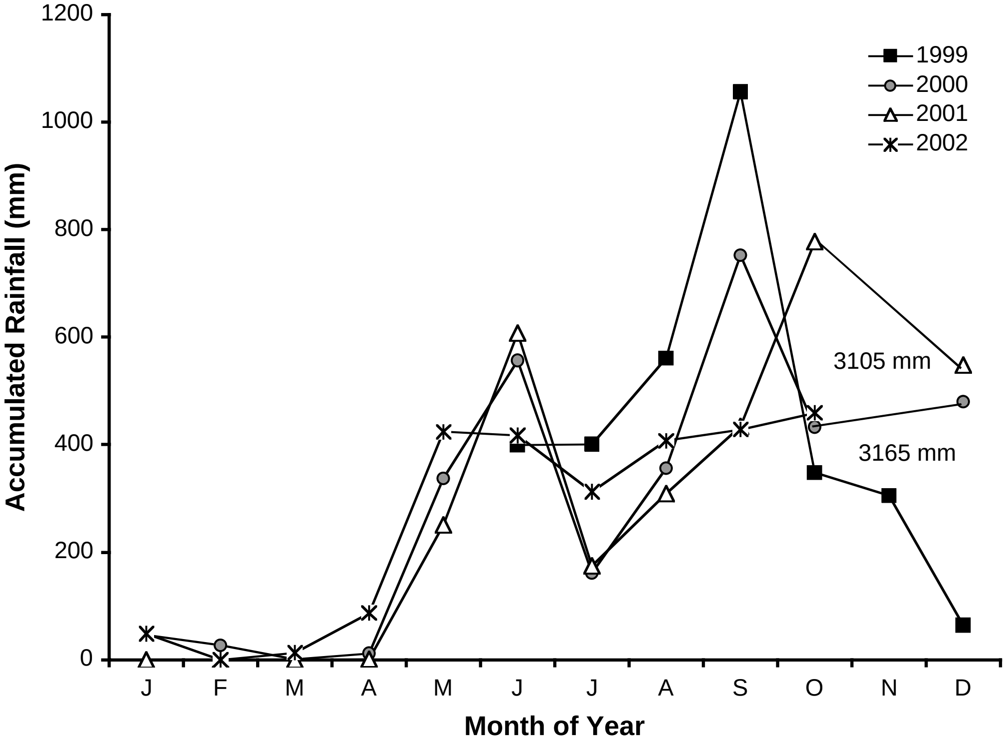


Figure 2. Location of forest zone study areas in relation to each other and the coastline on a topographic map of the region around Estación Biológica San Miguel, Reserva Absoluta Cabo Blanco.

Fig. 2, Chap II
Lindquist

Legend

A = Coastal zone

B = Inland Zone

↗ = Permanent Transect
(100 m in length)

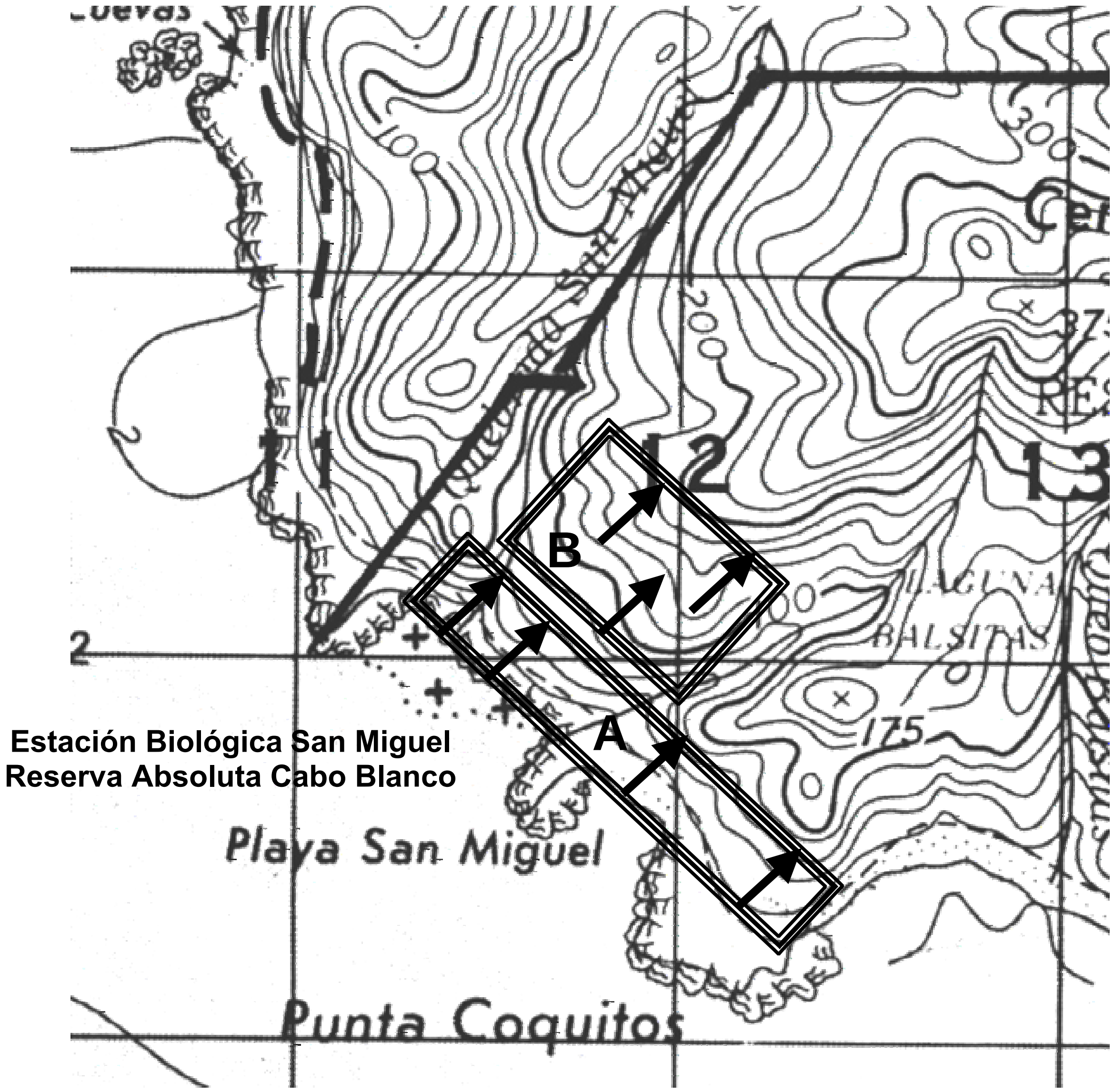


Figure 3. Species accumulation curve for the total number of stems sampled in the adult tree plots in the coastal and interior zones. The curve was generated from a random selection without replacement of the individuals found in all plots.

Fig. 3, Chap II
Lindquist

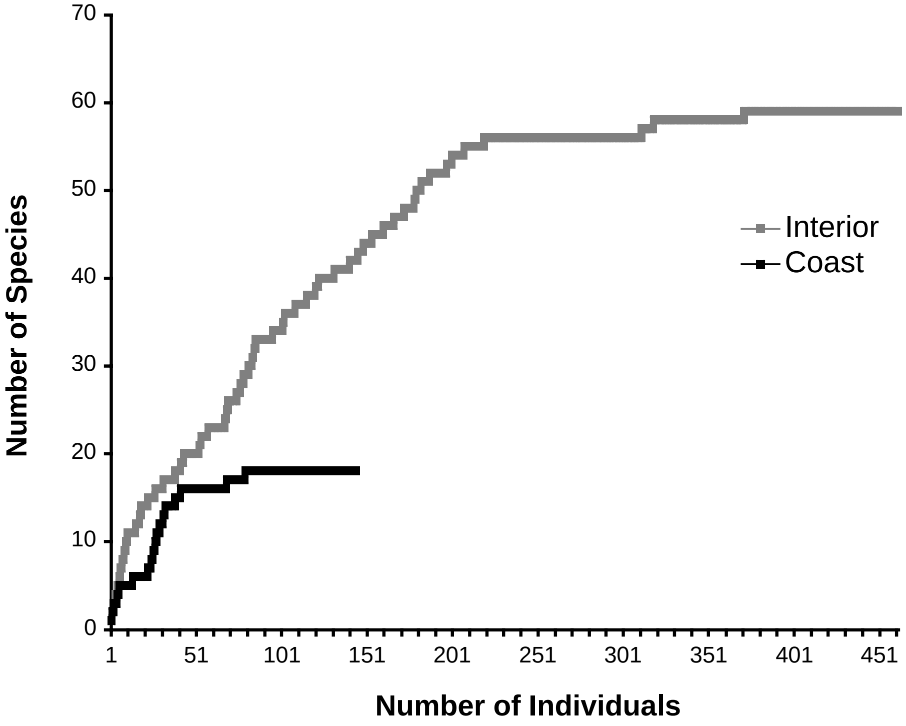


Figure 4. Distribution of tree diameter size-classes for all species, *Calycophyllum candidissimum*, *Bombacopsis quinata*, *Luehea seemannii*, *Cordia collococca*, and *Trichilia martiana* in the two sampling zones. The five size-classes are the following: (1) 2.5 cm ≤ x ≤ 5.0 cm, (2) 5.0 cm < x ≤ 10.0 cm, (3) 10.0 cm < x ≤ 20.0 cm, (4) 20.0 cm < x ≤ 30.0 cm, (5) 30.0 cm < x ≤ 50.0 cm, (6) x < 50.0 cm.

Fig 4, Chap II
Lindquist

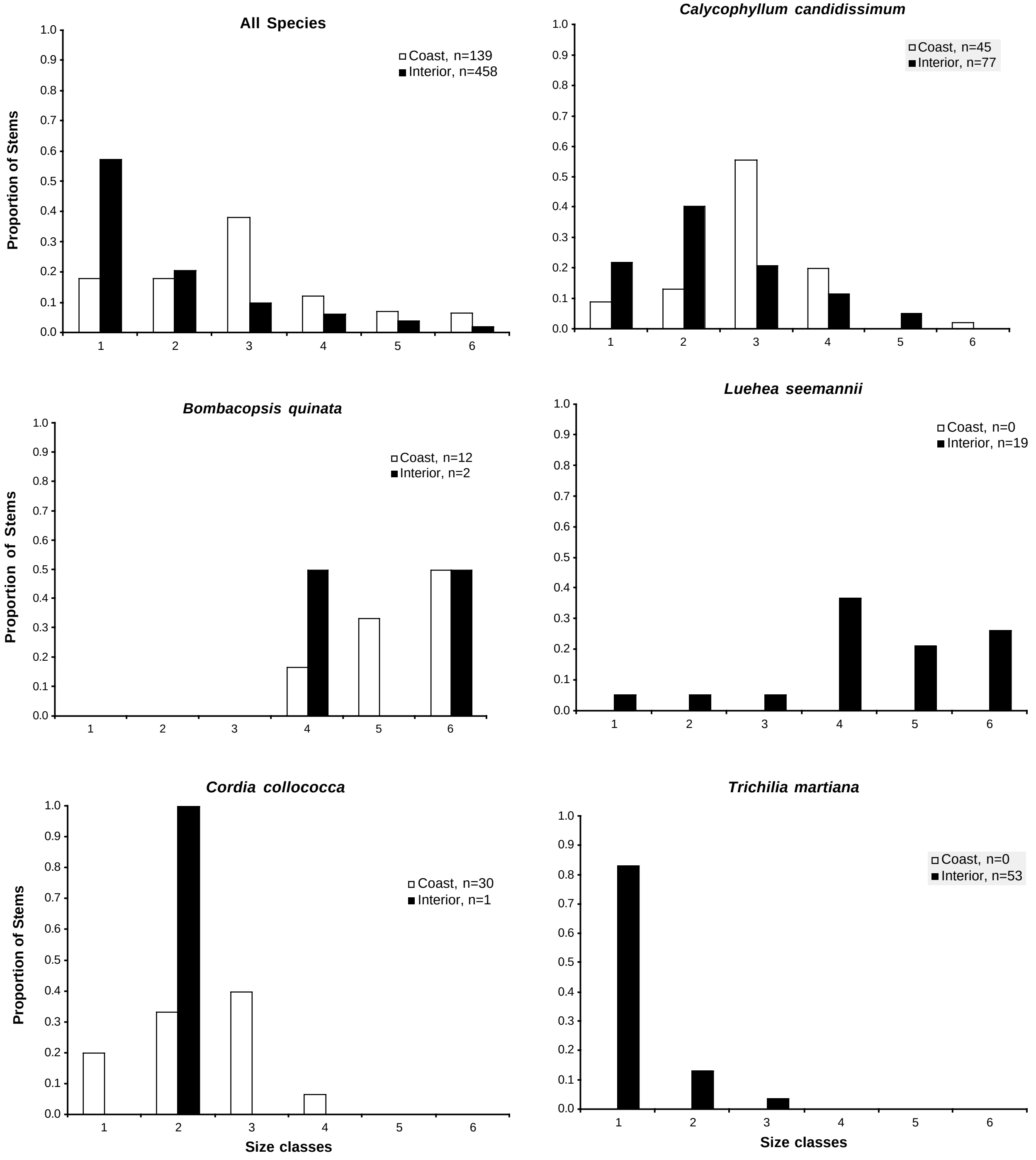


Figure 5. Altitude, slope, and aspect of the study quadrats along the permanent transects with relation to distance from shore.

Fig 5, Chap II
Lindquist

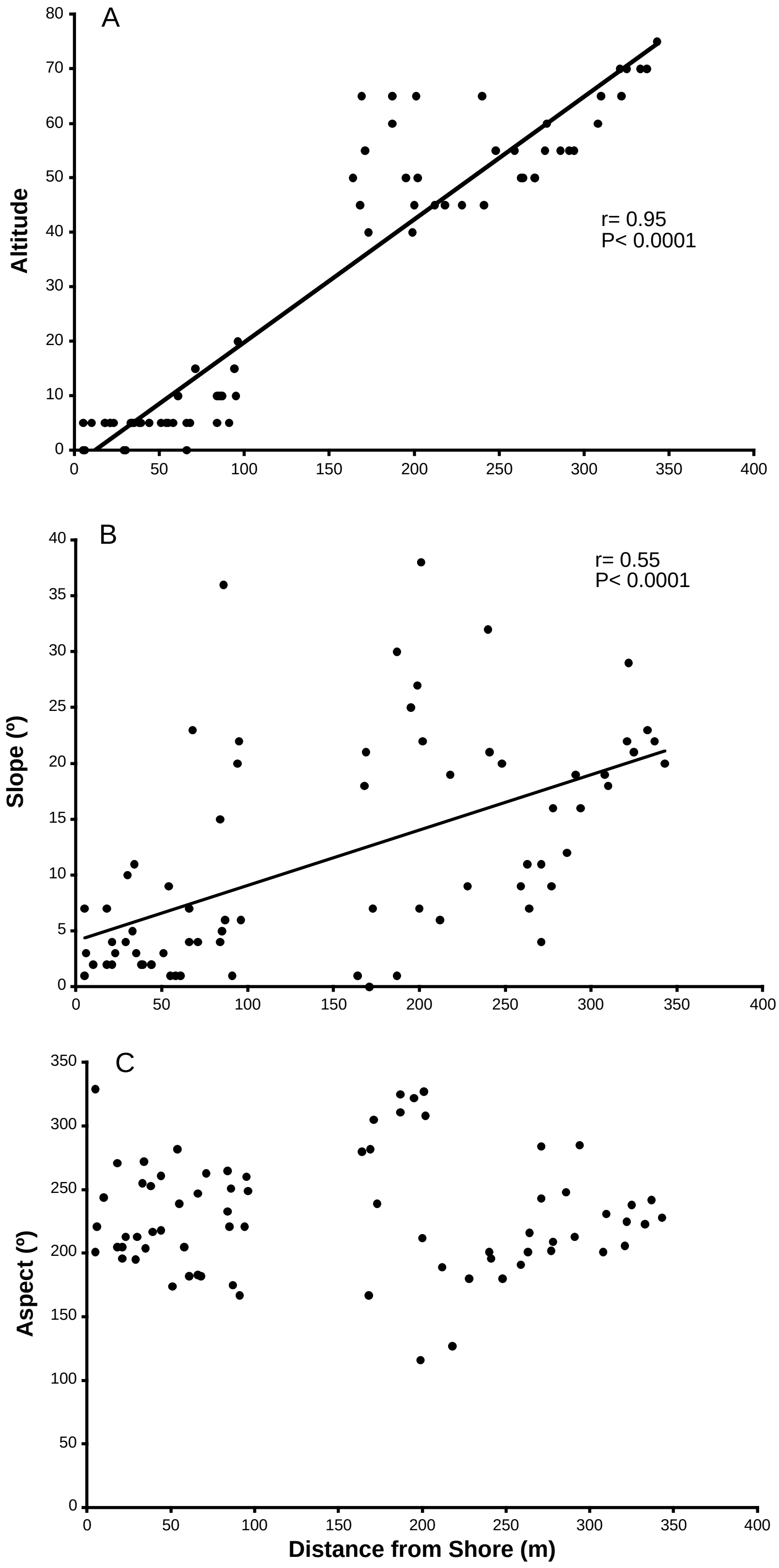
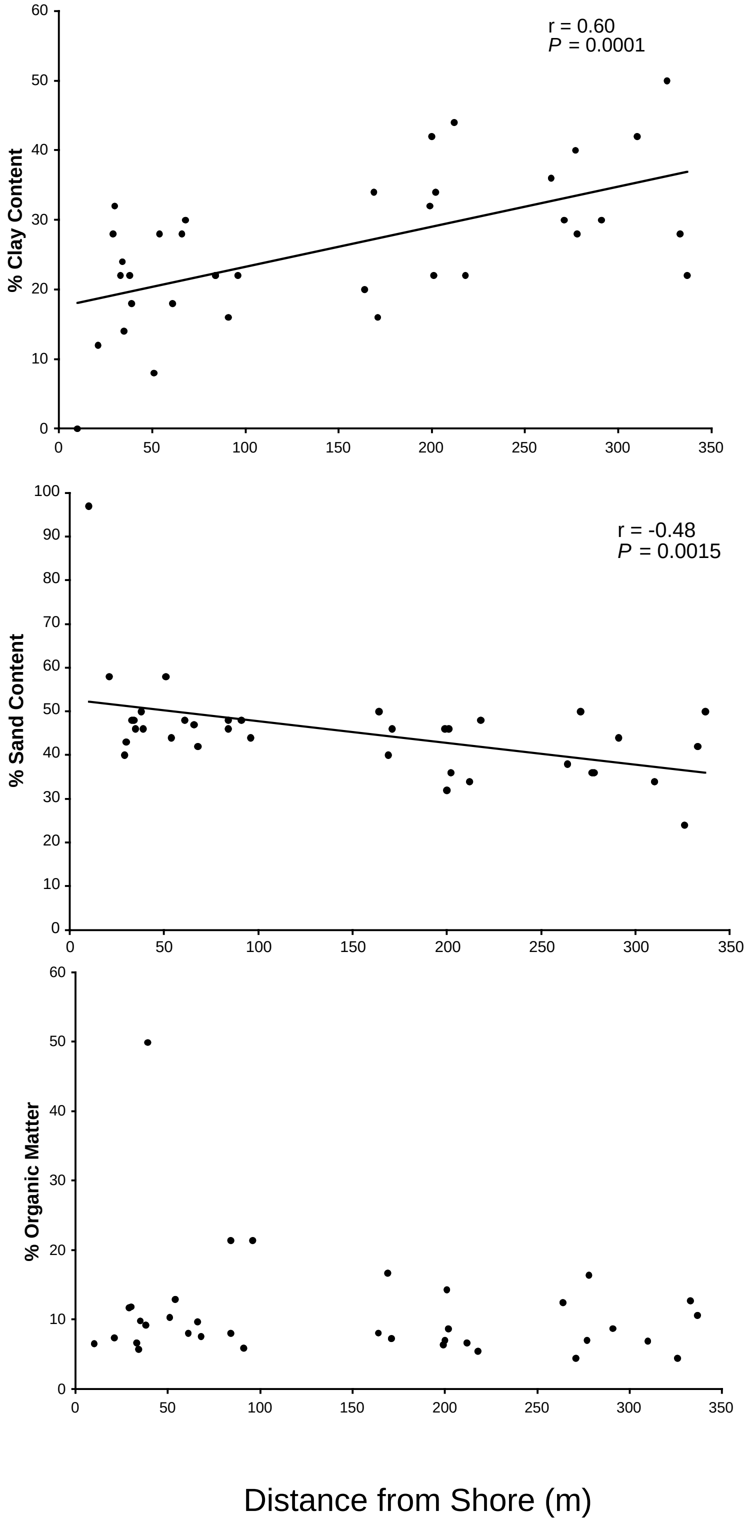
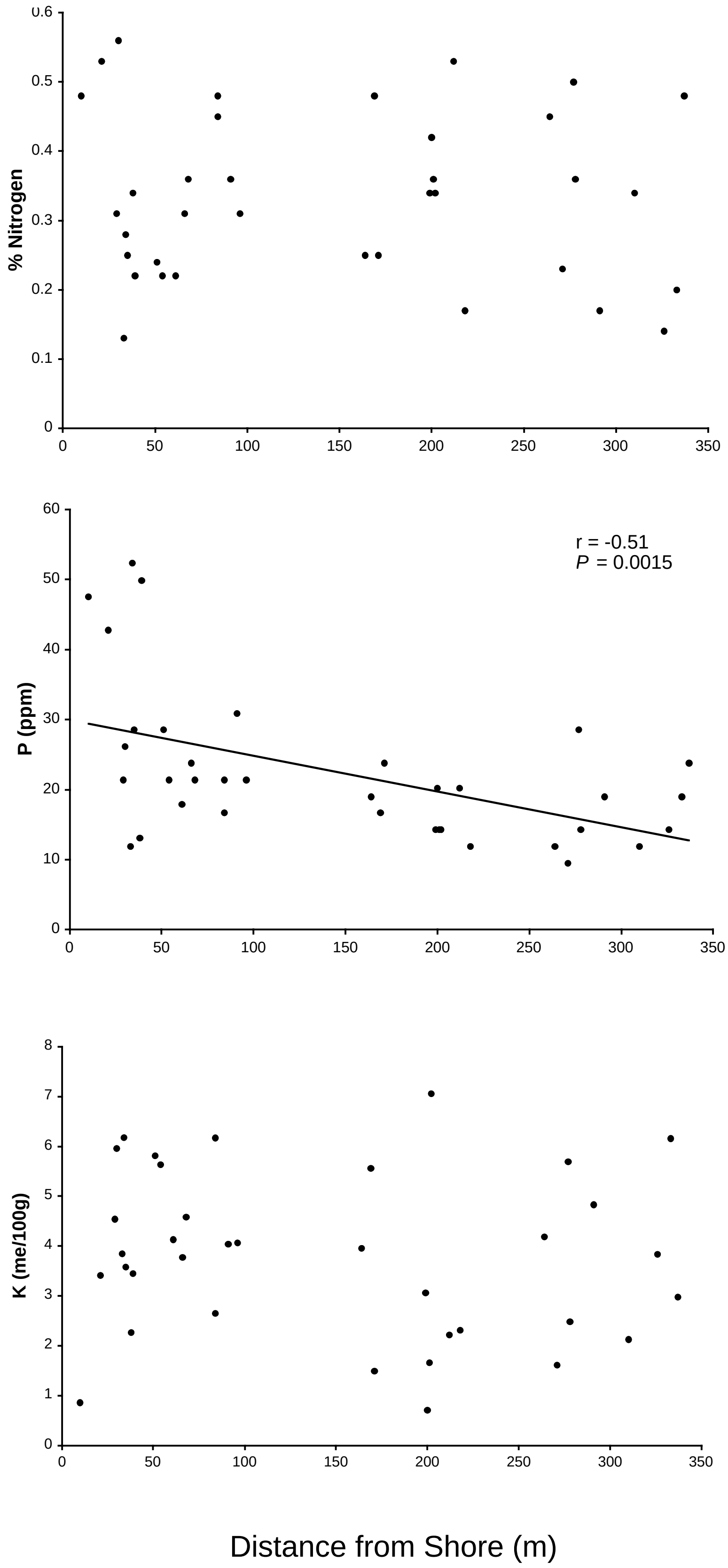


