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Effects of land crabs on seedling densities and distributions in a mainland neotropical rain forest

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ABSTRACT. The land crab, *Gecarcinus quadratus* (Gecarcinidae), affects plant diversity in a mainland, neotropical rain forest through selective seedling consumption. In Costa Rica's Corcovado National Park, *G. quadratus* lives in fossorial populations with up to six crabs m^{-2} in coastal forest extending *c*. 600 m inland from the Pacific Ocean. A narrow transition zone (*c*. 30 m) separates the crab zone from the crabless zone that comprises the remainder of the 55 000-ha park. The composition of dicotyledonous plants from the adjacent zones were distinct: crabless zone transects (240 m^2) contained 97 species representing 76 genera and 41 families; crab zone transects contained 46 species representing 38 genera and 25 families. Despite the narrow zonal separation, the crabless zone shared only 27.4, 29.9 and 52.8% of its species, genera and families, respectively, with the crab zone; in contrast, crab zone transects shared 56.5, 60.5 and 88% of their species, genera and families with the crabless zone. This abrupt diversity gradient suggests a powerful selection pressure in the crab zone preventing the establishment of certain dicotyledonous species. Two years of experimental crab exclusion suggested that *G. quadratus* reduces seedling density and diversity. Densities of seedlings (3–25 cm tall) within exclosures increased 144% over baseline values while control densities decreased. In contrast, seedlings at the cotyledon stage and taller (26–50 cm) were unaffected by crab exclusion. Preference tests conducted in the crab zone revealed a five-fold ratio of mortality rates for seedlings transplanted from the crabless zone and crab zone respectively. However, when protected from crabs, transplanted crabless and crab zone seedlings survived similarly well over 6 mo (83 and 70% respectively). Together, data from transects and experiments suggest that *G. quadratus* influences plant community composition.

KEY WORDS: community composition, Corcovado National Park, Costa Rica, *Gecarcinus quadratus*, Gecarcinidae, land crabs, seedling predation, tropical rain forest dynamics

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INTRODUCTION

Over the years, theoreticians have proposed many varied mechanisms to explain the maintenance of high species diversities for tropical rain-forest plants. With the notable exception of the Janzen–Connell model (Janzen 1970, Connell 1971), surprisingly few of these theories have incorporated the role of animals (J. Terborgh *pers. comm.*). A majority of the many studies addressing the survival patterns of tree propagules have wisely focused on the influence of abiotic and biotic factors upon the earliest stages of tree propagation (seed dispersal, survival and seedling emergence). Most propagules, however, must persist in the dark forest understorey for months or years before appropriate abiotic conditions allow growth (Clark & Clark 1992). During this period, slowly developing propagules are particularly vulnerable to herbivory and predation (Huntly 1991) by insects (Gange *et al.* 1991, Robertson *et al.* 1990), mammals (Howe 1990, Osunkoya *et al.* 1993, Terborgh 1992, Terborgh & Wright 1994), or combinations of taxa (Terborgh *et al.* 1993). Typical of many studies of plant propagule survival, predation studies have also primarily addressed the seed or cotyledon stages of plant recruitment (Augspurger & Kitajima 1992, Forget *et al.* 1994, Itoh *et al.* 1995, Kachi *et al.* 1993, 1995; McKee 1995, Reader 1991, Reader & Beisner 1991, Terborgh *et al.* 1993, Wright 1990) with relatively less attention given to older seedling stages (Howe 1990, Schupp 1988, Sork 1987).

In many systems, however, macrofauna alter seedling population densities and community diversities long after the vulnerable cotyledon stage (Green *et al.* 1997, Hanley *et al.* 1995, Osunkoya *et al.* 1993, Sork 1987, Terborgh & Wright 1994, Thomson *et al.* 1996, Turner 1990). In locations where seedlings must survive extended periods of predation pressure, predator density and predation intensity can affect probabilities of seedling survivorship (Green *et al.* 1997, Molofsky & Fisher 1993, Terborgh & Wright 1994). Under moderate predation pressures, seeds may be able to escape predation by germinating at a distance from the parent. Mechanisms such as this may well contribute to a higher plant diversity. However, when predation pressures on seeds and seedlings are high and predators ubiquitous, we might expect predation pressure to decrease tree diversity.