Figure 6. Correlations of (a) soil texture, (b) nutrient levels, (c) trace metals, and (d) pH and conductivity (as an index for soil salinity) with distance from shore. Note that the response variables and axes scales change in each graph, but x axis is constant. Trend lines, Pearson's correlation coefficients, and respective *P*-values are shown for those significant correlations

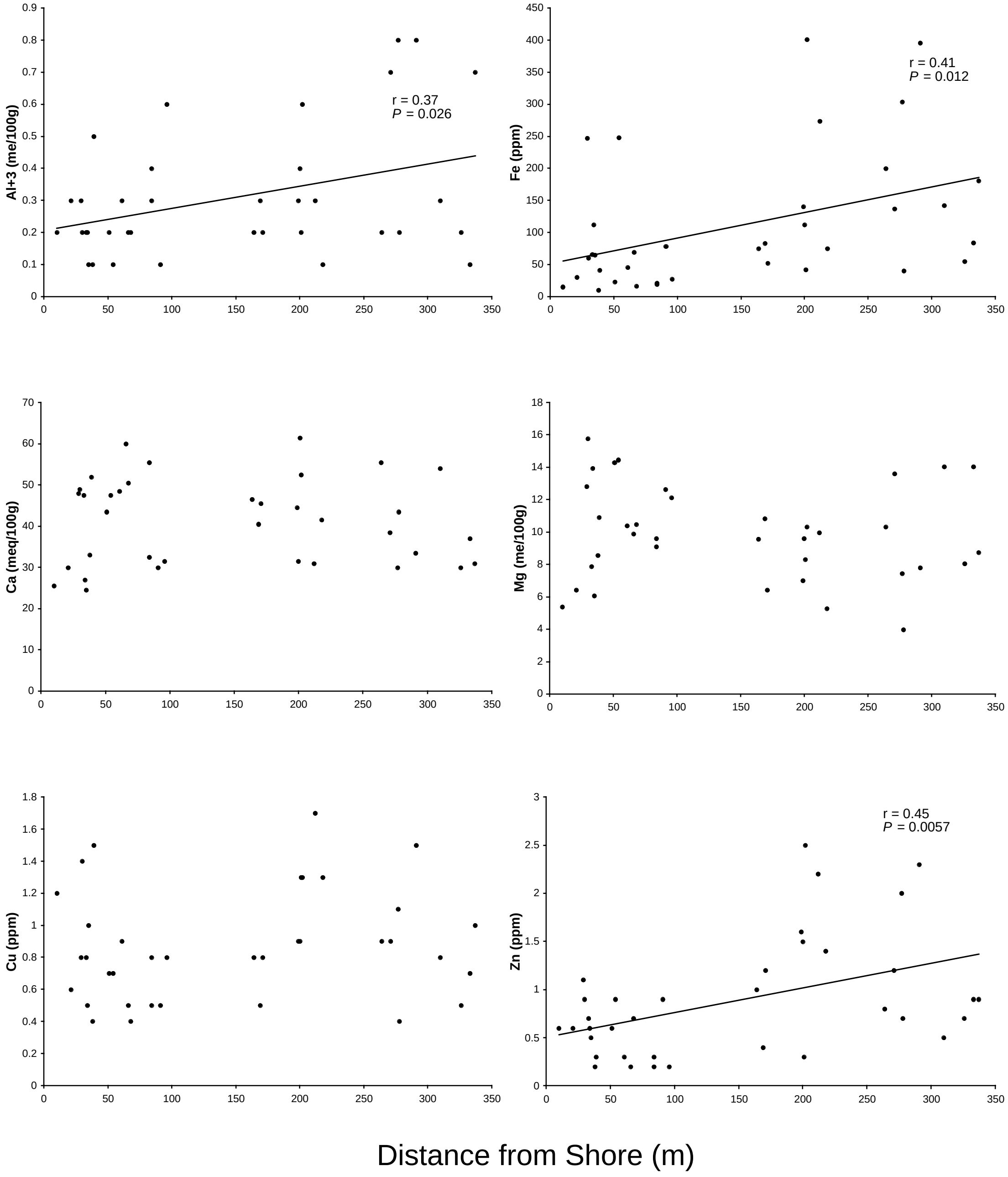
(a)


% Clay Content
r = 0.60
P = 0.0001
0
10
20
30
40
50
60
% Sand Content
r = -0.48
P = 0.0015
0
10
20
30
40
50
60
70
80
90
100
% Organic Matter
0
10
20
30
40
50
60
0
50
100
150
200
250
300
350
Distance from Shore (m)

(b)


% Nitrogen
0.6
0.5
0.4
0.3
0.2
0.1
0
0
50
100
150
200
250
300
350
P (ppm)
60
50
40
30
20
10
0
r = -0.51
P = 0.0015
0
50
100
150
200
250
300
350
K (me/100g)
8
7
6
5
4
3
2
1
0
0
50
100
150
200
250
300
350
Distance from Shore (m)

(c)


Al+3 (me/100g)
r = 0.37
P = 0.026
Fe (ppm)
r = 0.41
P = 0.012
Ca (meq/100g)
Mg (me/100g)
Cu (ppm)
Zn (ppm)
r = 0.45
P = 0.0057
0
50
100
150
200
250
300
350
Distance from Shore (m)

(d)

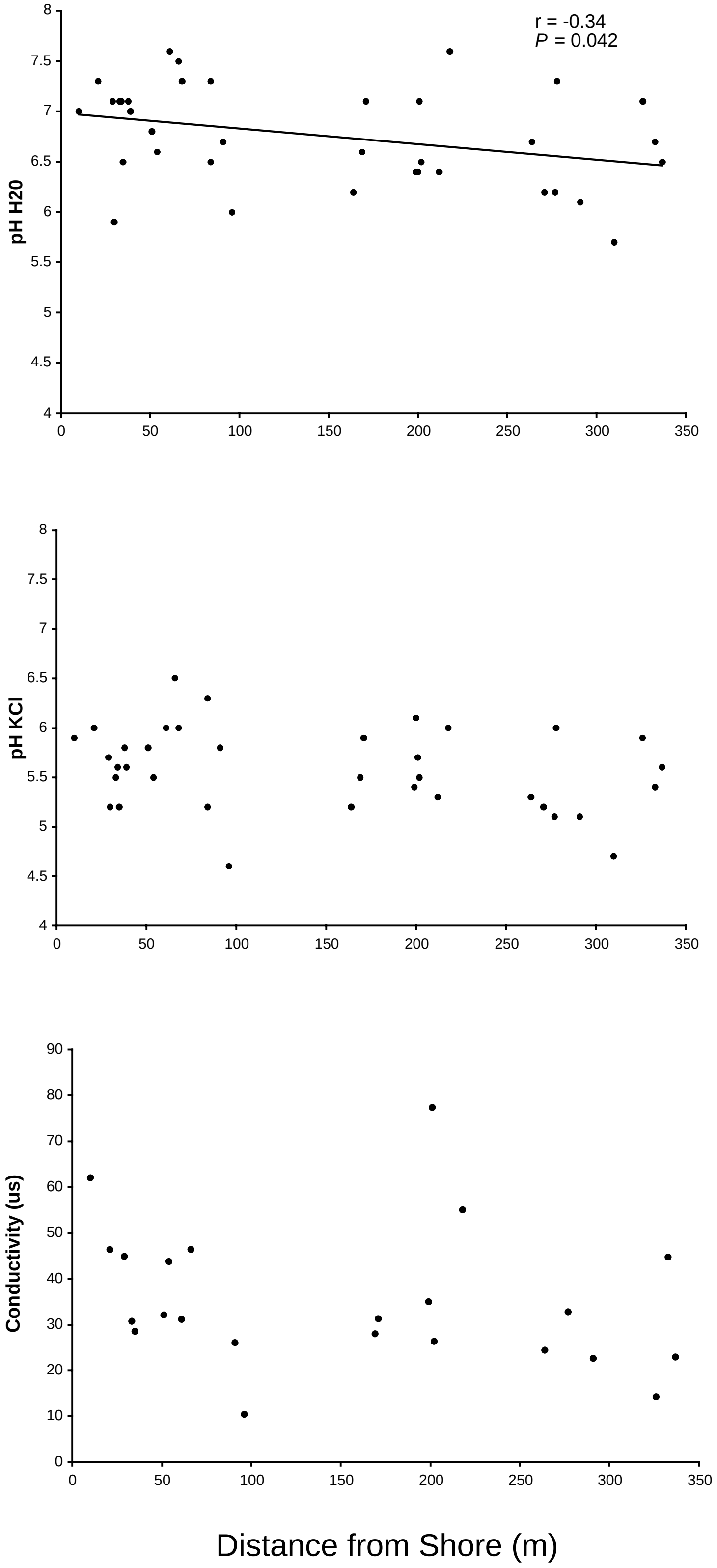

r = -0.34
P = 0.042
pH H20
8
7.5
7
6.5
6
5.5
5
4.5
4
0
50
100
150
200
250
300
350
pH KCl
Conductivity (us)
90
80
70
60
50
40
30
20
10
0
Distance from Shore (m)

Figure 7. Salt spray deposition, measured as conductivity (μs), in the coastal forest at 0, 10, 20, and 50 m intervals away from the shore. Samples were taken at 2 height intervals at each horizontal transect location: (1) 0.4 m above the ground and (2) 1.4 m above the ground. The control was an untreated filter-paper in distilled water.

Fig. 7, Chap II
Lindquist

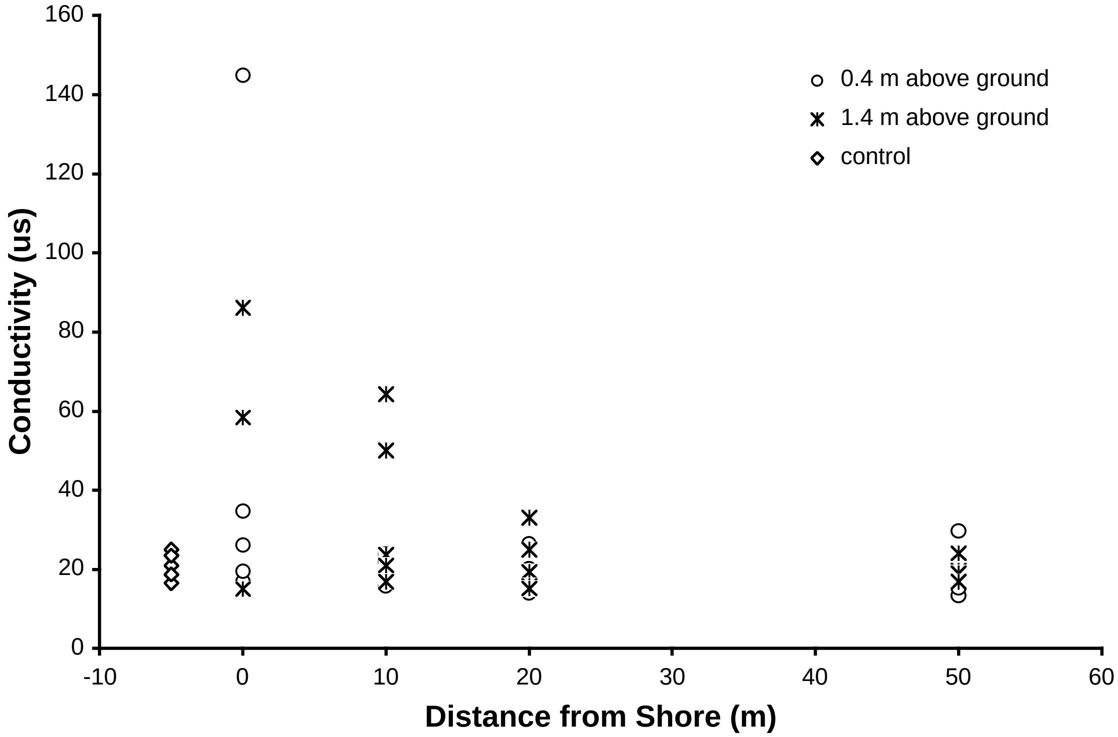


Figure 8. Correlations of canopy cover and land crab (*Gecarcinus quadratus*) hole densities with distance from shore.

Fig. 8, Chap II
Lindquist

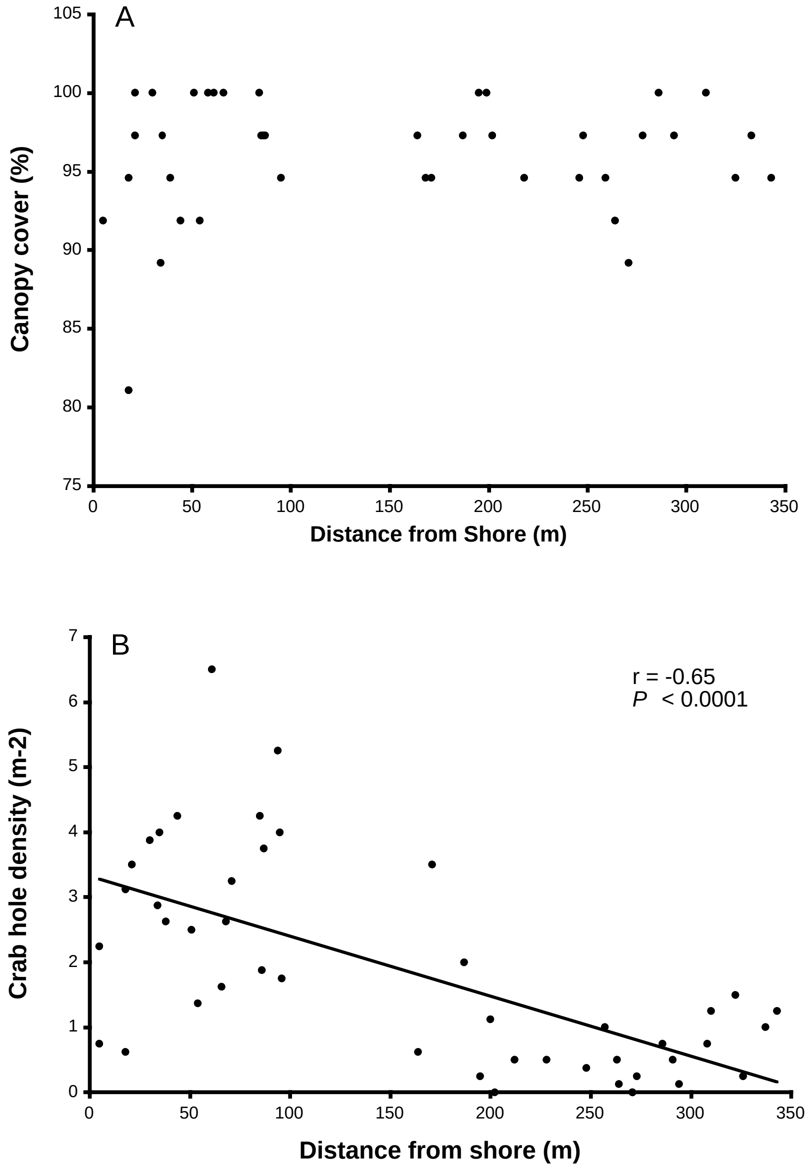
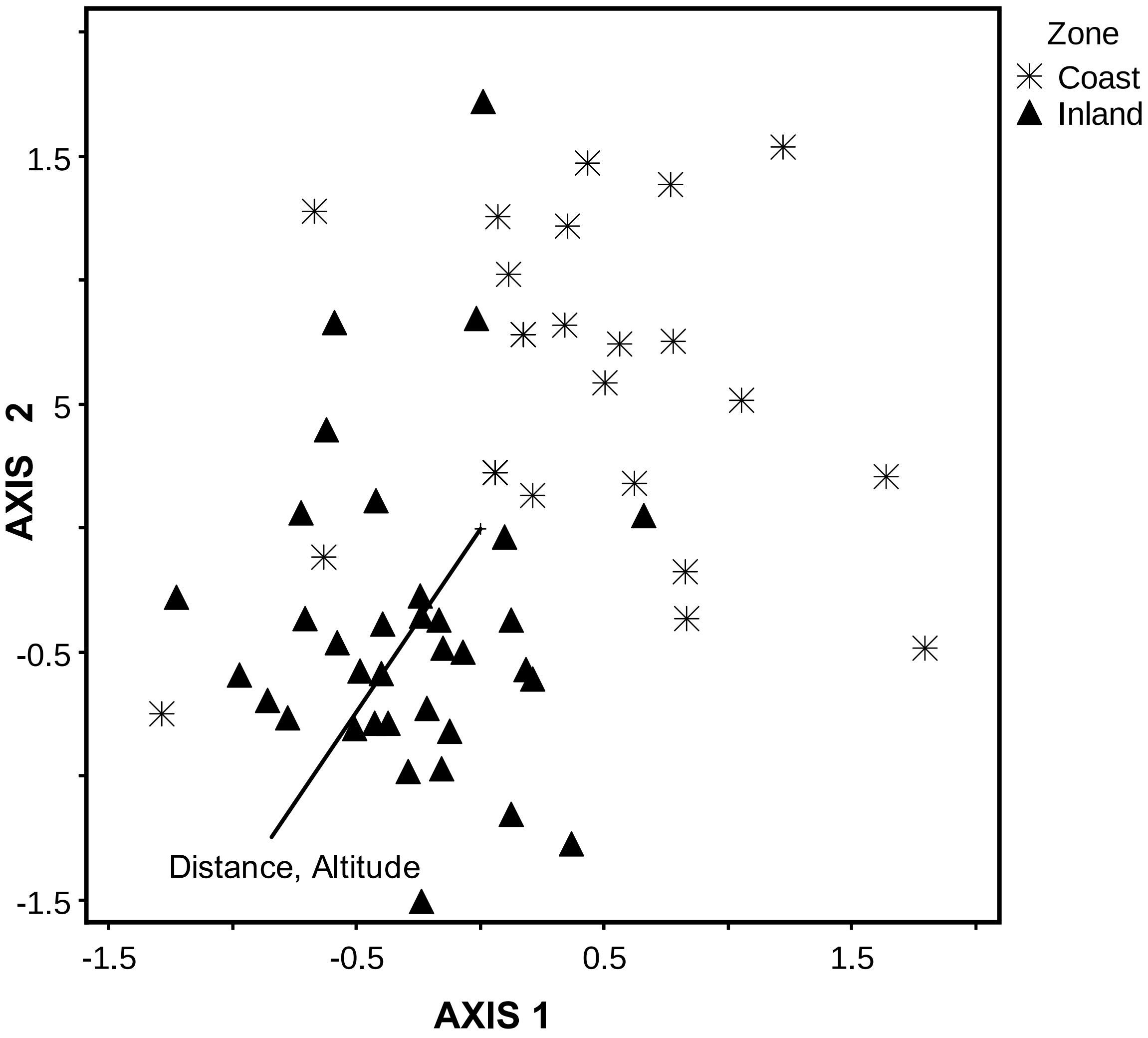
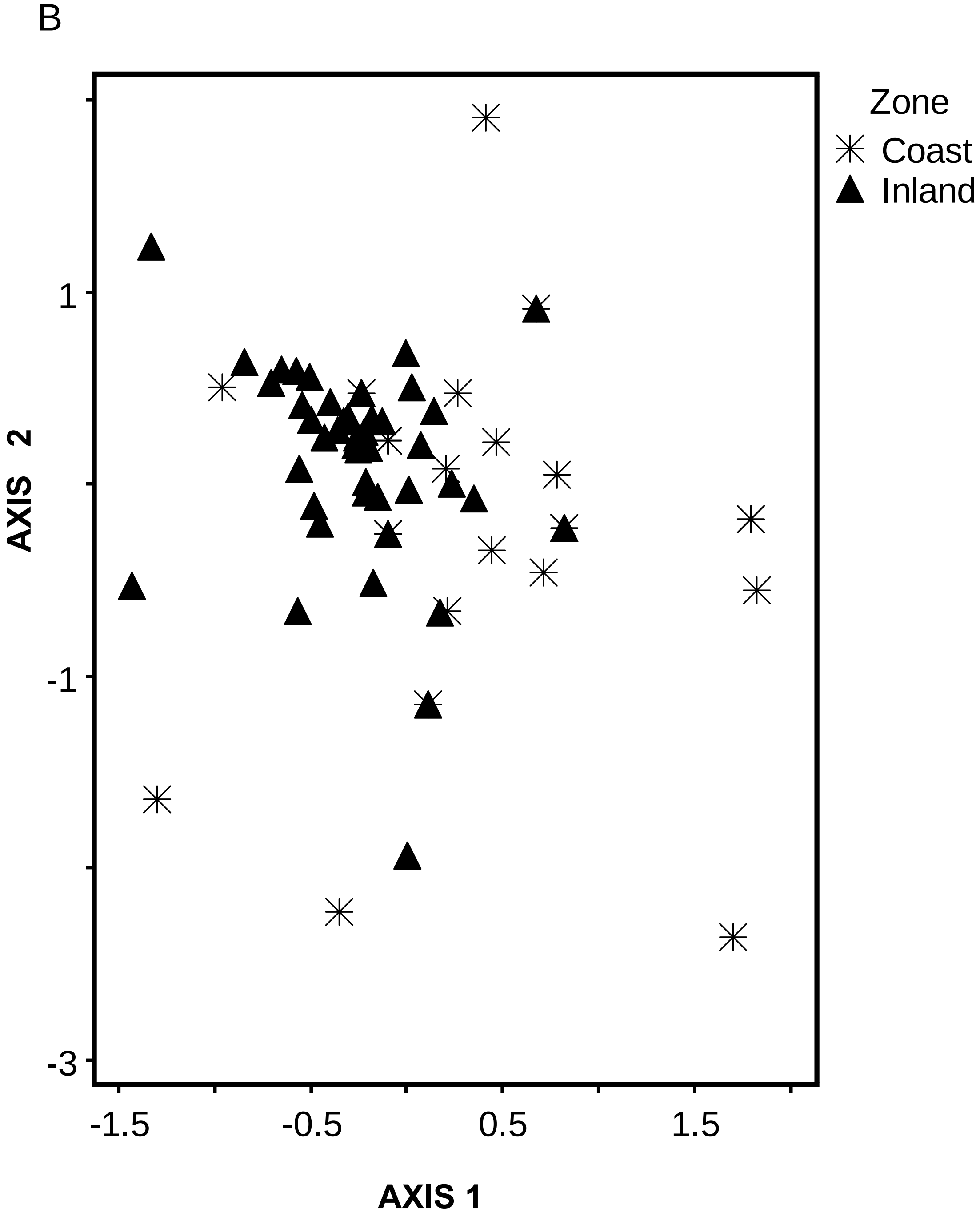


Figure 9. NMS ordination of (a) 62 adult tree plots and (b) 76 juvenile plots in species space. Plots are grouped into coastal (asterisks) and inland (triangles) categories. A joint plot of those environmental variables that explain at least 20% of the variation is overlayed on both graphs, with the vectors indicating the direction and strength of the their correlations with the axis scores. Only the distance/altitude variable made the joint plot cutoff in the adult plot ordination.

Fig 9, Chap II
Lindquist

A




B
Zone
✳ Coast
▲ Inland
1
-1
-3
-1.5
-0.5
0.5
1.5
AXIS 1
AXIS 2

SPATIAL AND SEASONAL VARIATION IN SEED RAIN COMPOSITION IN A COASTAL FOREST, COSTA RICA[1]

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[1] Lindquist, E.S., and D. Lieberman. To be submitted to Biotropica

Abstract

Dispersal limitation may promote high tree species diversity in old-growth tropical forests, and hinder recruitment in successional forests, yet support is insufficient for both hypotheses. We investigated the seed rain composition over space and time in a seasonal secondary forest on the Pacific coast of Costa Rica. Fifty seed traps were located along an environmental gradient away from the shore and examined every four weeks over a two-year period. We collected 65 species of woody plants over the duration of the investigation consisting of 28 tree species, 7 lianas, and 30 unidentified morpho-species. Tree phenological patterns were seasonal with the majority of species flowering, fruiting, and dropping their leaves in the dry season (December to May). Through a series of NMS ordination analyses, we observed variation in seed rain in both space and time. Seed rain composition changed with distance from shore. Yet we found evidence of long-distance dispersal events of greater than 50 m from the inland zone to the coastal zone. Most species' seed rain distributions were patchy (only 3 tree species were found in greater than 50% of the traps). Seed rain was very seasonal with higher densities and numbers of species falling in the dry season and early wet season (December to June) each of the two years. In summary, seed rain composition reflected the zonation of tree composition in the coastal forest, with some species' seed rain distributions extending beyond their adult distributions. Our results suggest that tree recruitment in a seasonal coastal forest undergoing regeneration is not dispersal limited, but possibly establishment limited.

Key words: dry tropical forest, dispersal, NMS ordination, seasonality, seed rain composition, spatial pattern, tree recruitment

Introduction

Currently, there is much debate over the factors that limit tropical tree recruitment. Hubbell et al. (1999) suggested that many tropical tree species experience dispersal limitation, or the failure of seeds to arrive at all suitable germination microsites. Dispersal limitation is one of several proposed mechanisms for maintaining species-rich forest communities (Hurtt and Pacala 1995).

Seed rain distribution is known to be spatially variable relative to light gaps (Augspurger and Franson 1988, Denslow and Gomez Diaz 1990, Loiselle et. al. 1996, Armesto et al. 2001), but its variability throughout a forested landscape, irrespective of forest gaps, largely remains a hypothesis. Because of the high diversity and spatial distribution of tree species in tropical forests, large spatial variation in the distribution of propagules in tropical forests is expected (Hurtt and Pacala 1995, Tilman 1999). However, only a few studies have shown spatial heterogeneity of seed rain in intact tropical forests (Loiselle et al. 1996, Grombone-Guaratini and Ribeiro 2002). The paucity of seed rain research is blamed on the difficulties in collecting, measuring, and analyzing seed rain, yet recent seed rain studies have proven to be very fruitful (Martínez-Ramos and Soto-Castro 1993, Grombone-Guaratini and Ribeiro 2002).

In addition to maintaining diversity, minimal seed dispersal is suggested to be a limiting factor in forest regeneration, or the recruitment of outside species into fragmented habitat. But again, there is a lack of data to test this hypothesis; only the early stages of regeneration have been investigated (Nepstad et al. 1996, Holl 1999, Wijdeven and Kuzee 2000, Holl 2002). Seed rain is known to be heterogeneous in regenerating pastures because of the patchy distribution of shrubs and trees, and subsequently animal seed dispersers (Holl 2002). Once forest regeneration exceeds these early stages where tree recruitment is restricted to patches, it is not well understood how seed rain is distributed through a forest matrix.

Besides spatial variation in seed rain composition, there are seasonal patterns of fruiting within and between years that cause temporal variation in propagule recruitment (Foster 1985, Frankie et al. 1974, Morellato 1995, White 1994, Young et al. 1987). Few studies have investigated the interannual and seasonal variation in the composition and distribution of seed rain in tropical dry or seasonal forest communities (but see Grombone-Guaratini and Ribeiro 2002).

Coastal forests provide a unique opportunity to study how seed rain spatial composition relates to the spatial zonation of the tree species with respect to the coastal gradient (Louda 1989). In a coastal terrestrial forest in Costa Rica, forest species composition, forest structure, and juvenile densities changed with distance from shore (Lindquist and Lieberman 2003). If the seed rain composition varies along the coastal gradient, then it may be an important factor influencing the change in forest composition and structure (Louda 1989). Yet no seed dispersal studies, outside mangrove forests (Delgado et al. 2001), have investigated the role of spatially variable seed dispersal in structuring plant communities along coastal gradients.

In order to investigate the recruitment role of seed dispersal in the coastal forest, we investigated the seed rain composition over space (relative to coastline) and time (over two years). Fifty seed traps were located at different distances from shore on the vegetation transects used in Lindquist and Lieberman (2003). All seeds of woody species were collected, identified, and described every four weeks over a two-year period. Tree phenological observations were also recorded over the same period. In order to assist seed identification and assess seed viability, we sowed the collected seeds and assessed rates of germination. Based on the previously described forest composition and species distributions, we predicted shifts in seed rain composition relative to local tree community composition and distance from coastline. Besides spatial heterogeneity, we predicted temporal variation in the seed rain because of the high seasonality of rainfall in a dry-humid tropical forest. This study is the first study to assess the spatial and temporal variation of seed rain composition in a seasonal coastal tropical forest.

Study Site

We conducted the study in the coastal terrestrial forest surrounding the Estación Biológica San Miguel (EBSM) of the Cabo Blanco Absolute Nature Reserve, Costa Rica (9˚ 35’ N and 85˚ 08.5’ W). A full study site description can be found in Lindquist and Lieberman (2003). The forest is classified as a transitional dry to wet tropical forest. Annual precipitation ranges from 2500 to 3200 mm year^{-1} (mean of 3000 mm year^{1}), with almost all the annual rain (95 to 100%) falling during the wet season (May to November; Lindquist and Lieberman, 2003). Average annual temperature is 27˚C, with average low and high temperatures of 24˚C and 32˚C respectively. Eighty-five percent of the 1250 protected hectares is 36-year-old secondary forest that has naturally regenerated from cattle pasture and small subsistence farms that grew primarily corn, beans, and other vegetables (Lindquist and Lieberman 2003). The remaining 15 percent consists of primary forest found in the upland slopes of the reserve.

Our study area, contained entirely within the secondary forest, is situated along a 1 km stretch of coastline and extends 350 meters away from the coastline (Lindquist and Lieberman 2003). For sampling methodology, the study area was divided into two sub-study areas, or forest zones: (1) the "coastal" zone is contained within the first 100 meters (100 m X 1000 m, or 10,000 m^{2} = 10 ha) of the coastline, and (2) the "inland" zone extends inward after the rock shelf; approximately 150-350m from the coastline (200 m X 500 m, or 10,000m^{2} = 10 ha). Nine permanent 100 m-long belt-transects running perpendicular to the shoreline were established in February 2000 in each forest zone (Lindquist and Lieberman 2003).

Methods

Phenology

From 2000 to 2002 we took note of the timing and duration of flowering, fruiting, and canopy abscission events of tree species in the study area. In particular, the monthly phenology of a group of tagged trees (n= 56, S= 21) along the coastal trail of EBSM was noted.

Seed rain

We placed one seed trap randomly within each 20 m of 10 belt-transects (5 in each forest zone) for a total of 50 traps (25 in each zone). The circular PVC-constructed seed traps had a collecting surface area of 0.28 m^2 (D= 0.6m) made of window-screen (square holes= 4 mm^2), and were 0.4 m above the ground. When necessary, we replaced the window-screen at collection periods.

Every four weeks for two years (from 19, 20 August 2000 to 14, 15 July 2002) we collected all seeds from each of the 50 traps (Table 1). Each collection typically lasted two days. Note that one data collection (27, 28 April 2002) was lost due to theft. We sorted through all material collected in the traps in the field: disposing of all leaf litter and other non-seed items, while collecting all intact fruits and seeds. We also collected pieces of seed-pods or other pieces of fruits to note their presence in the traps at that collecting period. In the laboratory, we sorted through the seeds trap by trap and identified the seeds to species using field guide descriptions and herbarium voucher specimens (Gentry 1993, Holdridge et al. 1997, Quesada et al. 1997, Poveda and Sánchez-Vindas 1999, Zamora et al. 2000), or morpho-species if the species was not known. Morpho-species were described, and vouchers made for future collection times. Seed vouchers were deposited in the Herbarium of EBSM.

In January and February 2001, we tested if there was significant seed loss (from wind and animal removal agents) from the traps within the four-week interval between checks. We placed 5 marked seeds of two species in 24 randomly-selected traps (of 50, 12 in each zone), *Enterolobium cyclocarpum* (animal-dispersed) and *Terminalia oblonga* (wind-dispersed), and checked their presence during weekly censuses. After 4 weeks, all *E. cyclocarpum* seeds remained, whereas a significant number of *T. oblonga* seeds were removed (9.2% removed) from the traps compared to the *E. cyclocarpum* seeds (0% removed; paired *t*-test, $t_{1,24} = -1.97$, $P = 0.031$). Some loss of wind-dispersed seeds was expected, therefore, during the four-week collecting intervals.

Seed germination

To determine percent germination, and assist in identification of collected seeds and seedlings, seeds were transported to shade-houses at Universidad Nacional Autonoma (UNA) in Heredia, San Jose within one week of collection. We sowed the seeds in alluvial sand to a depth approximately equal to the longest width of the seed. Species were separated in the germination beds by barriers. The seeds were watered by hand once or twice a week. We noted germination of seeds once a week. If seeds did not germinate in 6 months, they were removed and considered not germinated. The last germination check was October 4 2002 before the shade-house flats were cleaned out unexpectedly.

Unknown species were identified from germinated seedlings in the shade-house flats. Seedling vouchers were taken and placed in the EBSM Herbarium. Digital photographs were also taken of germinated seedlings to be used as vouchers for future seedling studies at EBSM.

Data Analyses

Seed rain composition was ordinated with nonmetric multidimensional scaling (NMS) analyses using PC-ORD software on the matrices of plots (traps) by species (S= 65) (Kruskal 1964, Mather 1976, McCune and Mefford 1999, McCune and Grace 2002). Four ordinations were conducted: (1) total seeds fallen into each trap (n = 50) over the entire study to compare seed rain distribution among coastal and inland traps; (2) total seeds fallen into each trap within each year (t = 13 for each year) to assess interannual variation; (3, 4) total seeds fallen into each trap within the wet ($t = 9$) and dry seasons ($t = 4$) for first year (3) and second year (4) to compare within-year seasonal variation.

The advantage of NMS over other ordination techniques is that it is based on ranked distances, and does not assume linear relationships among variables (McCune and Grace 2002). The ranked distances linearize the relationship between ordination distances measured in species and environmental space. Before the analyses, Beals smoothing was used to transform the heterogeneous compositional data for the adult and juvenile plots because of the high frequency of zeros (McCune and Grace 2002). Plots with no individuals of any species (all 0 frequencies), and outliers that were at least 2.3 standard deviations from the average distances between plots, were excluded from the analyses after preliminary runs with the entire data set (McCune and Grace 2002).

For the four analyses, we used the Sorenson distance measure recommended by McCune and Grace (2002) for NMS analysis of community data. We started each analysis with a random configuration, and conducted 15 runs with the real data, and 30 runs with the computer-generated random data. The number of dimensions was selected by PC-ORD; it found the best solution for each dimensionality (lowest stress or the inverse measure of fit to the data), and added additional dimensions only if they reduced the final stress 95% of the time or more ($p \leq 0.05$ for the Monte Carlo test). Forest zones, collection year, or season were used to group the plots (traps) for their respective NMS ordination.

Results

Phenology

Of 97 woody plant species known to be present in the forest around EBSM, 29 species were observed to have flowers at least once throughout the 3-year study, in addition to 50 species that had fruit, and 18 species that abscised their canopy for at least one individual (Table 2). Of those observed, the majority of these species flowered, bore fruit, and dropped their leaves in the dry season (December to May), when rainfall was minimal (Figure 1). The few species that flowered outside the dry season were *Attalea butyracea, Calycophyllum candidissimum, Cedrela fissilis, Piper tuberculatum, Plumeria rubra*, and *Simarouba glauca* (Table 2). Species that fruited outside the dry season were *A. butyracea, Bactris major, Bauhinia ?manca, Cedrela odorata, Crescentia cujete, Diospyros digyna, Miconia argentea, Piper tuberculatum, Sapium glandulosum, Spondias mombin, Tabebuia rosea,* and *Terminalia catappa* (Table 2).

Seed rain

Seeds of 65 species of woody plants were collected from the 50 traps over the two years of collections (26 collections total, Table 3). Thirty of the 65 species were not identified to family, genus, or species due to low seed numbers, minimal germination rates, or loss of seeds (bus theft). Of those woody species identified to at least genus, 28 were trees and 7 were lianas.

Luehea seemannii (Tiliaceae), a wind-dispersed canopy tree species, was the most abundant and common seed, with a mean density of 1030 seeds m^{-2} ± 2100 and a relative frequency of 60% (Table 3). *Calycophyllum candidissimum* (Rubiaceae), another wind-dispersed canopy species, was the second most abundant species (140 seeds m^{-2} ± 250) and was very common (frequented 70% of traps). The most abundant and common animal-dispersed tree species were *Inga vera* (Fabaceae, 30 seeds m^{-2} ± 130, 22%), *Brosimum alicastrum* (Moraceae, 3.9 seeds m^{-2} ± 7.1, 38%), and *Diospyros digyna* (Ebenaceae, 1.0 seeds m^{-2} ± 2.2, 22%; Table 3). Animal-dispersed species had much lower frequencies, with a range of 2% (one trap) to 38%. Two species of wind-dispersed liana had high seed densities and trap frequencies: *Serjania mexicana* (Sapindaceae, 59 seeds m^{-2} ± 300, 62%) and *Combretum cacoucia* (Combretaceae, 27 seeds m^{-2} ± 90, 46%; Table 3). One unknown morpho-species, UNKMMM, was abundant (110 seeds m^{-2} ± 240) and common (76%; Table 3).

The abundance and distribution (trap frequency) of the seed rain was spatially variable. We found high coefficients of variations for species' densities (Table 3), and a low mean number of species per trap (0.86 species ± 0.84; Figure 2). Furthermore, twenty-four species (37% of all species collected) had very localized dispersal; they were found in only 1 of the 50 traps over the two-year study. Species' seed rain distributions also varied with respect to distance from the shore; 23 species were found only in the inland zone, whereas 16 species arrived at traps in the coastal zone only.

In addition to varying in space, seed rain frequency, abundance, and richness varied with the seasons. Twenty-five species (2 tree species, 1 liana species, and 22 unknowns) only were found at 1 collection date over the two years (Table 3). The seed rain was more species rich in the dry season than in the wet season (Figure 2a), as well as more abundant (Figure 3). Mean number of species per collection period also increased during the dry months (Figure 2b). Inter-annually, seed rain richness (Figure 2) and density (Figure 3) were higher in Year 1 than in Year 2 but the intra-annual patterns were similar among the two years. *L. seemannii* was the most frequently collected tree species over time (58% of collections), while *Cedrela odorata* (Meliaceae, 50%) and *Lonchocarpus minimiflorus* (Fabaceae, 42%) were also common through time. *Bauhinia ?manca* (Fabaceae, 54%) was the most frequent liana species in time.

Ordinations: Seed rain composition

For Ordination 1, Axis 1 and 2 explained 41% and 54% respectively, for a total R^2= 94.4%, and stress was minimized at 10.5. The Axis 2 scores for the coastal and inland traps differed ($t_{1,46}$ = -4.4, P < .0001; Figure 4a). Two coastal traps on 1 transect differed more than two standard deviations from the mean axes scores and were excluded from the analysis. Much of the variation in axes scores was due to several species that only dispersed seeds in the coastal zone– *Tabebuia rosea, Terminalia catappa, Plumeria rubra, Sterculia apetala, Trichilia americana, Bombacopsis quinata*– which are all found in the lower half of Figure 4b.

When the interannual composition of seed rain in space was analyzed, 85% of the total variation among traps in species space was explained by the two axes (Axis 1 =

44%, Axis 2 = 41%) in Ordination 2. Five coastal traps were excluded from the analysis because they were significant outliers (> 2 SD), 1 of which had 0 propagules during Year 2. Axis 1 scores for individual traps from the first year to the following did not effectively change from their original positions in species space ($t_{1,44}$ = -0.082, P = .53; Figure 5). The few coastal zone traps that varied from all other traps in Ordination 1, showed the same patterns in each of the individual years. Although the overall seed rain composition did not vary significantly between the two eyars, we collected several species in only one year. Seeds from *Copaifera aromatica*, *Tabebuia rosea*, and *Trichilia martiana*, and 22 unknowns were only collected in Year 1. Whereas seeds from *Attalea butyracea*, Bignoniaceae sp., *Ficus* sp., Moraceae sp., *Spondias mombin*, *Posoqueria latifolia*, and 4 unknowns were only found in Year 2.

Ordinations 3 and 4 showed that seed rain composition among the traps did vary considerably between the wet and dry seasons (Figure 6a,b). In both years, the species composition of traps within a season had similar ordination scores, but the composition changed from one season to the next. In Ordination 3 (Year 1), Axis 1 and 2 represented 59% and 28% of the variation. Ordination 4 (Year 2) explained 81% (Axis 1= 43%, Axis 2 = 39%) of the species composition variation among the traps. In Year 1, five traps (all coastal) did not receive any propagules in the wet season, but all traps in the dry season received seeds. In Year 2, eight traps (7 coastal, 1 inland) received nothing during the wet season, and 6 traps (4 coastal, 2 inland) were empty throughout the dry season.

Germination

We observed low germination rates in the shade-house (Table 3). Mean germination for all species combined was 18% ± 29. Of the 56 species sown, only 30 species (21 tree, 6 vine, and 3 unknown) had at least 1 seed germinate. Many of the unknown species did not have seeds germinate (87%, 20 of 23 sown species) and consequently were not identified. The species with highest germination rates, excluding those that only had 1 seed germinate, were *Trichilia americana* (Meliaceae, 73%) and *Bombacopsis quinata* (Bombacaceae, 67%; Table 3).

Discussion

Differential seed dispersal may be a major factor structuring plant communities along gradients (Louda 1989), and may limit recruitment in many tropical forests (Hubbell et al. 1999). Our study, as the first to investigate seed rain patterns in a coastal tropical forest, did find that seed rain composition changed along the coastal gradient and was spatially variable (Figure 4). Much of this variation in the seed rain reflects the changes in the composition of the parental tree community with respect to distance from shore (Lindquist and Lieberman 2003). For example, of the species represented in the seed rain (Table 3), 3 species—*Sterculia apetala*, *Terminalia catappa*, and *Triplaris malaenodendron*—are found only in the coastal zone as adults (Lindquist and Lieberman 2003), and subsequently only dispersed seeds in the coastal zone.

The majority of species dispersed seeds in less than half of the traps. Only 3 species of trees—*Calycophyllum candidissimum* (Rubiaceae), *Cedrela odorata* (Meliaceae), and *Luehea seemannii* (Tiliaceae)—dispersed seeds to more than 50% of the traps (Table 3). Similarly, over a ten-year study on BCI, only 7 species (of 314 total species) dispersed seeds to more than 75% of the trap sites (Hubbell et al. 1999). However beyond the reasonable explanation that the heterogeneity in our seed rain merely reflects the spatial heterogeneity of parent trees in the coastal forest, several other factors may have affected the low trap frequency and high spatial variability of seed rain. Firstly, we only collected seed rain over a two-year sampling period when many species may not produce large quantities of seed every year (Turner 2001). Yet we found no differences in the species composition of the seed rain among the two years of the study (Figure 5). Secondly, the small sample area of the traps (sum area = 14 m^2) may have minimized the probability of collecting rare species. Even though many collected species had low spatial frequencies (Table 2) and not all species present in the forest were present in the seed rain (Lindquist and Lieberman 2003), we found a diverse group of species in spatial distribution (in both adults and juveniles), growth strategy, dispersal mode, and temporal frequency represented in the seed rain. With the addition of the unidentified species and multiple years of study, we expect seed rain species richness to increase and the composition to reflect the local tree community composition.

Assuming the seed rain composition was a representation of the surrounding tree community (Lindquist and Lieberman 2003), our findings do not indicate that seed dispersal is the primary factor limiting the establishment of species along the gradient. In some species, spatial distribution of seed rain paralleled or surpassed adult distribution (Lindquist and Lieberman 2003). For example, the most abundant species in the seed rain, *L. seemannii*, was only found in 18% of all adult plots (36% of inland plots), yet was present in 60% of the traps (including some coastal traps > 50 m from any known parent trees; Table 3). Moreover, of the 47 species present only in the interior zone in the juvenile and adult stages, and of those collected in the seed rain (n = 10), 8 species dispersed propagules into the coastal zone traps (Table 4). Hence, we found evidence of long-distance dispersal (> 50 m) by both wind and animal agents (Table 4) from the inland zone to the coastal zone. Thus recruitment limitation of these species in the coastal zone seems to occur not at the dispersal stage but in the later stages of establishment.

Of the four main agents of seed dispersal—gravity, wind, water, and animals—wind here was the most common vector. Wind dispersal is known to be a more common dispersal agent in seasonally dry forests (Gentry 1982, Grombone-Guaratini and Ribeiro 2002). Although the most common adult species of EBSM that produced large amounts of seeds were wind-dispersed species (*Luehea seemannii* and *Calycophyllum candidissimum*), there were also several common animal-dispersed species (*Inga vera*, *Diospyros digyna*, and *Brosimum alicastrum*; Table 3). Dispersal mode affects seed shadow sizes; wind-dispersed seeds are known to travel shorter distances on average (less than 100 m) than animal-dispersed seeds (see Turner 2001 for a review). Some bird-, bat-, and primate-dispersed species are known to disperse seeds 300 to 500 m from the parent tree (see Turner 2001 for a review). In general, the mean dispersal distance for tropical tree species with varying dispersal modes is in the range of 20 to 200 m (Augspurger 1986). Thus dispersal along our coastal gradient of greater than 50 m is reasonable.

Besides tree species, lianas were also abundant in the seed rain, especially the wind-dispersed species *Combretum cacoucia* and *Serjania mexicana* (Table 3). Several other studies in semi-deciduous neotropical forests found an abundance of woody climbers in the seed rain, and most were wind-dispersed species (Martínez-Ramos and Soto-Castro 1993, Grombone-Guaratini and Ribeiro 2002).

Spatial and temporal patterns of forest recruitment are closely tied to the seasonal patterns of seed arrival (Young et al. 1987, Grombone-Guaratini and Ribeiro 2002). In the coastal forest, we observed seasonality in the reproduction and canopy abscission of woody species (Figure 1). The majority of species flowered, fruited, and dispersed their seeds in the dry season from January to April when there was little to no rainfall (Table 1). Furthermore, of those species that dispersed seeds in the wet season, the majority were animal-dispersed species (Table 1, 2). At least 28% of the EBSM tree species were deciduous and dropped the majority of their leaves in the dry season (Figure 1). This pattern of seasonal canopy abscission, seed production, and seed dispersal during the dry period is common among seasonally dry forest types (Frankie et al. 1974, Jackson 1981, Bullock and Solís 1990, Grombone-Guaratini and Ribeiro 2002). Wind-dispersed seeds are more effectively dispersed in the dry season when much of the canopy is open and there is minimal rain (Turner 2001). Finally, it is advantageous for the species to disperse their seeds in the dry season so that the seeds can germinate with the first rains of the year and have the longest possible growing period until the next dry season when growth is hindered.

Germination rates were low (Table 3), but because of unfavorable shadehouse conditions, we believe they are not accurate estimations of seed viability. The shadehouse was not located at the study sites, but in Heredia, San Jose at 1400 m above sea level with strong trade winds much of the year. Consequently, the germination ambient conditions were much different than those at EBSM at sea level (higher temperatures and humidity). In addition there was loss of seeds due to germination bed destruction. Finally, the alluvial soil at times was found contaminated with non-EBSM seeds and pathogens. Although germination rates are not reliable, the value of the germination experiment was in the observation and collection of germinated seedlings vouchers to aid in seed identification.