For example, voles, *Microtus pennsylvanicus*, with densities up to 380 ha^{-1}, selectively devastated populations of enclosed tree seedlings in less than 1 y (Ostfeld & Canham 1993). Most studies of forested systems, however, address substantially lower predator densities. In contrast, land crab systems routinely support adult densities in excess of 10 000 individuals ha^{-1}. Land crabs of the family Gecarcinidae are shown here to represent a potentially significant selection pressure for seedling populations in a primary tropical rain forest on mainland Costa Rica.

Land crabs as seedling predators

In many tropical coastal rain forests, herbivorous land crabs (Gecarcinidae) conspicuously impact the local biological communities. With densities of land

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crabs commonly ranging from 7500 to over 50 000 crabs ha^{-1} (Costa Rica – P. Sherman, pers. obs.; Christmas Island – Green 1997, Hicks 1985, O'Dowd & Lake 1989; Veracruz, Mexico – Kellman & Delfosse 1993), few spatial or temporal avenues of escape may exist for preferred seedling species. Predation of seedlings by crabs may even dominate over other pressures influencing plant community composition (Green *et al.* 1997).

Nevertheless, despite the conspicuous presence of land crabs in many tropical coastal forests, their ecological role in the formation and maintenance of community composition and ecosystem dynamics has attracted surprisingly little attention. The majority of published work investigates other crab families (Sesarminae, Grapsidae and Ocypodidae) and their manipulation of leaf litter, plant propagules and the soil characteristics of the intertidal zones, mangrove communities and oceanic islands (Camilleri 1989, Clarke & Myerscough 1993, Emmerson & McGwynne 1992, Lubchenco *et al.* 1984, Louda & Zedler 1985, McIvor & Smith 1995, Micheli 1993, Robertson 1986, 1991; Robertson & Daniel 1989, Smith 1987a, b; Smith *et al.* 1991). Interestingly, the more we learn about Gecarcinidae the more we find that the various families play analogous ecological roles.

The published ecological work with Gecarcinidae and seed predation can be quickly and comprehensively summarized. Seed predation and dispersal by land crabs has only been documented in a few locations around the world. *Cardisoma carnifex* has been shown to disperse and consume seeds selectively in the central Pacific (Lee 1985, 1988), *Gecarcoidea natalis* in the Indian Ocean (Green *et al.* 1997, 1999; O'Dowd & Lake 1991) and *Gecarcinus lateralis* in the Gulf of Mexico (Garcia-Franco *et al.* 1991). Essentially, these studies implicate land crabs as potentially important seed predators. Another study, however, suggests that crabs do not significantly affect forest seed banks (Green *et al.* 1999).

Similarly, few studies have been published on the killing of seedlings by crabs of any species. Until recently, only anecdotal observations of crabs occasionally uprooting seedlings or negative associations between densities of crabs and seedlings were available (Alexander 1979 and Beever *et al.* 1979 with Sesarminae; Degener & Degener 1974 and Lee 1988 for *Cardisoma carnifex*.) Clark & Myerscough (1993) found that intertidal crabs of various unnamed taxa reduced seed survivorship of the mangrove *Avicennia marina*, but after 12 mo of exclusion experiments, the authors were unable to discern significant effects on seedling survivorship. In contrast, Robertson (1991) and Smith (1987a), compared the effects of sesarmid crabs on five different mangrove species and found that *Avicennia marina* was the most severely affected. McGuinness (1997) also found that crabs exerted severe predation pressures on mangrove propagules but that the selectivity of their predation was not predictable from an evaluation of adult tree dominance patterns.

The amount of work done on seedling consumption by Gecarcinidae is far more sparse; to the best of my knowledge, only four published studies exist.