Although we were able to identify many of the species from seed or from seedling voucher, there were still 30 unidentified species at the end of the experiment (Table 3). Many of these unknown morpho-species had only a few seeds, of which some or all did not germinate. In addition, the ability to identify seeds to morpho-species of numerous student field assistants and ourselves improved in the second year, and this may explain why there are more unidentified species from the first year than the second. Also, there may be some error due to minimally trained field assistants who separated species out into morpho-species during collecting periods, particularly in the first year when there were fewer seed vouchers and assistants had less experience. Once good descriptions (with sketches and measurements) were established for each morpho-species, along with voucher specimens, then many of the original unknown morpho-species were found to duplicate species. Some of the remaining unknown species may therefore still be duplicate species of others identified.

Previous studies in tropical forests found that seed rain limited juvenile recruitment in both shade tolerant species (Martinez-Ramos and Alvarez-Buylla 1995, Hubbell 1999) and shade intolerant species (Dalling et al. 1998, Holl 1999). In the previous study (Lindquist and Lieberman 2003), we found that juvenile densities were very low throughout the EBSM forest, and especially near the coast. Assuming the seed rain is sufficiently dispersing seeds, these findings suggest that tree recruitment is more influenced by establishment limitation, or the failure of seeds to germinate and establish as seedlings, than dispersal limitation. Indeed, in a series of manipulative experiments at EBSM, we found evidence of high mortality at the seedling stage; crab predation of seeds and seedlings significantly limited seedling establishment and growth in the EBSM forest (Lindquist and Carroll 2003). In the same study, canopy cover also affected seedling survival and growth, particularly for those seedlings that escaped initial crab predation.

In summary we conclude that although seed rain varied spatially and temporally, these patterns do not suggest limited tree recruitment at the seed dispersal stage. Seed rain species richness and abundance were considerable in the coastal areas near the shore, where juvenile densities were minimal. There were large pulses of seed rain in the dry season during both years of the study as expected in a seasonally dry semideciduous forest. It appears that tree species in the coastal forest are not limited by dispersal but rather establishment.

Acknowledgements

This work was supported by the NSF Dissertation Improvement Grant (DEB-0104791), Sigma Xi, and various field and travel award grants from the University of Georgia given to E. Lindquist. We are grateful to the Costa Rica MINAE administration of San Miguel Biological Station, Cabo Blanco Absolute Nature Reserve for allowing this study to be conducted in such a restricted area, and expressing interest in the study's findings. Many field assistants and students at the Universidad Nacional Autonoma (UNA), Heredia made this study possible: Minor Cedeño (UNA), Fabricio C. Céspedes (UNA), José Castro (UNA), Mónica Castro (UNA), Kerry Brewster (UGA), Chrissie Case (UGA), Stephanie Conrad (UGA), Priyanka Gill (UGA), Rachel Holcomb-Gurley (UGA), Shane Keebaugh (UGA), and Laura Wainer (UGA). We would also like to thank Marcelo

Ardón, C. Ronald Carroll, Bob Cooper, Mark Hunter, Al Parker, and Chris Peterson for their comments on earlier versions of the manuscript.

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Table 1. Collection times for seed traps. Seeds were collected from traps approximately every four weeks over two years.

Collection Time	**Year 1**	**Year 2**
1	19-20 Aug 00	14-15 Aug 01
2	19 Sept 00	9-10 Sept 01
3	18 Oct 00	17-18 Oct 01
4	13 Nov 00	9-10 Nov 01
5	11 Dec 00	7-8 Dec 01
6	9-11 Jan 01	3-4 Jan 02
7	5-6 Feb 01	31 Jan- 1 Feb 02
8	5-6 Mar 01	26-27 Feb 02
9	4-5 April 01	25-26 Mar 02
10	27-28 April 01	27-28 April 02
11	26-30 May 01	28-29 May 02
12	19-20 June 01	16 June 02
13	20-21 July 01	14-15 July 02

Table 2. Observed phenology of woody species in Cabo Blanco Absolute Nature Reserve, Costa Rica. The observed period when a particular species had flowers, fruit, and no leaves is noted, along with the growth habit of the species. For those non-deciduous species, "not applicable (NA)" is noted. If flowers, fruit, or no leaves (for deciduous species) were not observed during any time of the 3-year study (June 1999-July 2002), then nothing is noted.

Species	**Flowers**	**Fruit**	**No leaves**	**Habit**
Acanthaceae				
Aphelandra scabra	Feb-March	-	NA	Shrub, liana
Anacardiaceae				
Anacardium excelsum	Jan-Feb	March	NA	Canopy tree
Astronium graveolens	-	-	-	Canopy tree
Spondias mombin	Feb	Jan-June	Jan-Feb	Canopy tree
Annonaceae				
Annona reticulata	-	-	NA	Shrub
Annona purpurea	-	-	NA	Shrub
Oxandra venezuelana	-	-	NA	Shrub
Apocynaceae				
Plumeria rubra	May-Dec	Jan-March	Jan-March	Subcanopy tree
Thevetia sp.	Feb	Feb-March	NA	Subcanopy tree
Arecaceae				
Attalea butyracea (*Scheelea rostrata*)	May-July	Jan-Aug	NA	Palm
Bactris major	`-	July-Oct	NA	Palm
Bignoniaceae				
Amphitecna latiflolia	Feb	March	NA	Understory tree
Adenocalymna inundatum	-	-	NA	Shrub, liana
Arrabidaea conjugata	Nov-March	Feb-April	NA	Liana
Crescentia cujete	-	Jan-July	NA	Understory tree
Tabebuia impetiginosa	-	-	-	Subcanopy tree
Tabebuia ochracea	Feb-May	Feb	-	Subcanopy tree
Tabebuia rosea	Feb-March	May-July	Dec-April	Subcanopy tree
Bombacaceae				
Bombacopsis quinata	Jan-March	Feb-April	Jan-April	Canopy tree
Ochroma pyramidale	Feb-March	Feb-March	NA	Canopy tree
Pseudobombax septenatum	Jan-March	Feb-April	Jan-April	Canopy tree
Quararibea asterolepis	-	-	NA	Subcanopy tree
Boraginaceae				
Cordia collococca	Mar-April	-	April	Subcanopy tree
Burseraceae				
Bursera simarouba	-	-	-	Canopy tree
Capparidaceae				
Capparis amplissima	-	-	NA	Shrub
Capparis verrucosa	-	-	NA	Shrub
Cecropiaceae				
Cecropia peltata	-	Feb-March	NA	Subcanopy tree
Chrysobalanaceae				
Licania arborea	-	-	NA	Subcanopy tree

Licania platypus	-	-	NA	Subcanopy tree
Combretaceae				
Combretum cacoucia	Feb-March	Feb-March	NA	Shrub, liana
Conocarpus erectus	-	Jan-May	NA	Mangrove
Terminalia catappa	Jan-March	Jan-Aug	NA	Subcanopy tree
Terminalia oblonga	Jan-Feb	Feb-March	NA	Canopy tree
Ebenaceae				
Diospyros digyna	-	June-July	NA	Canopy tree
Elaeocarpaceae				
Muntingia calabura	Jan-May	Jan-May	March	Subcanopy tree
Sloanea terniflora	-	-	-	Subcanopy tree
Euphorbiaceae				
Alchornea costaricensis	-	-	-	Subcanopy tree
Alchorneopsis floribunda	-	-	-	Subcanopy tree
Hippomane mancinella	-	Feb-April	NA	Subcanopy tree
Sapium gladulosum	-	March-June	Mar-April	Subcanopy tree
Fabaceae, Caesalpinioidae				
Bauhinia ?manca	-	Feb-Oct	NA	Liana
Cassia grandis	Feb	Feb	NA	
Copaifera aromatica	-	-	NA	Treelet
Hymenaea courbaril	-	-	NA	
Schizolobium parahybum	Dec-Feb	Feb-April	Dec-April	Canopy tree
Mimosoideae				
Acacia collinsii	-	-	-	Treelet/shrub
Cojoba arborea	-	-	-	Canopy tree
Enterolobium cyclocarpum	-	Feb-July	Dec-April	Canopy tree
Inga vera	-	Feb-April	March-July	Canopy tree
Samanea saman	-	-	-	Canopy tree
Papilionidae				
Andira inermis	-	March	-	Canopy tree
Dalbergia retusa	-	-	-	Subcanopy tree
Lonchocarpus felipei	Feb-March	Feb-March	Jan-April	Canopy tree
Lonchocarpus minimiflorus	-	Jan-March	Jan-April	Canopy tree
Swartzia simplex	-	-	-	Shrub
Flacourtiaceae				
Casearia commersoniana	-	-	NA	Treelet
Casearia sylvestris	-	-	NA	Treelet
Lacistema aggregatum	-	-	NA	Treelet
Lauraceae				
Ocotea veraguensis	Feb	Feb	NA	Subcanopy tree
Malpighiaceae				
Heteropterys laurifolia	-	-	-	-
Malvaceae				
Hibiscus tilieaceus	-	Jan	NA	Shrub
Melastomataceae				
Miconia argentea	-	May-June	NA	Subcanopy tree
Miconia sp.	-	-	NA	Subcanopy tree
Meliaceae				

Cedrela fissilis	May-June	-	Jan-April	Canopy tree
Cedrela odorata	-	Apil-July	Jan-April	Canopy tree
Guarea glabra	-	-	NA	Subcanopy tree
Trichilia americana	-	Feb-April	Jan-March	Canopy tree
Trichilia martiana	-	-	-	Subcanopy tree
Trichilia pleeana	-	-	-	Subcanopy tree
Menispermaceae				
Hyperbaena tonduzii	-	Jan-May	NA	Treelet
Moraceae				
Brosimum alicastrum	-	Feb	NA	Canopy tree
Ficus goldmanii	-	Feb-March	NA	Canopy tree
Ficus trachelosyce (?maxima)	-	-	NA	Canopy tree
Sorocea sp.	-	-	NA	Treelet/Shrub
Trophis racemosa	-	-	NA	Subcanopy tree
Myrtaceae				
Psidium guayaba	-	Feb-April	NA	Subcanopy tree
Nyctaginaceae				
Guapira costaricana	-	-	NA	Treelet
Neea sp.	-	-	NA	Treelet
Piperaceae				
Piper tuberculatum	Jan-Oct	Jan-Oct	NA	Treelet
Polygonaceae				
Triplaris melaenodendron	-	-	-	Treelet
Rubiaceae				
Alibertia edulis	-	-	NA	Treelet
Calycophyllum candidissimum	Feb, Oct	Jan-June	April	Canopy tree
Macrocnemum roseum	-	-	NA	Canopy tree
Posoqueria latifolia	-	-	NA	Subcanopy tree
Randia monantha	-	-	NA	Treelet
Rutaceae				
Zanthoxylum setulosum	-	-	-	Canopy tree
Sapindaceae				
Serjania mexicana	-	Feb-June	NA	Liana
Sapotaceae				
Chrysophyllum cainito	-	Jan-May	NA	Canopy tree
Manilkara chicle	-	March	NA	Subcanopy tree
Pouteria reticulata	-	-	NA	Subcanopy tree
Pouteria campechiana	-	-	NA	Subcanopy tree
Simaroubaceae				
Picramnia latifolia	-	Feb	NA	Treelet
Simarouba glauca	Jan-May	Jan-Feb	NA	Canopy tree
Sterculiaceae				
Guazuma ulmifolia	Dec-April	Jan-April	NA	Subcanopy tree
Sterculia apetala	Jan-April	Feb-April	Jan-March	Canopy tree
Tiliaceae				
Luehea seemannii	Jan-Feb	Feb-June	NA	Canopy tree
Ulmaceae				
Trema micrantha	-	-	-	Subcanopy tree

Table 3. Cumulative density, frequencies, and germination rates for plant species present in seed traps. A species frequency is the percentage of traps (n= 50) it was found in over the two-year period. Germination rates were determined from germination experiments in a shadehouse in Heredia, San Jose, with the proportion germinated of total seeds sown in parentheses.

	Dispersal	**Density (m^{-2})**			**Space**	**Time**	**Germination**
Species name	**Mode**	**Mean**	**SD**	**CoV**	**Freq %**	**Freq %**	**Rate (%)**
All species	-	1650	2380	144	100	100	-
A.Trees							
Anacardium excelsum	animal	0.21	0.86	400	6.0	12	100 (2/2)
Attalea butyracea	animal	0.29	1.4	495	4.0	7.7	0 (0/1)
Bombacopsis quinata	wind	2.2	11	503	18	15	66.7 (4/6)
Brosimum alicastrum	animal	3.9	7.1	183	38	12	17.1 (7/41)
Calycophyllum candidissimum	wind	140	250	180	70	39	13.9 (326/2352)
Cedrela odorata	wind	11	25	241	52	50	5.5 (3/55)
Copaifera aromatica	animal	0.50	1.9	382	8.0	7.7	100 (3/3)
Cordia colococca	wind	1.1	2.4	226	18	12	17.3 (9/52)
Diospyros digyna	animal	1.0	2.2	217	22	12	10 (1/10)
Inga vera	animal/gravity	30	130	450	22	27	0.84 (1/119)
Lonchocarpus felipei	wind	1.3	5.8	452	10	23	16 (8/50)
Lonchocarpus minimiflorus	wind	12	32	271	48	42	1.3 (2/155)
Luehea seemannii	wind	1030	2100	203	60	58	5.1 (304/6002)
Picramnia latifolia	animal	0.79	2.6	335	12	15	14. (1/7)
Plumeria rubra	wind	1.4	7.0	490	8.0	27	16 (9/17)
Posoqueria latifolia	animal	3.2	23	707	2	3.8	0.0 (0/43)
Pseudobombax septenatum	wind	10.	42	415	24	35	18.6 (8/43)
Schizolobium parahyba	wind	3.1	13	422	8.0	23	0.0 (0/2)
Spondias mombin	animal	0.14	0.71	495	4.0	7.7	0.0 (0/0)
Sterculia apetala	animal/gravity	0.21	1.1	523	4.0	12	0.0 (0/1)
Tabebuia ochracea	wind	2.6	5.1	195	42	23	29 (11/38)
Tabebuia rosea	wind	1.6	7.0	424	12	7.7	2.6 (1/39)
Terminalia catappa	animal/water	0.29	1.6	556	4.0	15	0.0 (0/1)
Terminalia oblonga	wind	2.4	3.9	167	40	27	16 (6/38)
Trichilia americana	animal	2.0	7.8	390	8.0	27	73 (11/15)
Trichilia martiana	animal	0.21	0.86	400	6.0	3.8	25 (1/4)
Triplaris melaenodendron	wind	0.071	0.51	707	2.0	12	100 (1/1)
Ficus sp.	animal	0.21	0.86	400	6.0	3.8	25 (1/4)
Moraceae unknown	animal	0.071	0.51	707	2.0	12	100 (1/1)

B. Lianas

Arrabidaea conjugata	wind	5.2	8.3	159	46	31	28	(29/103)
Bauhinia ?manca	gravity/animal	8.9	22	244	46	54	16	(18/114)
Begoniaceae sp1	wind	9.1	25	274	44	42	60	(3/5)
Bignoniaceae sp1	wind	0.71	1.6	226	18	3.8	33	(3/9)
Combretum cacoucia	wind	27	90.	332	46	31	16	(40/247)
Serjania mexicana	wind	59	300	510	62	31	5.5	(20/63)

C. Unknowns

UNKAAA	-	5.7	31	547	22	23	0.0	(0/35)
UNKBBB	-	0.071	0.51	707	2.0	3.8	0.0	(0/2)
UNKCCC	-	0.071	0.51	707	2.0	3.8	-	
UNKDDD	-	0.071	0.51	707	2.0	3.8	0.0	(0/1)
UNKEEE	-	0.071	0.51	707	2.0	3.8	-	
UNKFFF	-	0.14	1.0	707	2.0	3.8	0.0	(0/2)
UNKGGG	-	0.071	0.51	707	2.0	3.8	0.0	(0/1)
UNKHHH	-	0.071	0.51	707	2.0	3.8	-	
UNKIII	-	0.071	0.51	707	2.0	3.8	0.0	(0/1)
UNKJJJ	-	0.64	4.5	707	2.0	3.8	0.0	(0/9)
UNKKKK	-	0.14	0.71	495	4.0	7.7	0.0	(0/2)
UNKLLL	-	0.14	1.0	707	2.0	7.7	0.0	(0/2)
UNKMMM	-	110	240	217	76	19	-	
UNKNNN	-	0.071	0.51	707	2.0	3.8	100	(1/1)
UNKOOO	-	0.21	0.86	400	6.0	3.8	0.0	(0/1)
UNKPPP	-	0.14	0.71	494	4.0	7.7	25	(1/4)
UNKQQQ	-	0.071	0.51	707	2.0	3.8	50	(1/2)
UNKRRR	-	0.071	0.51	707	2.0	3.8	0.0	(0/1)
UNKSSS	-	0.071	0.51	707	2.0	3.8	-	
UNKTTT	-	0.071	0.51	707	2.0	3.8	-	
UNKUUU	-	0.071	0.51	707	2.0	3.8	0.0	(0/1)
UNKVVV	-	43	300	707	2.0	3.8	0.0	(0/123)
UNKXXX	-	0.071	0.51	707	2.0	3.8	0.0	(0/1)
UNKYYY	-	0.071	0.51	707	2.0	3.8	0.0	(0/1)
UNKZZZ	-	1.7	12	707	2.0	3.8	0.0	(0/1)
UNKAAB	-	1.7	8.1	471	8.0	7.7	0.0	(0/9)
UNKABB	-	0.071	0.51	707	2.0	3.8	0.0	(0/1)
UNKACC	-	0.57	3.6	623	4.0	7.7	0.0	(0/8)
UNKADD	-	0.14	0.71	495	4.0	7.7	-	
UNKAEE	-	0.36	2.1	580	4.0	3.8	0.0	(0/5)

* Voucher specimens are deposited in the San Miguel Biological Station Herbarium, Cabo Blanco Absolute Reserve, Puntarenas

Table 4. Coastal trap frequency and number of seeds collected for tree species found in inland tree plots only. Number of coastal traps frequented (n= 25) and seed numbers are for the 26 collecting periods combined.

Species name	Mode of Dispersal	Number of Coastal Traps	Number of Seeds
Brosimum alicastrum	animal	8	22
Cedrela odorata	wind	12	48
Copaifera aromatica	animal	2	3
Diospyros digyna	animal	6	6
Inga vera	animal	0	0
Luehea seemannii	wind	6	25
Picramnia latifolia	animal	2	5
Posoqueria latifolia	animal	0	0
Tabebuia ochracea	wind	12	24
Terminalia oblonga	wind	8	9

Figure 1. Phenology of woody species over a three-year observation period (June 1999-July 2002) relative to annual average rainfall over the same period. Number of species observed with flowers, fruits, and no leaves are shown.

Fig 1, Chap III
Lindquist

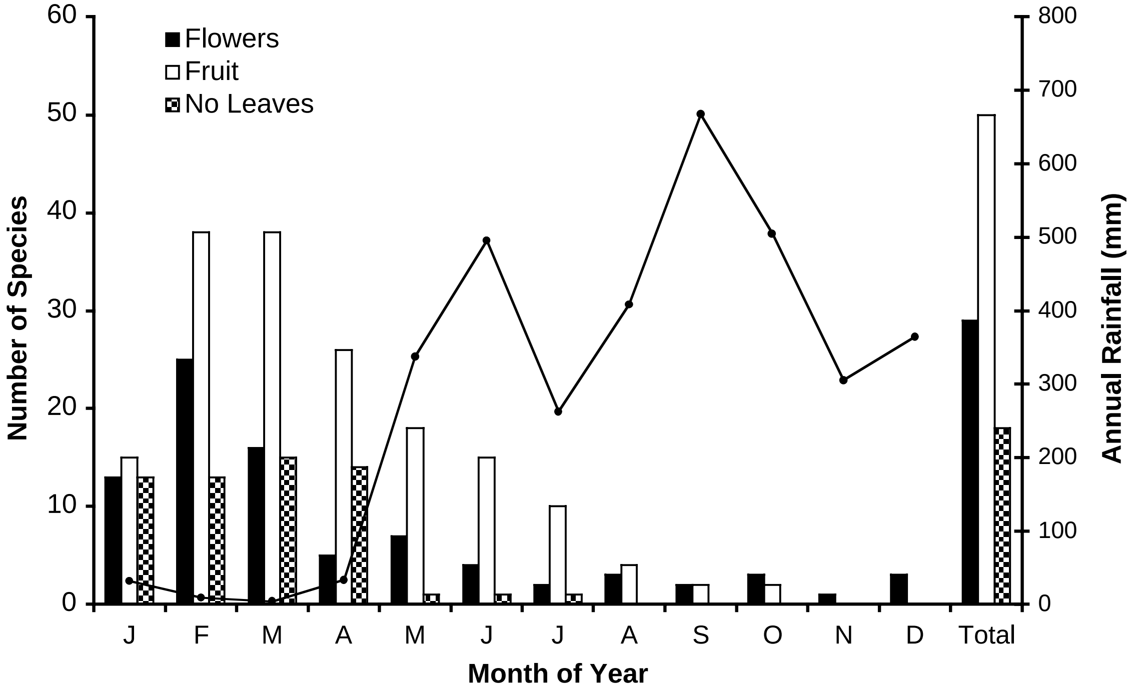


Figure 2. Total number (a) and mean number (b) of woody plant species collected in traps for each collection period over the two-year period. Collection periods are the same as in Table 1 and approximate months are labeled on x-axis.

Fig 2, Chap III
Lindquist

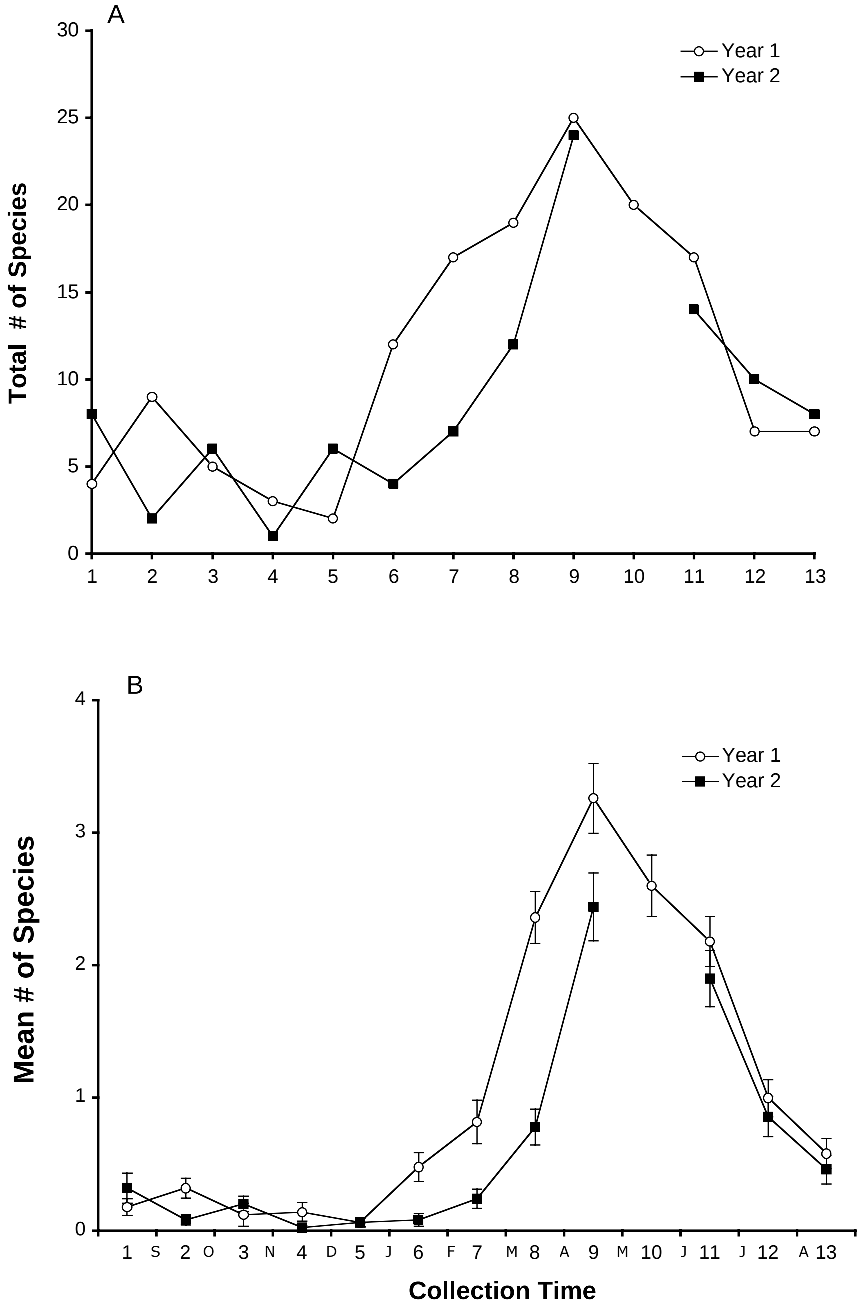


Figure 3. Mean number of seeds collected in traps over the two-year collection periods (Table 1). Error bars represent standard error of the mean for each collection period (n= 50).

Fig 3, Chap III
Lindquist

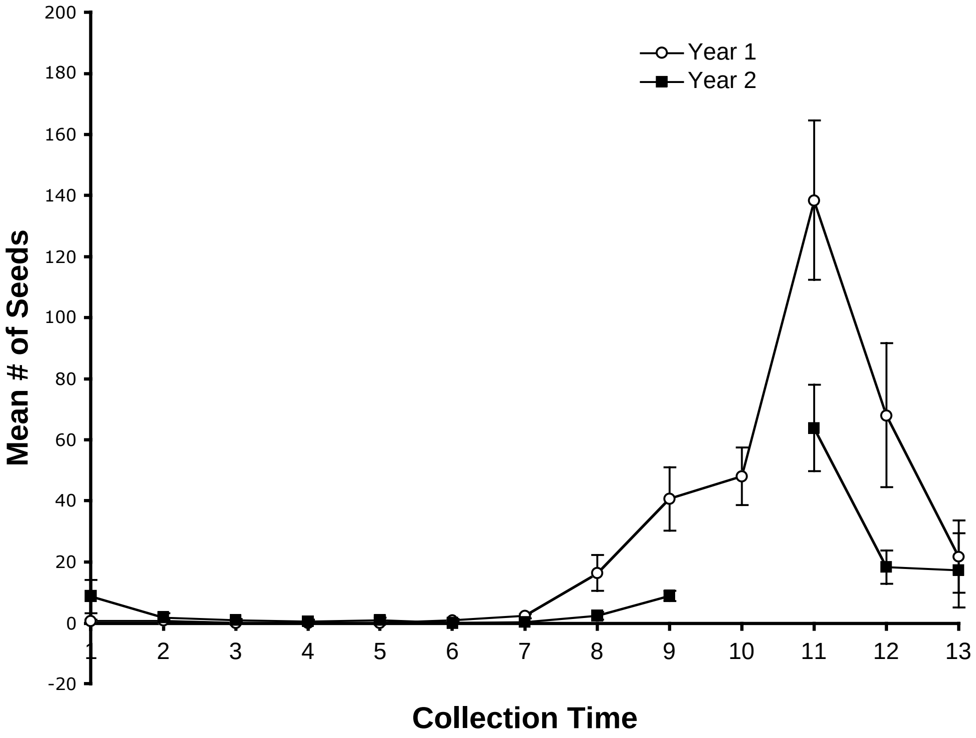


Figure 4. NMS ordination axes scores for (a) seed traps in species space, and (b) woody species in trap (plot) space. In (a) zone 1 (asterisks) is the coastal zone and zone 2 (triangles) is the inland zone. Trap numbers (e.g.,TP12) in (a) refer to the location of the trap along the transects. Species names' codes in (b) are referenced in Appendix 1.

Fig 4a, Chap III
Lindquist

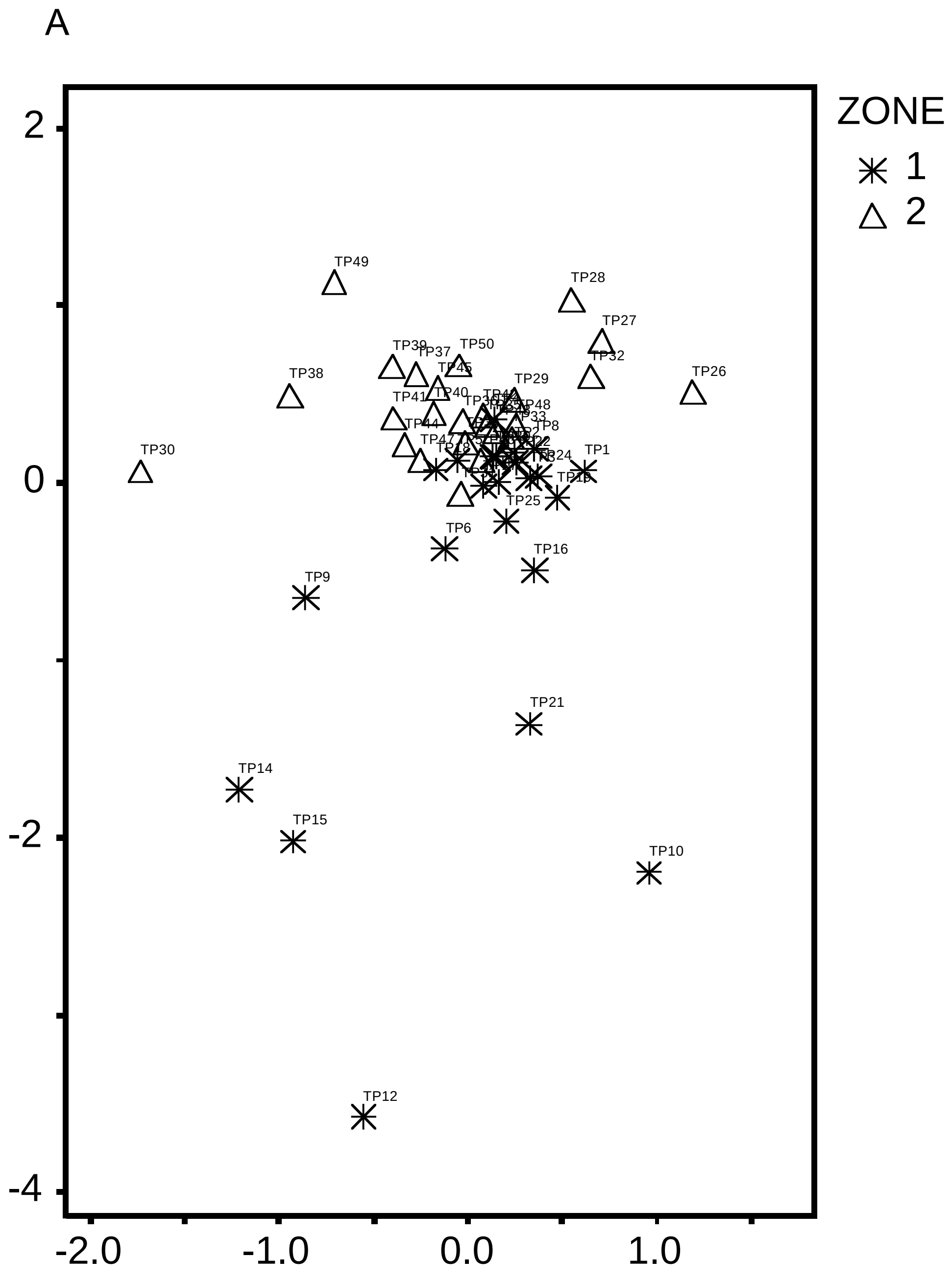


Fig 4b, Chap III
Lindquist

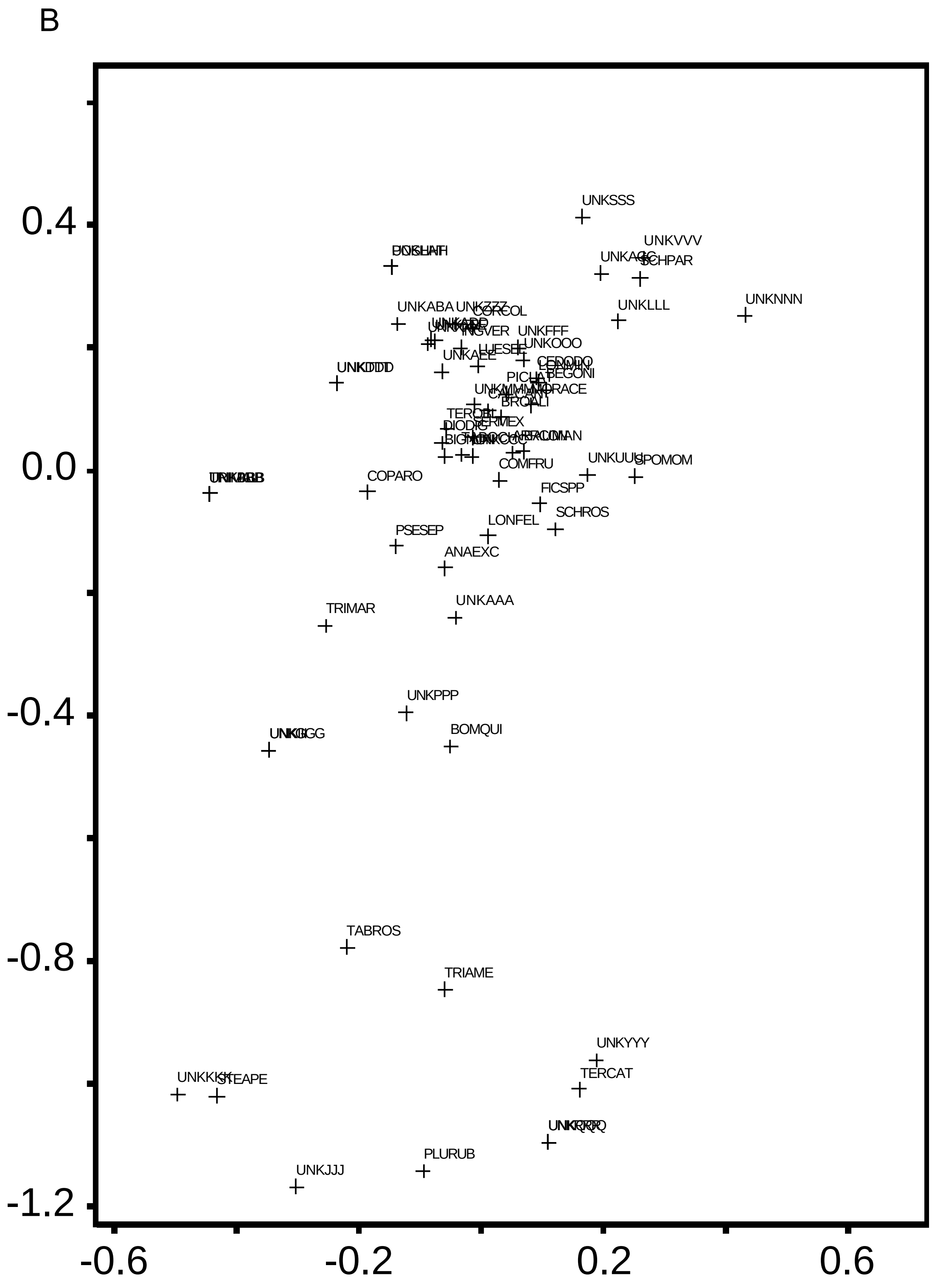


Figure 5. NMS ordination axes scores for seed traps in Year 1 (August 2000- August 2001) and Year 2 (August 2001-August 2002). Trap numbers (e.g.,TP15A) in refer to the location of the trap along the transects and the collection (A= Year 1, B= Year 2). For outlier traps, arrows represent the change in trap composition from Year 1 to Year 2, with some labeled outside the plot's area because they were excluded from the analysis during Year 1 or 2.

Fig 5, Chap III
Lindquist

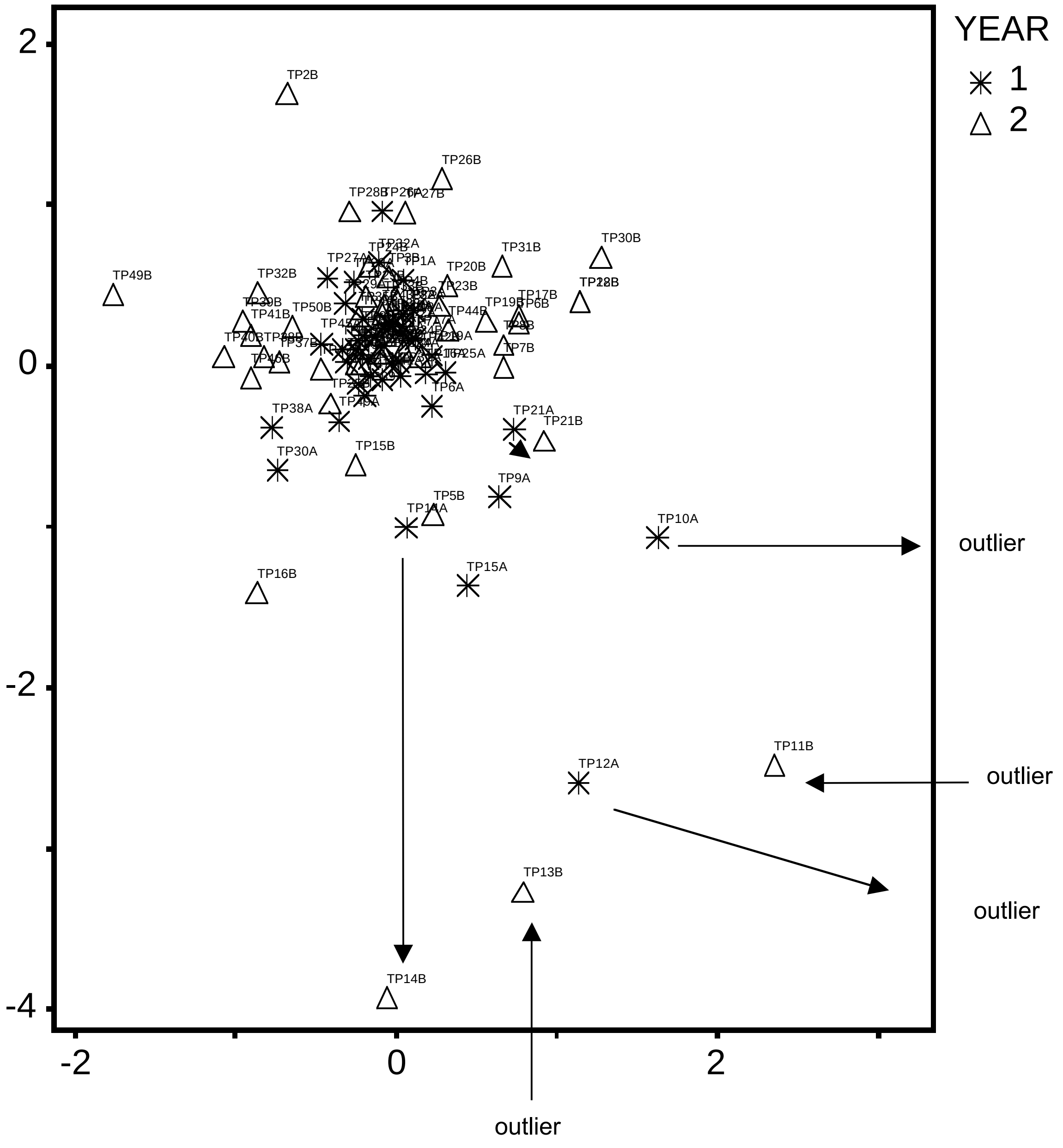
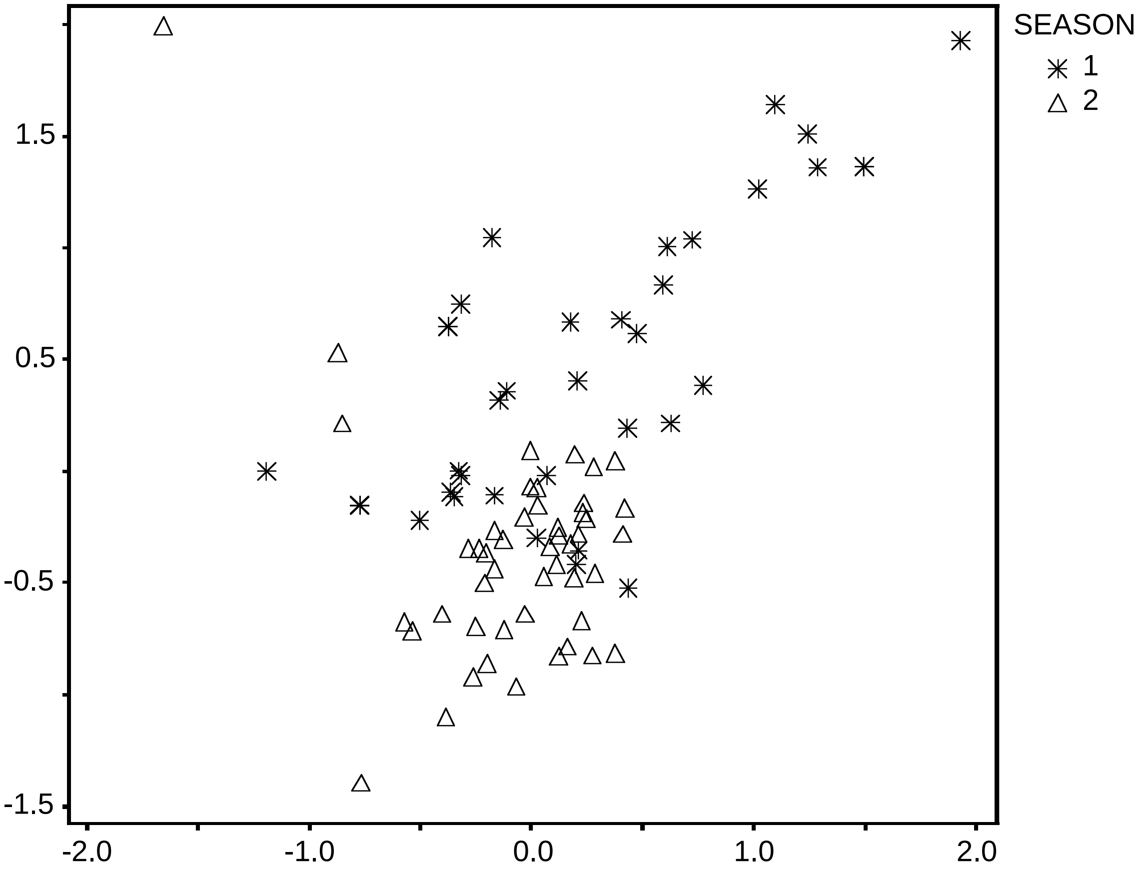


Figure 6. NMS ordination axes scores for (a) Year 1 (b) Year 2 by season. Season 1 (wet season, asterisks) represents seed trap totals for collection periods between May and December. Season 2 (dry season, triangles) combines seed trap seed rain from January to April.

Fig 6a, Chap III
Lindquist

A : Year 1



Appendix 1. List of plant species present in tree, sapling, seedling, or seed plots with their respective species code used in ordinations. Herbarium specimens and seed vouchers are also included.

Sp code	*Species name*	*Author and Herbarium specimen*	*Seed voucher*	*Family*
A.TREES				
ANAEXE	Anacardium excelsum	Bertero & Balb. ex Kunth (Lindquist 1048)	46	Anacardiaceae
ASTGRA	Astronium graveolens	Jacq. (Lindquist 1037)	-	Anacardiaceae
SPOMOM	Spondias mombin	L. (Lindquist 1077)	67	Anacardiaceae
OXAVEN	Oxandra venezuelana	R. E. Fr. (Lindquist 1021)	-	Annonaceae
PLURUB	Plumeria rubra	L.	19	Apocynaceae
BACMAJ	Bactris major	Jacq.	-	Arecaceae
COCNUC	Cocos nucifera	L.	-	Arecaceae
SCHROS	Attalea butyracea	(Mutis ex) L.f. Wess. B	68	Arecaceae
AMPLAT	Amphitecna latifolia	(Mill.) A.H. Gentry	-	Bignoniaceae
CRECUJ	Crescentia cujete	L.	-	Bignoniaceae
TABIMP	Tabebuia impetiginosa	(Mart. ex DC.) Standl.	-	Bignoniaceae
TABOCH	Tabebuia ochracea	(Cham.) Standl. (Lindquist 1049)	65	Bignoniaceae
TABROS	Tabebuia rosea	(Bertol.)D.C. (Lindquist 1044)	72	Bignoniaceae
BERFLA	Bernoullia flammea	Oliv.	-	Bombacaceae
OCHPYR	Ochroma pyramidale	(Cav. ex Lam.) Urb.	-	Bombacaceae
BOMQUI	Bombacopsis quinata	(Jacq.) Dugand	44	Bombacaceae
PSESEP	Pseudobombax septenatum	(Jacq.) Dugand	41	Bombacaceae
QUAAST	Quararibea asterolepsis	Pittier	-	Bombacaceae
CORCOL	Cordia collococca	L.	38	Boraginaceae
BURSIM	Bursera simaruba	(L.) Sarg.	-	Burseraceae
CASGRA	Cassia grandis	L. f.	-	Caesalpinioidae
COPARO	Copaifera aromatica	Dwyer (Lindquist 1012,1080)	31B	Caesalpinioidae
SCHPAR	Schizolobium parahybum	(Vell.) S. F. Blake	29B	Caesalpinioidae
CAPAMP	Capparis amplissima	Lam. (Lindquist 1005)	-	Capparidaceae
CAPVER	Capparis verrucosa	Jacq. (Lindquist 1011)	-	Capparidaceae
CONERE	Conocarpus erecta	L.	-	Combretaceae
TERCAT	Terminalia catappa	L. (Lindquist 1038)	13	Combretaceae
TEROBL	Terminalia oblonga	(Ruiz & Pav.) Steud. (Lindquist 1052)	36	Combretaceae
LICARB	Licania arborea	Seem. (Lindquist 1050)	-	Chrysobalanaceae
LICPLA	Licania platypus	(Hemsl.) Fritsch (Lindquist 1051)	-	Chrysobalanaceae
DIODIG	Diospyros digyna	Jacq. (Lindquist 1058,1064)	23, 70	Ebenaceae
MUNCAL	Muntingia calabura	L. (Lindquist 1075)	-	Elaeocarpaceae
SLOTER	Sloanea terniflora	(Moc. & Sesse ex DC.) Sta (Lindquist1075)	-	Elaeocarpaceae
ALCFLO	Alchorneopsis floribunda	(Benth.) Mull.Arg.	-	Euphorbiaceae
HIPMAN	Hippomane mancinella	L.	-	Euphorbiaceae
SAPGLA	Sapium glandulosum	(L.) Morong (Lindquist 1039)	-	Euphorbiaceae
CASCOM	Casearia commersoniana	Cambess.	-	Flacourtiaceae
CASSYL	Casearia sylvestris	Sw. (Lindquist 1033)	-	Flacourtiaceae