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Only two of these studies are experimental and these both document strong effects of selective seedling consumption by *Gecarcoidea natalis* on Christmas Island, Indian Ocean (Green *et al.* 1997, O'Dowd & Lake 1990). The third study records observations of *Gecarcinus lateralis* consuming propagules of *Bromelia* spp. in Veracruz, Mexico (Garcia-Franco *et al.* 1991), and the fourth records negative correlations between densities of *Gecarcinus planatus* and young plants on Socorro Island, Mexico (Jiménez *et al.* 1994). Delfosse (1990) is a fifth unpublished study where preliminary data from exclusion plots suggest a negative impact of *Gecarcinus lateralis* on seedling densities in Veracruz, Mexico.

The work from Christmas Island remains the most compelling. In the first of the consecutive studies, O'Dowd & Lake (1990) transplanted four seedling pairs of seven species exposing one to, and protecting the other from, crabs. In the wet season, crabs killed or defoliated 28.6% of the 28 uncaged seedlings in 3 d. At the end of the dry season, crabs damaged or killed 35% of 74 uncaged seedlings. Crabs were found to be selective in their seedling predation during the wet but not the dry season. Additionally, the authors revealed negative correlations between seedling chemistry (total N, neutral detergent fibre and total phenolic concentrations) and crab predation rates providing a possible basis to seedling selectivity by crabs.

More recent work by Green *et al.* (1997) on the same population of crabs extends the initial findings of O'Dowd & Lake (1990). Using 25-m^2 experimental quadrats inside and outside of forest light gaps, Green *et al.* report that after 2 y, the exclusion of crabs resulted in large increases in seedling density and diversity relative to open control quadrats where few species survived. It seems that *Gecarcoidea natalis* strongly reduce some seedling populations while neglecting others. The authors suggest that *G. natalis* dominates the low-diversity forests of Christmas Island as a result of their density, biomass, and selectively intense impact on the vegetation. The authors hypothesize that wherever land crabs reach such high densities their impact on surrounding communities may be similarly strong. The data presented here strongly support this hypothesis.

In this paper, survey and experimental data are presented to document the effects of *Gecarcinus quadratus* de Saussure (Gecarcinidae) on seedling densities and distributions within a primary rain forest on mainland Costa Rica. Survey methods were used to test the hypothesis that the diversity of dicotyledonous plants would be relatively lower in forest areas where crabs live. Experimental exclosure and enclosure trials were used to test whether (1) seedling densities increase in response to predator-release from *G. quadratus* and (2) land crabs are selective in the species of seedlings they consume.

STUDY SITE AND SPECIES

Gecarcinus quadratus de Saussure (Gecarcinidae) lives in the coastal forests of the neotropics, and is considered by some authorities to be synonymous with

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Gecarcinus lateralis Freminville (Burggren & McMahon 1988, Turkay 1973). Populations of *G. quadratus* extend from Florida, through the Antilles down the Atlantic Coast of Central America to Guyana, and down the Pacific Coast of Latin America from Mexico to Peru (Burggren & McMahon 1988). My study was conducted at the Sirena Biological Station of Costa Rica's Corcovado National Park, situated on the Pacific's Osa Peninsula, between 8°27′ and 8°30′N and 83°25′ and 83°45′W. The region is described as tropical wet rain forest and it receives over 5 m of rain annually with individual storms precipitating over 350 mm of rain in under 12 h (Sirena station's data; Hartshorn 1983). Conditions support a forest canopy *c.* 30–70 m tall. The dry season extends from January to late March, during which time monthly rainfall ranges from *c.* 10 to 75 mm. The Osa Peninsula is known to have at least 2142 different plant species from over 185 families (Quesada *et al.* 1997) and a more recent estimate documents 2618 different species (R. Aguilar, *pers. comm.*) The Peninsula has one of the neotropic's most species-rich forests, partly because it is an area of overlap for the northern-most and southern-most extensions of many plant species, originating from the southern and northern hemispheres respectively. The study location is considered to be primary forest (R. Aguilar and O. Vargas, *pers. comm.*) and although limited selective removal of adult trees for local construction may have occurred before the area was designated a National Park in 1975, no physical evidence (stumps, mounds, light gaps without fallen trees etc.) remains to suggest recent interference.