OCOVER	Ocotea veraguensis	(Meisn.) Mez	-	Lauraceae
NECSP	Nectandra ?membranacea		-	Lauraceae
LACAGG	Lacistema aggregatum	(Bergius) Rusby (LIndquist 1008,1009)	-	Lacistemataceae
MICARG	Miconia argentea	(Sw.) DC.	-	Melastomataceae
CEDFIS	Cedrela fissilis	Vell.	-	Meliaceae
CEDODO	Cedrela odorata	L.	16,26,47	Meliaceae
GUAGRA	Guarea glabra	Vahl (Cespedes X) (Céspedes 1059)	-	Meliaceae
TRIAME	Trichilia americana	(Sesse & Moc.) T. D. Penn	17,18	Meliaceae
TRIMAR	Trichilia martiana	C. DC. (Lindquist 1002,1022)	30	Meliaceae
TRIPLE	Trichilia pleeana	(A. Juss.) C. DC. (Lindquist 1030)	-	Meliaceae
HETLAU	Heteropterys laurifolia	(L.) A. Juss.	-	Malpighiaceae
HYPTON	Hyperbaena tonduzii	Diels (Lindquist 1040)	-	Menispermaceae
ENTCYC	Enterolobium cyclocarpum	(Jacq.) Griseb.	-	Mimosoideae
INGVER	Inga vera	Willd. (Lindquist 1001)	42	Mimosoideae
INGSP	Inga sp2		-	Mimosoideae
COJARB	Cojoba arborea	(L.) Britton & Rose	-	Mimosoideae
BROALI	Brosimum alicastrum	Sw. (Lindquist 1003,1013)	43	Moraceae
FICGOL	Ficus goldmanii	Standl. (Lindquist 1054)	-	Moraceae
FICTRO	Ficus trachelosyce	Dugand (Lindquist 1026)	-	Moraceae
SORSP	Sorocea sp.	-	-	Moraceae
TRORAC	Trophis racemosa	(L.) Urb. (Lindquist 1014,1061)	-	Moraceae
EUGSOL	Eugenia salamensis		-	Myrtaceae
GUACOS	Guapira costaricana	(Standl.) Woodson (Lindquist 1034)	-	Nyctaginaceae
NEESP	Neea sp.		-	Nyctaginaceae
ANDINE	Andira inermis	(W. Wright) Kunth (Lindquist 1036,1054)	-	Papilionidae
LONFEL	Lonchocarpus felipei	(N/D) N. Zamora ined.	11,12,54	Papilionidae
LONMIN	Lonchocarpus minimiflorus	Donn. Sm. (Lindquist 1027)	29	Papilionidae
SWASIM	Swartzia simplex	(Sw.) Spreng. (Lindquist 1032)	-	Papilionidae
PIPTUB	Piper tuberculatum	Jacq.	-	Piperaceae
TRIMEL	Triplaris melaenodendron	(Bertol.) Standl. & Steye	-	Polygonaceae
ALIEDU	Alibertia edulis	(Rich.) A. Rich (Lindquist 1029,1081)	-	Rubiaceae
CALCAN	Calycophyllum candidissimum	(Vahl) DC.	3	Rubiaceae
MACROS	Macrocnemum roseum	(Ruiz & Pav.) Wedd. (Lindquist 1019)	-	Rubiaceae
POSLAT	Posoqueria latifolia	(Rudge) Roem. & Schult. (Lindquist 1062)	71	Rubiaceae
RANMON	Randia monantha	Benth.	-	Rubiaceae
ZANSET	Zanthoxylum setulosum	P. Wilson	-	Rutaceae
CHRCAI	Chrysophyllum cainito	L. (Lindquist 1063)	-	Sapotaceae
MANCHI	Manilkara chicle	(Pittier) Gilly (Lindquist 1006,1076)	-	Sapotaceae
POURET	Pouteria reticulata	(Engl.) Eyma (Lindquist 1007,1016)	-	Sapotaceae
POUCAM	Pouteria campechiana	(Kunth) Baehni	-	Sapotaceae
PICLAT	Picramnia latifolia	Tul. (Lindquist 1010)	63	Simaroubaceae
SIMGLA	Simarouba glauca	DC. (Lindquist 1047)	-	Simaroubaceae
GUAULM	Guazuma ulmifolia	Lam. (Lindquist 1017)	-	Sterculiaceae
STEAPE	Sterculia apetala	(Jacq.) H. Karst.	31	Sterculiaceae
LUESEE	Luehea seemannii	Triana & Planch.	33	Tiliaceae
TREMIC	Trema micrantha	(L.) Blume	-	Ulmaceae

FICSPP	Ficus sp	-	75	Moraceae
MORACE	?Moracaceae	-	76	Moraceae
B. LIANAS				
BEGUNK	Begoniaceae sp1	-	25,27	Begoniaceae
ARRCON	Arrabidaea conjugata	(Vell.) Mart.	35,39	Bignoniaceae
BIGNON	Bignoniaceae sp1	-	72	Bignoniaceae
BAUSPP	Bauhinia ?manca	-	1,28	Caesalpinioidae
COMSPP	Combretum cacoucia	Exell (Lindquist 1067, 1068)	34	Combretaceae
SERMEX	Serjania mexicana	(L.) Willd. (Lindquist 1071)	5,37,57,65	Sapindaceae
C. UNKNOWN				
UNKAAA	-	-	2,2A	-
UNKBBB	-	-	4	-
UNKCCC	-	-	6	-
UNKDDD	-	-	7	-
UNKEEE	-	-	8	-
UNKFFF	-	-	9	-
UNKGGG	-	-	10	-
UNKHHH	-	-	14	-
UNKIII	-	-	15	-
UNKJJJ	-	-	20	-
UNKKKK	-	-	21	-
UNKLLL	-	-	24	-
UNKMMM	-	-	32	-
UNKNNN	-	-	45	-
UNKOOO	-	-	48	-
UNKPPP	-	-	49	-
UNKQQQ	-	-	50	-
UNKRRR	-	-	51	-
UNKSSS	-	-	52	-
UNKTTT	-	-	53	-
UNKUUU	-	-	58	-
UNKVVV	-	-	59	-
UNKXXX	-	-	60	-
UNKYYY	-	-	61	-
UNKZZZ	-	-	62	-
UNKAAB	-	-	64	-
UNKABB	-	-	66	-
UNKACC	-	-	69	-
UNKADD	-	-	73	-
UNKAEE	-	-	74	-

* Voucher specimens are deposited in the San Miguel Biological Station Herbarium, Cabo Blanco Absolute Reserve, Puntarenas

EFFECTS OF CRAB PREDATION AND CANOPY COVER ON SEEDLING ESTABLISHMENT IN A COASTAL TROPICAL FOREST[1]

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[1] Lindquist, E.S., and C.R. Carroll. To be submitted to Oecologia

Abstract

The effects of predators on terrestrial plant community structure is central to our understanding of plant distributions, yet has been the topic of few studies. Recently, several studies have debated the significance of differential seed and seedling predation versus plant response to environmental conditions in mangrove communities, yet no comparable investigations have been conducted in coastal terrestrial forests. We investigated the potential relative and differential effects of seed and seedling predation by land crabs, *Gecarcinus quadratus*, and hermit crabs, *Coenobita compressus*, and canopy cover on seedling establishment. We conducted seed removal, seedling establishment, and seedling growth experiments over a two-year period. Exclosure and open control treatments manipulated crab consumption pressure; seeds and seedlings of seven different tree species and four growth stages were transplanted into experimental gap and non-gap plots. The results of our study were: (1) crab predation pressure significantly affected seed and seedling survival rates and stem height; (2) crab predation pressure decreased with distance from shore (as crab density increased); (3) crabs differentially preferred seeds and younger seedlings over older seedlings but showed no species preferences; and (4) canopy cover affected seedling survival and stem height increment change. In summary, we conclude that crab predation of seeds and seedlings, and secondarily canopy cover, are important factors affecting the tree regeneration in this secondary coastal forest. Our study emphasizes the need for ecologists to incorporate multiple factors into their experimental designs to elucidate a better understanding of the relative importance of hypothesized mechanisms causing species distribution shifts and abundances.

Key words: coastal tropical forest, canopy cover, land crab, seed and seedling predation, seedling establishment, tree recruitment

Introduction

One of the most pertinent objectives of plant ecology is to better understand the factors determining the distribution and abundance of species (Whittaker 1975, Harper 1977, Louda 1989). Janzen (1970) and Connell (1971) proposed that predation on tree seeds and seedlings is a major mechanism that structures biological communities, particularly diverse tropical forests. Since then, numerous studies have affirmed that seed predators and herbivores have significant impacts on plant recruitment at the seed (Schupp 1988, Smith et al. 1989, Wright 1990, Clarke and Myerscough 1993, Terborgh et al. 1993, Hart 1995; McKee 1995, Blate et al. 1998) and seedling (Sork 1987, Schupp 1988, Howe 1990, Molofsky and Fischer 1993, Osunkoya et al. 1992, Hart 1995, Green et al. 1997, Terborgh and Wright 1994, Turner 2001, Sherman 2002) stages. However, it remains unclear how important predation is relative to other possible biotic and abiotic factors that are known to influence species distributions (but see Smith 1987a,b, Sork 1987, Howe 1990, Osborne and Smith 1990, Clarke and Myerscough 1993, Molofsky and Fischer 1993, McKee 1995, McGuinness 1997).

Coastal terrestrial forests are well suited for disentangling biotic and abiotic factors because of their interface between marine and terrestrial ecosystems, and their potentially harsh environmental gradients. Although there is a paucity of literature on coastal terrestrial forests, especially for those in the tropics, they provide a distinctive model to test how consumer movements across the marine and terrestrial interface and spatial changes in environmental conditions can affect prey distribution, productivity, and community composition (Polis and Hurd 1996, Polis et al. 1997).

The majority of the work addressing the effects of predator pressure on community structure in coastal forest systems has been conducted in mangrove habitats (Smith 1987, Smith 1988, Smith et al. 1989, Clarke and Myerscough 1993, McKee 1995, McGuinness 1997, Sousa and Mitchell 1999, Krauss and Allen 2002), and in oceanic island (Lee 1985, Lee 1988, O’Dowd and Lake 1991, Green et al. 1997) communities.

Mangrove crabs (Families Sesarminae, Grapsidae, and Ocypodidae) have been found to be significant consumers of mangrove propagules and some have suggested that crab consumption pressure is the main factor influencing mangrove species’ distributions (see Smith 1992 for a review). Contrary to this proposed "dominance-predation model", other investigators discovered that high levels of seed predation by crabs did not correlate with mangrove species' abundances and concluded that physiological adaptation to variable abiotic conditions is the key mechanism causing apparent zonation of mangrove communities (Clarke and Myerscough 1993, McKee 1995, Sousa and Mitchell 1999).

Only a few researchers have begun to investigate the impacts of terrestrial land crab seed and seedling predation on plant recruitment in coastal terrestrial forests, (*Gecarcoidea natalis*, Christmas Island, Indian Ocean, O'Dowd and Lake 1990, O'Dowd and Lake 1991, Green et al. 1997; and *Gecarcinus quadratus*, Costa Rica, Pacific Ocean, Sherman 2002). In many coastal forests around the tropics, land crabs (Family Gecarcinidae) and hermit crabs (Family Pagaridae) are very abundant. Terrestrial hermit crabs may spend a portion of their foraging time in the intertidal zone, but only the larval stage of terrestrial land crabs is spent in the marine habitat before the crabs come to shore, and spend the remainder of their lifetime in the coastal forest (Burggren and McMahon 1988). Although land crabs are known to be omnivorous, they have been found to forage predominantly on fruits, seeds, seedlings, and leaf litter (Lee 1985 and 1988, O’Dowd and Lake 1990, O'Dowd and Lake 1991, Green et al. 1997, Sherman 2002). Impacts of hermit crab consumption of seeds, fruit, or seedlings on plant recruitment have not been investigated in any study, although they are known to forage on fruits and leaves of plants (Ball 1972, Burggren1988, Thacker 1996, Thacker 1998).

In the only mainland terrestrial forest study assessing the effects of land crabs on seedling densities and distribution, Sherman (2002) found both significant effects of crabs on seedling densities over time and differential preference by land crabs for seedling species not present in the crab zone. His differential predation findings are similar to those found in mangrove communities. From these studies with crabs in coastal communities, it appears that terrestrial crabs, like mangrove crabs, can have major impacts on plant productivity through their very intense consumption of seeds and seedlings, and on plant distribution through their preferential predation on particular species. In addition, the investigators suggested that crab predation pressure may be the major factor influencing terrestrial plant community composition in coastal forests, but none directly investigated the effects of land and hermit crabs on tree recruitment.

Besides consumption pressure, other abiotic and biotic factors can influence plant community composition at various stages of plant recruitment and most studies have found that mortality factors at the earliest stages of tree recruitment (seed production, seed dispersal, seedling establishment) are the most influential (see Clark et al. 1999 for a review). This may be partly due to the emphasis placed on the early recruitment stages by past investigators, but it appears that microsite conditions such as light (e.g., Augspurger 1984), soil moisture (e.g., Veenendaal et al. 1996), soil nutrient status (e.g., Swaine 1996), soil salinity (e.g., Williams et al. 1998), predation and herbivory (e.g., Terborgh and Wright 1994), and inter- and intraspecific competition (e.g., Clarke et al. 1996.) promote differentiation of survival and growth at establishment among plant species. In particular, the influence of light on the survival and growth of tropical tree seedlings has been widely investigated, with the majority of studies finding that survival and growth are positively correlated with light availability (see Turner 2001b for a review).

Well-designed studies in mangroves incorporated abiotic environmental factors such as tidal inundation, soil salinity, and canopy cover into their crab consumption experiments, and found that none of the factors alone regulate mangrove recruitment (McGuinness 1997, Krauss and Allen 2002). When comparing the relative effects of light and crab consumption pressure on seedling establishment in mangroves (McGuinness 1997), and oceanic island terrestrial forests (Green et al. 1997), seedling survival and growth was found to be higher in shadier canopy microhabitats than in gaps, and the investigators concluded that light was secondarily important to seedling success after crab predation pressure. There is also some evidence that canopy cover may affect crab foraging patterns, thereby indirectly affecting seedling success. Osborne and Smith (1990) found that crab predation rates were negatively correlated with gap size in an Australian mangrove, whereas Sousa and Mitchell (1999) found that canopy cover (gap or non-gap) did not affect crab predation rates on mangrove propagules. It is apparent from these studies that there is no consensus as to how canopy cover and other environmental conditions directly and indirectly affect plant community spatial patterns, and how their influence relates to that of crab predation pressure.

With few empirical comparative studies conducted in coastal terrestrial forests, it is still unknown how changing microsite conditions and predation pressure along a gradient work independently, and/or interact with each other to structure plant communities. In this study we investigated the combined and differential effects of seed and seedling predation by both land crabs (*Gecarcinus quadratus*) and hermit crabs (*Coenobita compressus*) on seedling establishment and growth in a mainland coastal terrestrial forest community in Costa Rica. By manipulating crab predation pressure on transplanted seeds and seedlings with exclosure and control treatments, and canopy cover with natural light gaps and nearby non-gap sites, we examined the relative effects of crab herbivory and canopy cover. To investigate how crabs may affect plant composition differentially in space and time, we assessed how predation pressure varies with distance from shore, time of year, tree species, and seedling age.

We predicted that crab predation pressure would significantly affect seed and seedling survival and growth, while light would affect seedling growth more than survival in those seedlings that escaped crab predation as a secondary influential factor. Assuming crab densities correlate with crab predation pressure, we predicted that seed and seedling survival and growth would be less in the coastal zone than in the inland zone. We also predicted that preferential crab predation would cause differences in survival and growth rates among different tree species and different ages of seedlings, with preference for larger-seeded species and younger seedlings.

Methods

Study Site

We conducted the study in the coastal terrestrial forest surrounding the San Miguel Biological Station of the Cabo Blanco Absolute Nature Reserve, Costa Rica (9˚ 35’ N and 85˚ 08.5’ W). The forest is classified as a transitional dry to wet tropical forest. Annual precipitation ranges from 2500-3200 mm year^{-1} (mean of 3000 mm year^{-1}), with almost all the annual rain (95 to 100%) falling during the wet season (May - November; Lindquist and Lieberman 2003). Average annual temperature is 27˚C, with average low and high temperatures of 24˚C and 32˚C respectively. Eighty-five percent of the 1250 protected hectares, including our study area, is 36 year-old secondary forest that has naturally regenerated from cattle pasture. The remaining 15 percent consists of primary forest found in the upland slopes of the reserve and was excluded from this study.   A complete study site description can be found in Lindquist and Lieberman (2003).

Our study area was divided into two approximately 8 ha (80,000 m^2) sub-study zones: the "coastal" zone (0 to 100 m from shore, 0 to 20 m altitude,) and the "inland" zone (200 to 400m from shore, 40 to 70 m altitude). The coastal zone was 800 m long (parallel to coastline) and 100 m deep, whereas the inland study area was 400 m long and 200 m deep. Our study area was restricted for two reasons: (1) we excluded a steep limestone rock shelf stretching the length of the study area between 100 and 200 m from shoreline, and (2) stream gorges restricted the length of the study area in the inland zone.

Prior to the experimental treatments, we assessed tree species distributions and densities in our study area. Stratified-randomly selected circular quadrats were used to sample tree seedlings in each study zone (stems < 0.5m in height; quadrat radius = 2 m;

n=20 each zone), saplings (stems $\geq$ 0.5 m, diameters < 5 cm; quadrat radius = 3 m; n=20 each zone), and adults (diameters $\geq$ 5 cm; quadrat radius = 5 m; n=20 each zone). In the 0.10 ha total area sampled in each of the two study zones for adults, 15 tree species were represented within the 61 adult individuals encountered in the coastal zone, while 44 species were represented within the 152 adults tagged and measured in the inland zone. When species number is controlled for any density effect, the coastal zone had 0.25 species adult stem^{-1} while the inland zone had 0.29 species adult stem^{-1}. Only five species occurred in both zones. For juveniles (seedlings and saplings combined; dbh < 5 cm) the pattern is similar; the number of species was much less in the coastal zone (6 species) than in the inland zone (45 species). Although the adult density was much higher for the inland zone (1500 trees ha^{-1}) than the coastal zone (610 trees ha^{-1}), the sum basal areas of the two zones were very similar (24 m^2 ha^{-1} and 25 m^2 ha^{-1} respectively). Juvenile densities also differed between the two zones with 0.08 and 0.65 stems m^2 in the coastal and inland zones respectively. Juvenile densities are very low for both zones, but extremely low in the coastal zone. In brief summary, compared to the inland zone, the coastal zone had fewer species and lower density of juveniles.

The most common tree species in the coastal zone include *Bombacopsis quinata* (Bombacaceae), *Calycophyllum candidissimum* (Rubiceae), *Hyperbaena tonduzii* (Menispermaceae), and *Attalea butyracea* (Arecaceae). *Brosimum alicastrum* (Moraceae), *C. candidissimum,* and *Trichilia martiana* (Meliaceae) are the most common species in the inland zone (Lindquist and Lieberman 2003). Two vines, *Bauhinia sp.* (Fabaceae/Caesalpinioideae) and *Adenocalymna inundatum* (Bignoniaceae), are also very abundant in the coastal zone.

Crab distribution and densities

Gecarcinus quadratus se Saussure (Gecarcinidae), the Harlequin land crab, lives and forages in coastal forests along both the Atlantic (Florida to Guyana in northeastern South America) and Pacific (Mexico to Peru) coasts of the Americas, and may be synonymous with *Gecarcinus lateralis* Freminville (Burggren and McMahon 1988*)*. The terrestrial hermit crab, *Coenobita compressus* (Pagaridae), is also found on both Neotropical coasts, but their range from the shoreline is much more limited than that of the land crab.

In our study area, large populations of the fossorial Harlequin land crab, *G. quadratus*, and the terrestrial Hermit crab, *C. compressus* are present. Land crab burrows are present from the coastline to approximately 500 m inland with densities decreasing with distance from shore (from on average 3 crabs m^{-2} in the coastal zone to 1 crab m^{-2} in the inland zone). Terrestrial hermit crabs are absent from the inland zone.

Experimental plot design

In both the coastal and inland zones, experimental plots were located under two levels of forest canopy cover: natural light gap, and adjacent non-gap. Using a densiometer, 14 light gaps and non-gap paired plots (7 in each zone) were selected, and represented low and high levels of the natural range of canopy cover found in the study area (using randomly located transects to get baseline levels). The light gaps varied in ground area ($15m^2$ to $120\ m^2$) and percent canopy cover (Table 1) but did not differ in canopy cover between the inland and coastal zones.

Depending on the size of the light gap, 2 to 4 pairs of exclosure and control sites (no exclosure) in each light treatment were randomly placed in the study plots with each site 2 m from its nearest neighbor. Sites in the gap and non-gap treatments were separated by approximately 10 m. Each cylindrical aluminum sheet metal exclosure was 0.3m tall and 1m in diameter, with its interior-face spray painted an opaque gray to minimize microclimatic changes inside the exclosures compared to outside. Differences in the temperature microclimate in the interior and exterior of the exclosures were not detected during mid-day 2 hr measurement intervals. Exclosures were stabilized with two wooden stakes, and the base of each exclosure was flush with the ground, with the sheet metal not extending belowground. On the few occasions when a crab entered an exclosure from belowground, that particular exclosure observation was removed from the exclosure treatment database.

Exclosure treatments were designed only to exclude land and hermit crabs. Both species of crab can climb vegetation, wooden poles, and other rough materials that provide foot and claw holds (Lindquist personal observation). We used smooth sheet metal instead of mesh fencing to prevent crabs from climbing the exclosures. Other potential seed predators and seedling herbivores such as mammals and insects had access to seeds and seedlings inside the exclosures by stepping, jumping, bending, or flying over the 0.3 m tall exclosure. It's important to note here that no small mammals were trapped in the study area in three years of trapping in the wet and dry seasons (Bob Timm, unpublished data). Terrestrial crabs appear to exclude small mammals in areas where they have high densities (Bob Timm, personal communication).

During the establishment of the plots very little vegetative cover was altered. After the exclosures were in place, we ensured the absence of crabs inside the exclosures at the beginning of each experiment with two nights of Sherman live-trapping in each exclosure. If a crab was trapped, it was removed from the site, its hole covered up, and the trap was open for an additional two nights for that site.

In 2002, the second year of the study, we used two additional types of exclosures as procedural controls to test for any indirect effects of the exclosure and open control treatments. To test the validity of the open control treatment, we added a new control treatment with elevated metal exclosures 5 cm above the ground to allow crabs and other small animals to enter from below. Also, to minimize potential adverse effects on seedling survival and growth, we used exclosures with the same aluminum sheet metal used in the other exclosures in the upper half of the structure only (15 to 30cm above ground), and chicken wire mesh (square holes = 25 mm^2) in the lower half to allow more mixing of air, water, and soil between the interior and exterior of the exclosures. These new exclosures and controls were placed in the plots following the same methods as the others.

Seed removal

We used seeds of three native tree species that varied in their seed size, mode of dispersal, successional growth strategy, and distribution in the study area (Table 2). Seeds were collected from several sources to capture the normal range in seed quality. Dry *Terminalia oblonga* seeds from 5 parent trees within the study area were collected just after falling to the ground (no visual evidence of insect or fungal attack) in February 2001. Dry *Enterolobium cyclocarpum* seeds and *Anacardium excelsum* seeds were received from the CACH Forestry Seed Bank in Hojancha, Costa Rica (approx. 35 miles north of the study area) in July 2000. All 3 species naturally set and disperse fruit in the study area during the dry season when the experiments were conducted.

In the dry season of 2001 (15 Jan 01 to 1 March 01), 6 treatments were selected and divided among 144 sites (2 forest zones x 2 canopy cover levels x 2 predation levels x 18 replicates). In the dry season of 2002 (21 Feb 02 to 21 March 02), 6 treatments were selected and divided among 48 sites (1 forest zone x 2 canopy cover levels x 3 predation levels x 8 replications). One seed of each species was placed in each exclosure and control, 20 cm apart from any other seed in each. Leaf litter and debris were removed from each site in order for the status of the seed (removed/ not removed) to be clearly and easily censused. Seed removal was censused on days 1, 2, 4, 6, 9, 13, 18, 23, 29, 36, and 46 in 2001, and days 1, 2, 5, 7, and 28 in 2002. Seeds were marked as removed if $\geq$ 50% of the seed was gone from the experimental site. When a seed was not present at the site, we searched for it within a 5m radius of its original location, but on no occasions was the removed seed found. We equate removal of the seed from the site to its mortality because it was most probably consumed or buried deeply by crabs (their holes are at least 1 m in depth).

Seedling establishment: survival and growth

We transplanted seedlings of 7 different species and various ages from a common-garden to the experimental plots in the wet seasons of 2001 (9 Aug 01 to 4 Dec 01) and 2002 (14 June 02 to 24 July 02). Tree species were selected for the experiments because of their seed availability, and to embrace a range in: seed/seedling size, mode of dispersal, successional growth strategy, and distribution in the study area (Table 2). Seedlings were germinated in a common-garden before transplantation. Seeds of *Anacardium excelsum* and *Enterolobium cyclocarpum* were scarified with sandpaper and placed in a 1:10 bleach/water for 12 hours to break the hard seed coat and encourage rapid germination. Until germination, seeds were placed in Jiffy-7 Peat Pellets, and then transplanted after germination (minimum of two days) to black plastic forestry seedling bags (10 cm^3) with drainage holes. We filled the bags with a 50:50 soil mixture of Jiffy peat and sifted sand from the upper beach of the study area. Seeds and seedlings were watered either by natural rainfall or manually with non-chlorinated spring water when needed to prevent wilting.

Seedlings were transported to the study plots after the following post-germination times: 2 days (Age 1 class), 7 days (Age 2 class), and 255 days (Age 3 class) in 2001; and 2 days (Age 1 class) and 7 days (Age 2 class) in 2002. For any experiment, all seedlings were planted into the experimental plots on the same day no matter their age, species, or location. The bags containing the seedlings were placed in the ground at each site so that the lip of the bag was flush with the ground. Each seedling was labeled with a white plastic pot tag inserted into the seedling bag for identification during the censuses. Upon transplantation, the seedlings' stem length was measured from ground to apical meristem, and leaf number was noted. Stem length and leaf number were not measured for those young seedlings without a stem (Age 1 class in 2001 and 2002). In subsequent censuses of the seedlings, stem length and number of leaves were measured with the same protocol on days: 3, 14, 31, 71, 91, 118 in 2001; and 1, 3, 7, 14, 22, 30, 40 in 2002.

Seedling growth experiments

In 2001, 24 seedlings each of 3 species (*Cordia collococca*, ht = 5.5 cm ± 1.5; *Inga vera*, ht = 8.8 ± 2.2; and *Plumeria rubra*, ht = 11.4 cm ± 1.6) that vary in their distribution in the study area, growth strategy, and mode of dispersal (Table 2) were dug up and randomly transplanted into experimental exclosure and open control sites in the coastal and inland zones not used for the other experiments (6 replicates of each treatment combination). These sites were all situated randomly with respect to canopy cover. Seedlings of each species were collected from 2 to 4 parent trees in the study area, and their stem heights and diameters were approximately equal upon collection. Seedlings were potted in black seedling bags with the soil medium of their transplantation site. At each measurement census (days 0, 2, 5, 10, 22, 40, 80, 100, and 127) seedling stem height above the ground and leaf number were recorded.

Statistical Analyses

Survival rates (or the inverse removal rates) of seeds and seedlings for all experiments among all treatments were compared using Cox Regression Survival Analyses (JMP 4.0) with an accelerated failure-time model (Allison 1995, Fox 2001: called the parametric survival fitting model in JMP 4.0 and equivalent to the PROC LIFEREG in SAS 6.0) with a Weibull distribution. Because the shape of the survival curve was expected to be affected by the treatment covariates, we used the accelerated failure-time model that considers the timing of mortality (or high hazard; Fox 2001). The other regression model, proportional hazards, is best used only when the probability of failure will be affected by the different treatments. To assess significance of differences among treatments we used the Wilcoxon x^2 test statistic, rather than the Log Rank x^2 test statistic, because it puts more weight on the early survival times to emphasize the typically rapid effect of the crab exclosure treatment. All significant interactions among treatments were included as model main effects. To compare between treatment levels, we used simple Survival Analysis contrasts (JMP 4.0;

equivalent to PROC LIFETEST in SAS 6.0) and Bonferroni corrections (adjusted P-value = 0.05/ number of contrasts).

To compare growth patterns between the experimental treatments, particularly for the gap/non-gap treatment, we divided the seedlings that survived until the end of the experiments into two groups: (1) "no growth" for those with negative or zero net growth and (2) "growth" for those with positive net growth. We compared the effects of our treatments on growth (no growth versus growth) with contingency tests using Pearson's x^2 test statistic.

To compare seedling growth among the age and species classes for those seedlings that survived until the end of the experiments and had positive net stem height growth, we conducted Kruskal-Wallis rank sum tests for two parameters: relative stem height growth rate (RHGR) and leaf growth rate (LGR).

Results

Seed removal

In the 2001 experiment, from the Parametric Survival Cox regression analysis we found that both presence of crabs and forest zone affected the number of seeds remaining over the duration of 46 days (Table 3). As predicted, the proportion of seeds remaining in the crab exclosures was higher than that in the unprotected controls (Figure 1), and seed removal was more rapid in the coastal forest zone than in the inland forest zone (Table 3). Canopy cover did not affect seed removal rates (Table 3). There was no difference in the removal rates among the three seed species (Figure 1; Table 3). Two interactions were also significant: (seed species x forest zone x canopy cover) and (crab treatment x seed species x forest zone x canopy cover) (Table 3).

In the 2002 experiment, the results were similar: (1) the crab exclosure treatment affected the rate of seed removal, with the seeds in the open controls removed more rapidly than those in the solid crab exclosure treatment (Figure 2; Table 3;); (2) no survival differences in regards to canopy cover; and (3) no survival differences among the three species (Table 3). Although the rate of seed removal in the elevated control did not differ from either the open treatment or the exclosure treatment (Table 3), it did lie between the two other failure rates (Figure 2). The two covariates in the experiment, canopy cover and seed species, did not affect removal rates of the transplanted seeds (Table 3).

Seedling establishment: Survival and growth

A. Seedling Age 2001 Experiment

In the 2001 experiment where we transplanted *Enterolobium cyclocarpum* seedlings of three ages into the coastal and inland gap/non-gap plots, we found that not only did the exclosure treatment affect seedling survival, but all covariates in the experiment also affected seedling survival rates: forest zone, canopy cover, and age of seedling (Table 4). As predicted we found that seedling mortality rates were higher: (1) in the control treatments compared to the exclosure treatments, (2) in the coastal zone compared to the inland zone, (3) in the non-gap compared to the gap sites, and (4) for the younger seedling age classes and decreased in each successive age class (Table 4). In addition, there were two significant interactions: crab treatment x canopy cover, and crab treatment x seedling age (Table 4).

Final seedling growth only varied between the three age classes (n= 32, df= 1, x^2= 8.727, *P*= 0.0127), not between forest zones (df=1, x^2= 0.142, *P*= 0.7061), crab treatment (df= 1, x^2= 0.970, *P*= 0.3248), or canopy cover (df= 1, x^2= 0.039, *P*= 0.8439) (Figure 3). When we assessed seedling growth rates in relation to canopy cover, we found a difference in the leaf growth rate (LGR) but not relative height growth rate (RHGR) (Table 5). In contrast, among the three age classes, RHGR differed but not LGR (Table 5).

B. Seedling Species 2001 Experiment

When we transplanted established seedlings of both *E. cyclocarpum* and *Bombacopsis quinata* into the coastal gap/non-gap plots, we found different results than in our 2001 seedling age experiment. The exclosure treatment did not affect seedling survival, nor did the covariate seedling species affect seedling mortality rate (Table 4). However, canopy cover did affect seedling survival rates, with survival rates higher in the gap sites than in the non-gap sites, as found in the experiment with different aged seedlings (Table 4). Canopy cover, however, did not affect growth (n= 44, df= 1, x^2= 0.074, *P*= 0.7857; Figure 3c). For those seedlings that experienced positive growth over the entire study, both RSHGR and LGR differed between the light gap and non-gap treatments (Table 5). With species, more *B. quinata* seedlings grew (75% of total) than *E. cyclocarpum* seedlings, especially in the gap, crab treatments (75% and 25% of initial total respectively). Yet, growth patterns (df= 1, x^2= 3.824, *P*= 0.0505; Figure 3c) and RHGR (Table 5) differed, but not LGR (Table 5). Finally, the growth patterns did not differ with the crab treatment (df= 1, x^2= 0.732, *P*= 0.3922; Figure 3c).

C. Seedling Establishment 2002 Experiment: Validating the experimental design

When testing the effects of the experimental exclosure design (open control and exclosure), we found no significant differences in seedling survival between the two control treatments (open control and lifted exclosure), and between the two exclosure treatments (solid sheet metal exclosure and half-mesh exclosure) as expected (Table 4). Moreover, the survivorships of individuals in both exclosure treatments were higher than those in the control treatments as expected (Figure 4), demonstrating the significant effect of crab predation on seed and seedling survival rates. In addition to crab presence, canopy cover affected the mortality rate of seedlings, with a higher failure rate for seedlings transplanted in the non-gap than compared to those in the gap sites (Table 4).

When we assessed stem growth patterns in the 2002 experiment, we found that, like survival, crab exclosure treatment (between the solid and mesh treatments) did not affect growth patterns (n= 25, df= 1, x^2= 0.337, *P*= 0.5615; Figure 4a,b) nor did canopy cover (df= 1, x^2= 1.963, *P*= 0.1612; Figure 4b). For those seedlings with positive stem growth, canopy cover only affected LGR, not RHGR (Table 5). Seedling age did affect growth (df= 1, x^2= 9.077, *P*= 0.0026; Figure 3a), along with RHGR but not LGR (Table 5).

Seedling growth experiments

A. Seedling Growth 2001 Experiment

When we translocated established seedlings from the study area into our experimental plots, we found that the exclosure treatment did not affect seedling survival, but that forest zone and seedling species did (Table 4). As we predicted, and seen in our other seed removal and seedling establishment experiments, seedling survival was greater in the inland zone than in the coastal zone (Table 4). Among the species, *Cordia collococca* experienced a higher failure rate than the other two species, *Inga vera* and *Plumeria rubra* (Table 4).

In the contingency analysis of growth we found no effects of the exclosure treatment (n= 41, df= 1, x^2= 0.997, *P*= 0.3179), forest zone (df= 1, x^2= 0.976, *P*= 0.3231), nor species (df= 2, x^2= 1.428, *P*= 0.4898) (Figure 5). Finally the growth rates, RSHGR and LGR, did not differ between the 3 species (Table 5).

Discussion

Seed removal

As we predicted, by limiting the availability of seeds to potential crab predation pressure, seed removal rates were significantly lower than for the unprotected seeds in both experiments (Figure 1, 2). Also as predicted, seed removal rates negatively correlated with the density of crabs; there was higher seed survival in the inland zone where *Gecarcinus quadratus* densities are significantly less and *Coenobita compressus* is absent. However, crabs may not differentiate among different species of propagule because we found no differences in removal rates among our three species. In addition we found no direct evidence that canopy cover indirectly affects seed removal rates by directly affecting crab foraging activity (Table 3), which agrees with the mangrove findings of Sousa and Mitchell (1999) but not Osborne and Smith (1990). Although we found no differences in seed survival among our gap/non-gap treatments and seed species (Table 3), the significance of interactions between crab treatment, seed species, forest zone, and canopy cover suggest that the magnitude of crab predation may not be entirely homogenous across microhabitats independent of crab density. In general, however, our findings agree with those past studies that found that crab predation is universally effective in removing seeds, and may have particularly damaging effects on plant recruitment in those coastal areas where crab densities reach extraordinarily high levels (Smith et al. 1989, Green et al. 1997, Sherman 2002).

Seedling establishment

From our four experiments with transplanted seedlings grown from seed we found, as predicted and similar to the findings from the seed removal experiments, that seedling survival was affected by varying crab consumption pressure: it was higher in the inland zone than in the coastal forest, and higher for older seedlings than for the younger ones (Table 4). However canopy cover also influenced seedling survival. The variation in canopy cover between the gap and non-gap plots could have caused microclimatic variation in solar radiation (Ostertag 1998), air temperature (Everham et al. 1996), soil temperatures (Pearson et al. 2002), and soil matric potential (Veenendaal et al. 1996). Our results reveal the importance of assessing multiple factors when determining the effect of any one potentially important variable.

In both the 2001 and 2002 seedling establishment experiment, the Age 1 and Age 2 seedling classes experienced far more predation pressure than the Age 3 class (Table 3). We believe crabs may be more attracted to the seed and young cotyledon seedling stages because of their higher nutritional reward. One of the most limiting nutrients in the diet of the omnivorous land crabs is nitrogen (Wolcott 1988), which is concentrated in seeds and young seedlings (Garwood 1996). Thus if a seedling is able to escape early crab predation, it may reach a size refuge from predation, and be subjected to other potential environmental and biological limiting agents, such as light availability.

In the seedling establishment study comparing species, both *B. quinata* and *E. cyclocarpum* survived better in the canopy gaps than in the non-gap sites (Table 4), a trend seen in the majority of past tropical tree/shrub seedling transplantation studies (Denslow et al. 1990, Boot 1996, Ashton et al. 1995, Kobe 1999, Turner 2001). Similarly, past studies show a correlation between seedling height growth and the light environment (Clark et al. 1993, Lieberman et al. 1990, Turner 1990b). But undeniably there is a gradient of seedling responses to light with some shade-tolerant understory species showing little difference in survival between gap and non-gap sites (Fraver et al. 1998). One must consider when interpreting our results that the two species we used are known to be light-demanding species commonly found in open sites and therefore may lie at the other end of this continuum.

Even though we found no effect of canopy cover on promoting growth, when we looked at only those few seedlings (n= 28) that had positive growth, there were higher stem and leaf growth rates in the gap than the non-gap sites (Table 5). There was some variability, however, among the species and experimental plots. *E. cyclocarpum* grew faster (more height increase per day) than *B. quinata*, especially in light gaps. Furthermore, the significant 3-way interaction between canopy cover, seedling species, and experimental site suggests to us that the two species had different growth responses to light and that these responses may also have varied among the different plots. Our inconclusive growth findings may thus be due to small sample sizes. Yet, the fact that we had only a few seedlings survive the intense crab consumption pressure and low light levels, demonstrates the importance of these two factors for plant recruitment, and diminishes the effects of any factors affecting growth after these initial mortality factors at the seed and young seedling stages.

Seedling growth experiment

When we translocated seedlings from the study area into our seedling growth experiments, we found that crab herbivory did not have an affect on seedling survival or growth, nor did these responses vary among the three species used (*Cordia collococca*, *Inga vera*, and *Plumeria rubra*) (Table 4, Figure 5). These findings agree with those from the seedling establishment experiments for the Age 3 seedlings; established seedlings of 5 months or older appear to be unaffected by crab predation.

We also found that seedling survival and growth were not related to the species adult distribution. If crab consumption pressure was the primary factor affecting the shift in tree species composition between the coastal and inland forests, as hypothesized by the dominance predation model, we would expect differential predation on species, inversely related to that species' abundance (Smith et al. 1989). Although *I. vera* did experience positive stem height change on average in the exclosure treatments only in the inland zone where it's predominantly found as an adult and has high juvenile density (Figure 5), its survival and growth did not significantly differ between the two forest zones. Both *C. collococca* and *P. rubra* experienced similar mortality and growth rates in the two zones, irrespective to their adult distributions (Table 2).

Because we found that crab predation pressure has more impact at the seed and young seedling stage in the seed removal and seedling establishment experiments, crabs may still have some differential influence on tree species distribution. However, the fact that we found no differential crab preference for seeds in the removal experiments, suggests that crabs alone may not regulate the observed shifts in forest composition.

Relative role of predation pressure in structuring forests

All of our experiments in this study, with the exception of the seedling growth experiment with older translocated seedlings, show clear evidence for the large impact of land crabs on seedling establishment. The majority of seeds and seedlings in the open or elevated exclosure treatments perished while those protected from crab predation pressure encountered far lower mortality rates. We thus believe that crab predation pressure plays a major role in limiting tree recruitment both in distribution and abundance, and explains much of the observed paucity in juveniles in the coastal forest, especially in the coastal zone. However, because species was not an important factor in our experiments even when we included wind dispersed species, we do not conclude that crabs differentially affect tree composition through species preferences. We suggest that species that produce copious amounts of seeds, such as the wind dispersed species dominating the coastal zone, may escape crab predation through quantity not quality of seeds.

A growing number of studies, like ours, demonstrate that animals as predators have large effects on plant recruitment (Smith et al. 1989, Molofsky and Fischer 1993, Terborgh and Wright 1994, Green et al. 1997, Sherman 2002). Because most animal predation and herbivory, like that of crabs, occurs typically in the seed and early seedling stages, it may have primacy in determining species establishment over other biotic and abiotic conditions at the establishment stage. However, it is important to not ignore other potentially important mechanisms such as adaptation to environmental conditions and competition (Louda 1989, McKee 1995a, McKee 1995b, McGuinness 1997). Our study shows clear evidence for the effect of canopy cover variability on seedling establishment for those propagules that escape mortality by predation. Our study, thus, emphasizes the need for ecologists to incorporate multiple factors into their experimental designs to elucidate a better understanding of the relative importance of the hypothesized mechanisms causing species distribution shifts and abundances.

Acknowledgements

Our work was supported by the NSF Dissertation Improvement Grant (DEB-0104791), Sigma Xi, and various field and travel award grants from the University of Georgia given to Erin Lindquist. We are grateful to the Costa Rica MINAE administration of San Miguel Biological Station, Cabo Blanco Absolute Nature Reserve for allowing this study to be conducted in such a restricted area, and expressing interest in the study's findings. This study wouldn't be possible without the unselfish field help of numerous field assistants, with particular thanks to Kerry Brewster for her painstaking dedication to every seedling in our study dead or alive. We would also like to thank Marcelo Ardón, Bob Cooper, Mark Hunter, Diana Lieberman, Al Parker, and Chris Peterson for their comments on earlier versions of the manuscript.

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Table 1. Percentage canopy cover of the gap and non-gap sites within the plots of the seed removal and seedling establishment experiments.

	n	Mean ± SD	Range
Coastal zone			
Gap sites	6	74% ± 5.4	67 – 82%
Non-gap sites	6	88% ± 1.0	86 – 89%
Inland zone			
Gap sites	4	77% ± 3.5	75 – 80%
Non-gap sites	4	89% ± 4.6	88 – 91%

Table 2. List of tree species used in the seed removal and the seedling establishment experiments. Family name, successional stage of prevalent recruitment, seed dry weight (n= 20), and dispersal mode (anemochorous= wind-dispersed, zoochorous= animal-dispersed) are given.

Scientific Name	Family	Growth strategy	Distribution	Dry Wt (g)	Dispersal Mode	Experiments Included
Anacardium excelsum	Anacardiaceae	late	Inland zone	3.2	animal	Seed removal Seedling establishment
Bombacopsis quinata	Bombacaceae	early	Coastal zone, Inland zone	0.045	wind	Seedling establishment
Cordia collococca	Boraginaceae	early	Coastal zone, Inland zone	NA	wind	Seedling growth
Enterolobium cyclocarpum	Fabaceae/ Mimosoidadae	early	Coastal zone, Inland zone	3.2	animal	Seed removal Seedling establishment
Inga vera	Fabaceae/ Mimosoidadae	late	Inland zone	NA	animal	Seedling growth
Plumeria rubra	Apocynaceae	early	Coastal zone	0.37	wind	Seedling growth
Terminalia oblonga	Combretaceae	early	Coastal zone, Inland zone	0.040	wind	Seed removal

Table 3. Results of Cox regression survival analyses for the seed removal experiments testing for effect of crab exclosure treatment, canopy cover, forest zone, and seed species on seed removal rates. Only significant interactions are included. Simple survival contrasts between treatments were calculated using the Bonferroni correction.

I. Seed removal experiment 2001

	df	**x^2**	**Contrast**
Total Model	9	94.9***	
Crab Exclosure	1	73.4***	
Open control			>
Solid exclosure			<
Canopy cover	1	0.0679	
Light Gap			
Non-gap			
Forest zone	1	28.3***	
Coastal zone			>
Inland zone			<
Species of Seedling	2	3.58	
Anacardium excelsum			
Entelobium cyclocarpum			
Terminalia oblonga			
Canopy x Forest x Species	2	6.8***	
Crab x Canopy x Forest x Species	2	15.5***	

II. Seed removal experiment 2002

	df	**x^2**	**Contrast**
Total Model	5	14.1*	
Crab Exclosure	2	13.3**	
Open control			a
Solid exclosure			b
Elevated exclosure			ab
Canopy cover	1	0.0273	
Light Gap			
Non-gap			
Species of Seedling	2	0.767	
A. excelsum			
E. cyclocarpum			
T. oblonga			

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, P-values calculated from the Wilcoxon x^2 test statistic

Table 4. Results of Cox regression survival analyses for seedling establishment experiment testing for effect of crab exclosure treatment, canopy cover, forest zone, seedling age, and seedling species on seedling survival for *Enterolobium cyclocarpum* (IA, IB, II), *Bombacopsis quinata* (IB), *Cordia colloccoca* (III), *Inga vera* (III), and *Plumeria rubra* (III). Only significant interactions are included. Simple survival contrasts between treatments were calculated using the Bonferroni correction.

	df	**x^2**	**Contrast**		**df**	**x^2**	**Contrast**
I. Seedling establishment experiment 2001				**II. Seedling establishment experiment 2002**			
IA. With Age							
Total Model	8	111***		Total Model	8	81.9***	
Crab Exclosure	1	17.8***		Crab Exclosure	3	67.4***	
Open control			<	Open control			a
Solid exclosure			>	Solid exclosure			b
Canopy cover	1	5.08*		Elevated exclosure			a
Light Gap			>	Mesh exclosure			b
Non-gap			<	Canopy cover	1	8.60**	
Forest zone	1	7.85**		Light Gap			>
Coastal zone			<	Non-gap			<
Inland zone			>	Age of Seedling	1	3.26	
Age of Seedling	2	63.7***		Germinated (Age 1)			
Germinated (Age 1)			a	Cotyledon (Age 2)			
Cotyledon (Age 2)			b	Crab x Canopy	3	20.1***	
Established (Age 3)			c				
Crab Treatment * Canopy	2	15.7***					
Crab Treatment * Age	1	5.58*		**III. Seedling Growth Experiment 2001**			
IB. With Species				Total Model	4	19.5***	
Total Model				Crab Exclosure	1	0.400	
Crab Exclosure	3	16.6***		Open control			
Open control	1	0.152		Solid exclosure			
Solid exclosure				Forest Zone	1	6.71**	
Canopy cover		14.6***		Coastal zone			<
Light Gap	1		>	Inland zone			>
Non-gap			<	Species of Seedling	2	13.9***	
Species of Seedling				*Cordia colloccoca*			a
B. quinata	1	1.66		*Inga vera*			b
E. cyclocarpum				*Plumeria rubra*			b

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, P-values calculated from the Wilcoxon x^2 test statistic

Table 5. Comparative statistics for relative stem height growth rate (RHGR) and relative leaf growth rate (RLGR) in seedling establishment (A, B) and seedling growth (C) experiments. Only seedlings that had positive stem height growth at the termination of the experiment are included here.

	RHGR (mm mm^{-1} day^{-1})				**LGR (leaves day^{-1})**			
Treatment Level	**n**	**Mean**	**SD**	**Kruskal-Wallis**	**n**	**Mean**	**SD**	**Kruskal-Wallis**
A. 2001 Seedling Establishment								
AI. With Age								
Age								
Age 1	8	3.80	1.23	df=2, x^2= 14.4	8	0.0795	0.0622	df=2, x^2= 4.63
Age 2	1	0.022	.	*P*= 0.0007	1	0	.	*P*= 0.0989
Age 3	11	0.00945	0.0144		11	0.0263	0.0317	
Canopy cover								
Light Gap	13	2.00	2.11	df=1, x^2= 6.26	13	0.0483	0.0503	df=1, x^2= 0.159
Non-gap	7	0.656	1.73	*P*= 0.0123	7	0.0424	0.0604	*P*= 0.690
AII. With Species								
Species								
B. quinata	19	0.0358	0.0318	df=1, x^2= 3.40	19	0.00308	0.0143	df=1, x^2= 7.39
E. cyclocarpum	9	0.0212	0.0323	*P*= 0.0651	9	0.0207	0.0169	*P*= 0.0066
Canopy Cover								
Light Gap	22	0.0373	0.0332	df=1, x^2= 6.07	22	0.0128	0.0159	df=1, x^2= 5.71
Non-gap	6	0.0085	0.0126	*P*= 0.0138	6	0.00620	0.0132	*P*= 0.0066
B. 2002 Seedling Establishment								
Age								
Age 1	15	5.94	0.730	df=1, x^2= 7.39	15	0.137	0.0773	df=1, x^2= 0.0043
Age 2	8	0.397	0.999	*P*= 0.0066	8	0.144	0.0623	*P*= 0.0168
Canopy cover								
Light Gap	20	4.21	3.97	df=1, x^2= 0.208	20	0.015	0.0661	df=1, x^2= 4.31
Non-gap	3	2.67	3.36	*P*= 0.648	3	0.0583	0.0520	*P*= 0.0378
C. 2001 Seedling Growth								
Cordia colloccoca	4	0.0281	0.0123	df=2	4	0.00582	0.0162	df=2
Inga vera	5	0.0175	0.0090	x^2= 3.03	5	0.00005	0.0111	x^2= 0.664
Plumeria rubra	5	0.0131	0.0109	*P*= 0.133	5	-0.0015	0.0187	*P*= 0.718

Figure 1. Proportion of dry seeds remaining in the 2001 seed removal experiment among the crab and control treatments and three species of seeds. Values are proportion remaining of total, and bars are standard errors for each treatment estimated by Cox Regression Analysis. Solid lines represent crab exclosure treatments and dotted lines are crab control treatments. Simple contrasts among the crab treatments were calculated using simple survival contrasts with Bonferroni corrections.

Fig 1, Chap IV
Lindquist

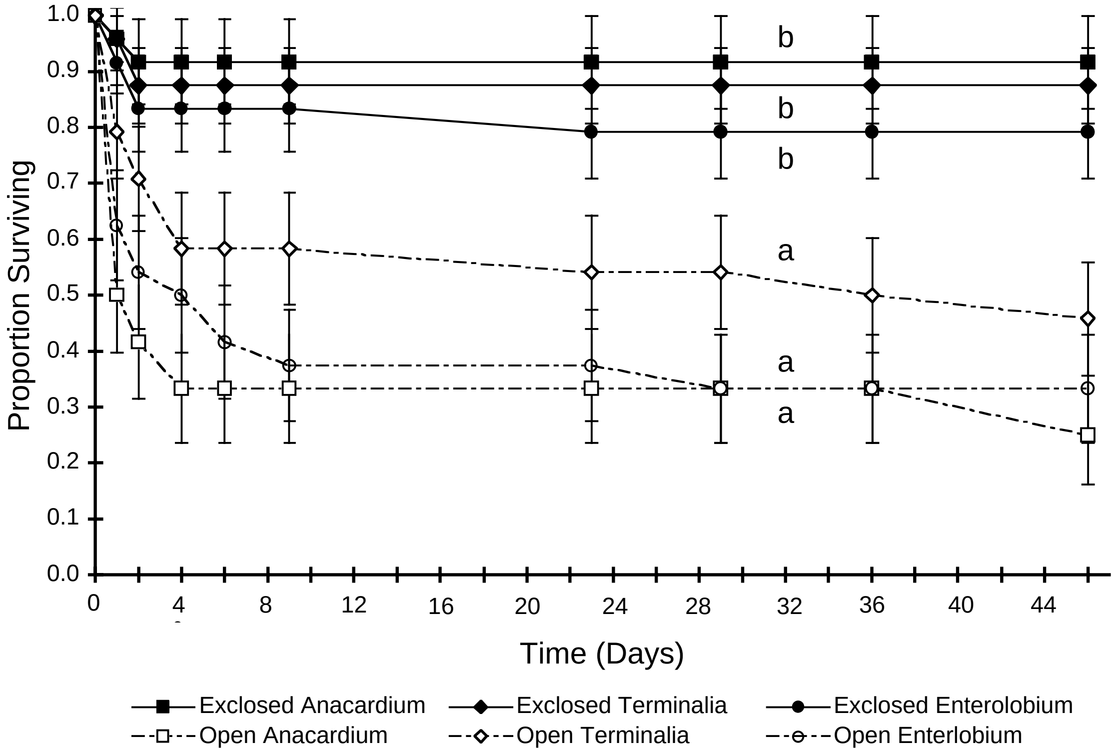


Figure 2. Proportion of dry seeds remaining in the 2002 seed removal experiment among the three crab exclosure treatments and three species of seeds (A, B, C). Values are proportion remaining of total, and bars are standard errors for each treatment estimated by Cox Regression Analysis. Solid lines represent crab exclosure treatments (solid exclosure) and dotten lines are crab control treatments (lifted exclosure and open exclosure). Comparisons among the 3 exclosure treatments were calculated using simple survival contrasts with Bonferroni corrections for the 3 species combined.

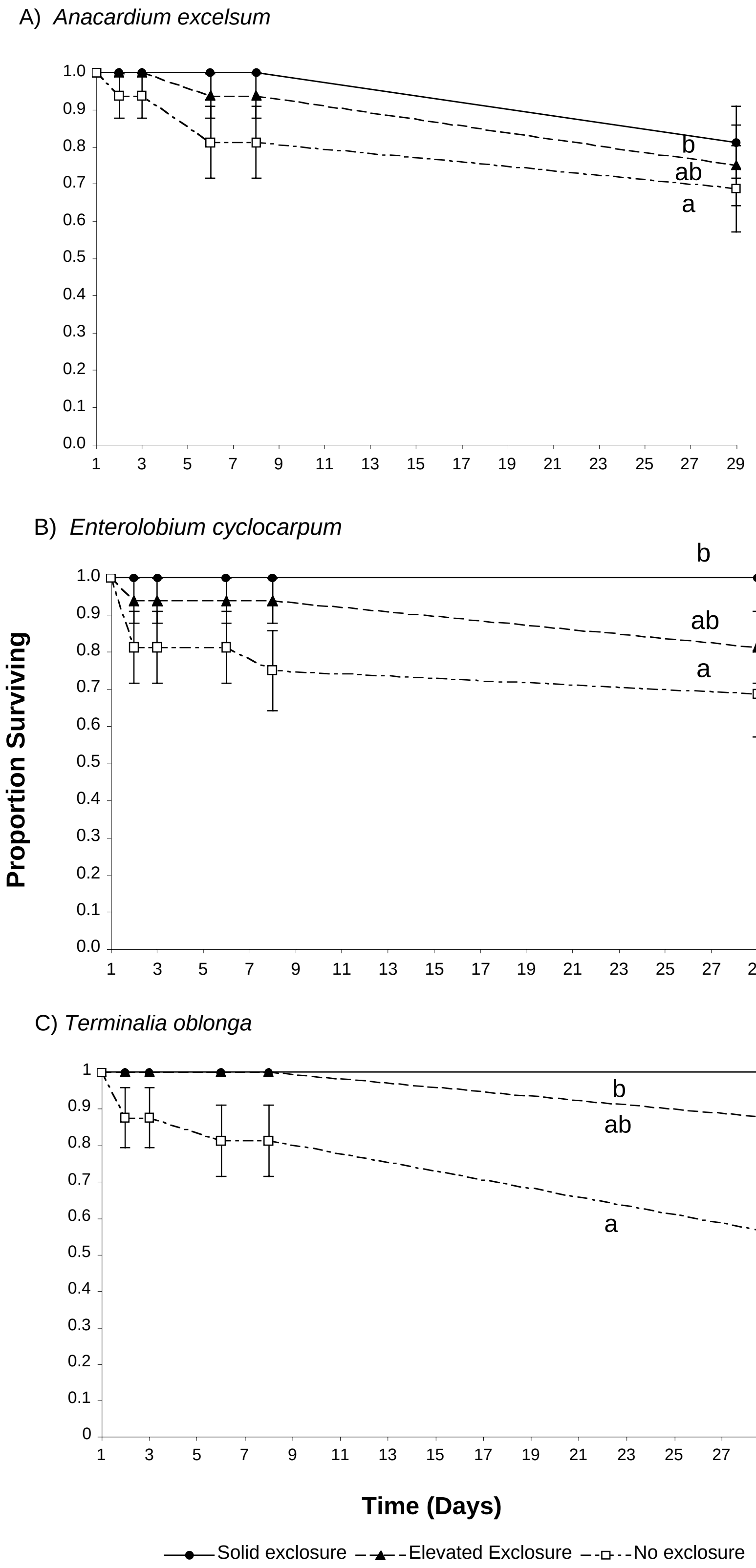
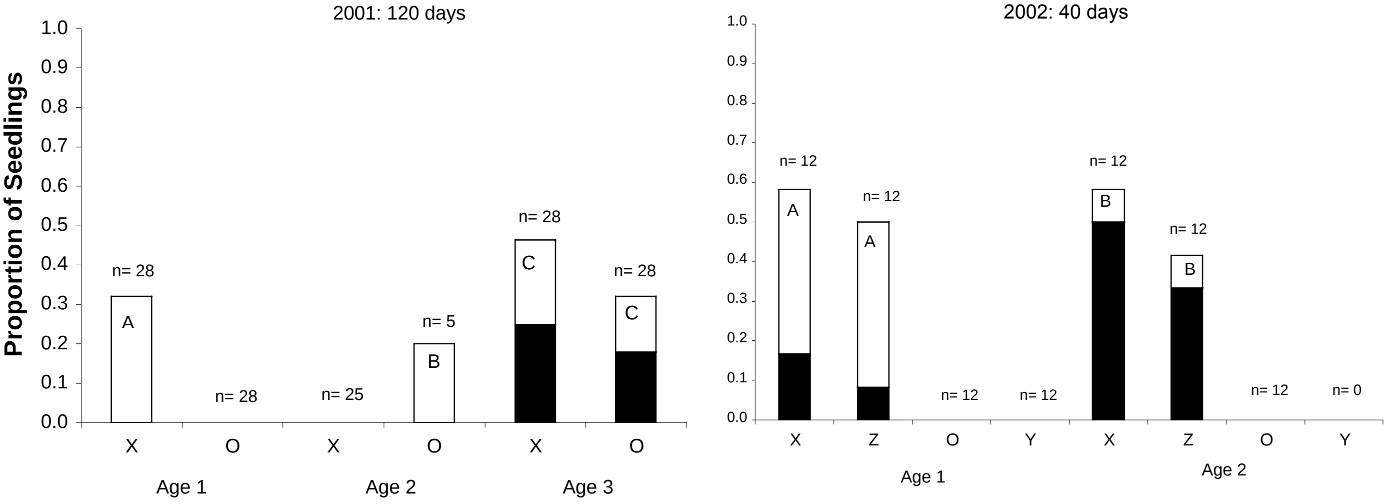
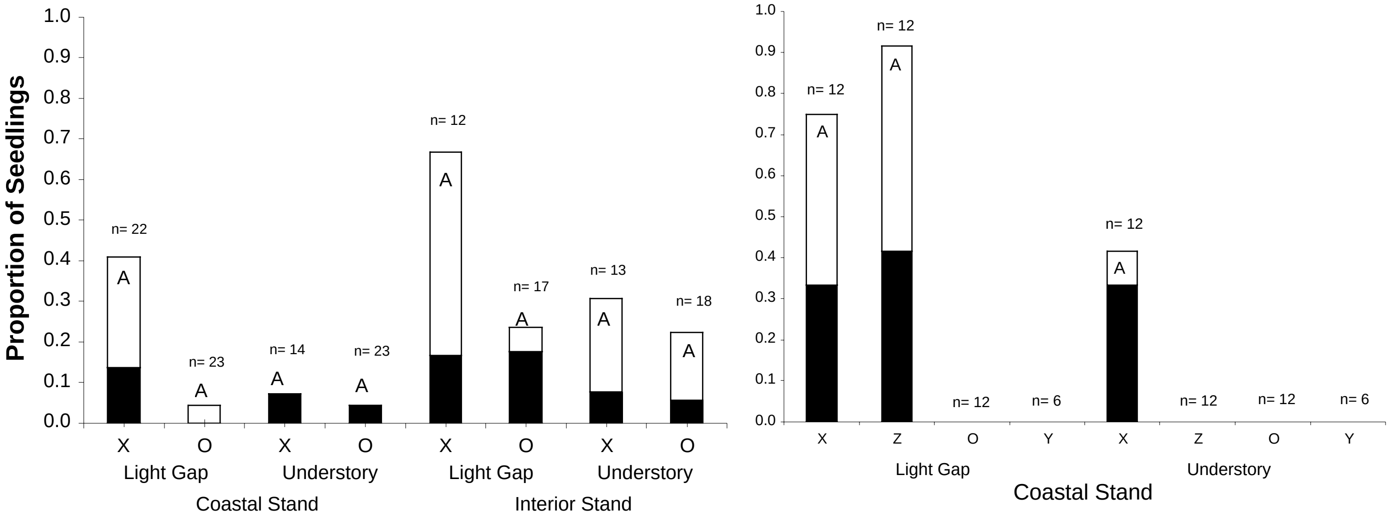

A) *Anacardium excelsum*
b
ab
a
B) *Enterolobium cyclocarpum*
b
ab
a
C) *Terminalia oblonga*
b
ab
a
Proportion Surviving
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
Time (Days)
—●— Solid exclosure
– –▲– – Elevated Exclosure
– -□- - No exclosure

Figure 3. Growth of seedlings that survived in 2001 (left side) and 2002 (right side) seedling establishment experiment. (A) Growth results in 2001 and 2002 experiments relative to the age class treatments (Age 1: 2 days old, Age 2: 7 days old, Age 3: 255 days). (B) Growth results in 2001 and 2002 experiments relative to forest zone and canopy cover treatments. (C) Growth results in 2001 in species experiment relative to canopy cover (coastal zone only). "No growth" (shaded bars) includes seedlings with negative or zero net growth, while "growth" (open bars) includes seedlings with positive net growth values only. The initial sample size for each treatment are given (including dead seedlings), and letters in the bars represent comparisons of growth (no growth vs. growth) within individual treatments from the X^2 Pearson Contingency Tests (trreatment levels that share the same letter are not significantly different in their growth patterns).

A) Age Experiment



B) With Age: Forest Stand and Canopy Cover



C) Species Experiment: Species and Canopy Cover

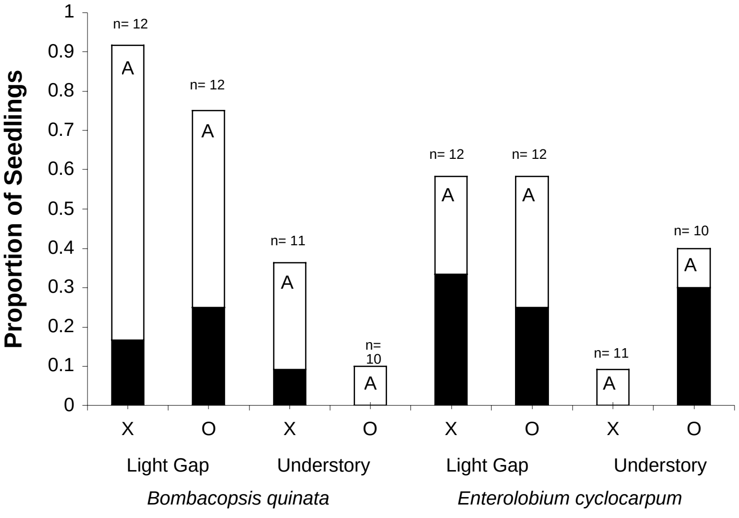


Figure 4. Survivorship of *Enterolobium cyclocarpum* seedlings in the 2002 seedling establishment study in the 4 crab exclosure treatments. Values are proportion remaining of total, and bars are standard errors for each treatment estimated by Cox Regression Analysis. Solid lines represent crab exclosure treatments and dotted lines are crab control treatments. Comparisons among the 4 treatments were calcuated using simple survival contrasts with Bonferroni corrections.

Fig 4, Chap IV
Lindquist

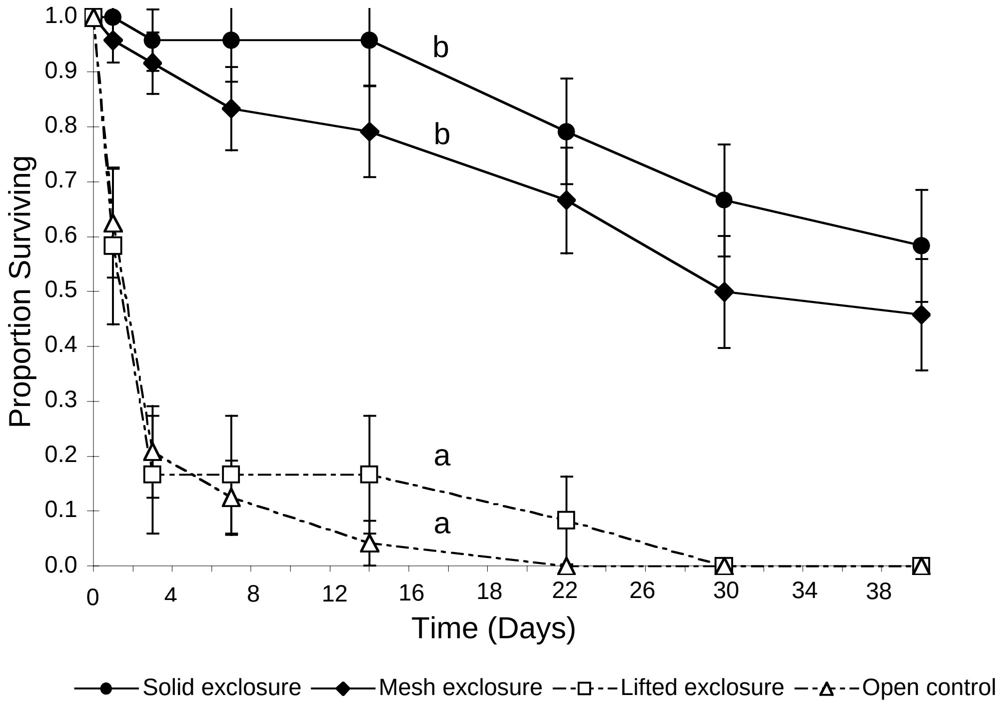
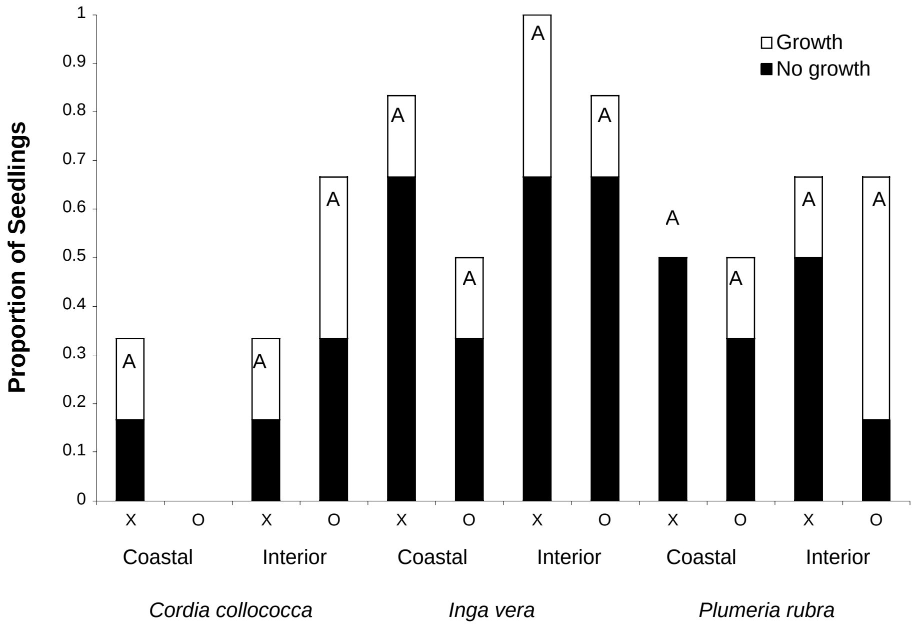


Figure 5. Growth of seedlings in 2001 seedling growth experiment of three species in two forest zones and two crab exclosure treatments (open control, open bars and solid exclosure, solid bars). "No growth" includes seedlings with negative or zero net growth, while "growth" includes seedlings with positive net growth values only. For all treatments, n=6. Letters in the bars represent comparisons of growth (no growth vs. growth) within individual treatments from the X^2 Pearson Contingency Tests (treatment levels that share the same letter are not significantly different in their growth patterns).

Fig 5, Chap IV
Lindquist



CONCLUSION

Whittaker (1975) stated "We can say something about a community by giving a list of its species composition, but a community is poorly described by such a list along." Connell and Slatyer (1977) described a community as "the set of organisms that occur together and that significantly affect each other's distribution and abundance. It is the interactions that make a community a unit worthy of study." These interactions include direct associations between species like competition, predation, and mutualisms, as well species' relationships with the environment. The purpose of this study, accordingly, was not only to examine the species composition of a coastal forest in Costa Rica, but also to investigate the interactions between the trees, their environment, and their natural enemies. The specific objectives of the study were to 1) describe the forest structure and tree recruitment patterns in the seed, seedling, sapling, and tree life stages, 2) compare these patterns to the environmental gradient in the coastal forest, and 3) determine the relative influences of crab predation pressure and canopy cover on seedling establishment.

Foremost, I found shifts in the forest structure and composition along the coastal gradient. Tree adult and sapling densities, species richness, and canopy height all were higher in the inland areas than in the coastal areas. Seedling densities did not differ between the two zones, but were relatively low throughout the study area. The coastal zone lacked recruitment in the sapling and small adult stem size-classes of all species whereas the interior zone lacked only small stems of several light-demanding canopy species. Several environmental and biotic variables correlated with distance from shore (altitude, soil texture, soil phosphorus content, soil pH, and land crab density). Only distance from shore, representing the complex environmental gradient, explained at least 20 percent of the compositional differences among adult plots in a NMS ordination. Secondly, seed rain composition varied both spatially and temporally, and did differ along the gradient Although most species' seed rain distributions were patchy, some species dispersed seeds over 50 m from the inland areas to the coastal areas. I found large pulses of seed rain occurring in the dry periods of both study years. Seed rain composition paralleled changes in tree composition with respect to the coastal gradient. These findings suggest that although seed rain is spatially restricted by the distribution of parent trees, tree recruitment in the coastal forest is not dispersal limited.

Finally, land crab predation hindered seed and seedling survival and growth. More specially I found: 1) crab predation pressure decreased with distance from shore proportional to crab densities, 2) seed removal and seedling survival rates did not vary among tree species, (3) crabs preferred seeds and younger seedlings over older seedlings, and (4) canopy cover affected seedling survival and stem height increment change.

From these findings, it appears that tree recruitment in the secondary coastal forest is not recruitment limited, but rather establishment limited. The seed rain effectively delivered tree propagules to the microsite, but after arrival microsite conditions (crab predation and canopy cover) hindered establishment. This study emphasizes the need for ecologists to incorporate multiple factors into their experimental designs in order to elucidate a better understanding of the relative importance of hypothesized interactions causing species distribution shifts and abundances.

A mere "snapshot" in the regeneration process of a coastal forest is presented here. Future work that follows the changes in forest structure and tree recruitment will provide indispensable information on the later stages of seasonal forest regeneration. These findings, present and future, will be of practical use in tropical and sub-tropical forest conservation and restoration efforts. The study provides land managers with the knowledge needed to encourage natural regeneration of tropical forests—especially seasonally dry forests—and actively restore a diverse tree community in deforested areas. Currently, there is an ecological urgency to establish biological corridors between existing forested fragments (Janzen 1988). Long-term research on patterns of regeneration, near and far from the coast, will help identify critical areas for these corridors. Once the land is protected, it will assist in the long-term monitoring and management of the ecosystem as its species composition and structure changes through time.

Finally, my collaboration with Area Conservación Tempisque, the faculty and students of the Universidad Nacional Autonoma (UNA), and the National Institute of Biodiversity (INBio) initiates an essential working research and educational relationship among individuals, private organizations, and public institutions of Costa Rica.

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