Corcovado's forested coastline forms the southern and western extensions of the Park and supports large populations of the fossorial land crab *G. quadratus* (the only Gecarcinid in the immediate study area termed the 'crab zone'). At Sirena station, this crab zone extends inland from the beach *c.* 600 m at which point there is a steep transition into the 'crabless zone' representing the remainder of the Park's 55 000 ha plus the large forested regions beyond the park boundary. I define this transition region by the perpendicular gradient of crab burrows that ranges from 0 to 1 m^{-2}. The transition zone is often as narrow as 15 m. As one moves inland over the transition-zone gradient, soils shift rapidly from a bare, sandy substrate to a more dense, clay substrate that contains leaf litter accumulations > 15 cm and a thick superficial root mat (Sherman 1997).

In addition to land crabs, many animals inhabit or visit the coastal forests including white-lipped and collared peccaries, tapir, agouti, paca, coati, various rodents, curosow and tinamou. Whilst not renowned for their seedling consumption (M. Altrichter and C. Foerster, *pers. comm.*, Stiles & Skutch 1989), these animals could influence seed and fruit density and distributions and, thereby, seedling populations. To the best of my knowledge, however, the land crab is the only major seed / fruit / seedling consumer exclusive to the 'crab zone'.

Experiments were run in forest bordering the Sirena River Trail, where crab

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burrow densities ranged from 0.75 to 6.0 m^{-2}. In the study area just before the transition zone, adult crab densities ranged from 0.75 to 1.7 m^{-2} which represents an estimated biomass of 600 to 800 kg crabs ha^{-1} considering that body mass of an adult live crab for the two sexes averages (± SE) 78 ± 3 g. These estimates are similar to those made from Christmas Island (Green 1997, Hicks 1985).

The activity patterns of *Gecarcinus quadratus* follow regional seasonality. Two years of observations revealed that crab activity decreased with the onset of the dry season in early January, remained low until the first rains of the wet season, and then increased with the strengthening rains in late April. During the first rains of March, much of the population migrated towards the ocean to breed and foraging was limited. Crabs remained active above ground until late December and may show activity peaks during July and August (P. Sherman, *pers. obs.*). Contrary to all other personal, communicated, and published accounts from Costa Rica and elsewhere with which I am familiar, *G. quadratus* of Sirena Station is strictly nocturnal.

METHODS

Floristic diversities within and outside of the crab zone

To document the plant diversity inside and immediately outside of the crab zone, I set up four 30-m × 2-m transects in each of the two zones for a total of 240 m^2 of forest sampled per zone. All transects were run in the forest to either side of the Sirena River Trail. Within these transects, all dicotyledonous stems over 130 cm tall were counted and identified to species. Along each transect, a 3-m^2 circular subplot was established at 10, 20 and 30 m within which all seedlings were counted and classified to species (where possible) and to one of two size classes (3–30 cm and 31–130 cm tall). Crabless zone transects were run within 50 m of the transition zone. Crab zone transects were located 200 m closer to the coastline from the crabless zone transects. All plant identifications were made by expert botanists O. Vargas and R. Aguilar. All voucher specimens are lodged at La Selva Biological Station in Costa Rica.

After sampling from the two zones, as described above, I developed the hypothesis that certain seedlings – known to be consumed by crabs and found only in our crabless zone transects – would be negatively correlated with the density of crab burrows. Four plant species that fitted these criteria were selected: *Brosimum alicastrum* Sw. (Moraceae), *Lacistema aggregatum* (Bergius) Rusby (Flacourtiaceae), *Protium ravenii* D. Porter (Burseraceae), and *Sorocea cufodontisii* W. C. Burger (Moraceae). A fifth species that was known from transects to be abundant in both zones was selected as a control: *Piper reticulatum* L. (Piperaceae). To test the hypothesized negative correlation between certain plant species and crab burrows, we searched for these five species along five additional transects (each 30-m × 2-m) established across the transitional region between the crabless and crab zones. Transects were located such that

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the first 15 m contained no crab burrows, the first burrow was encountered at *c.* 15 m, and burrow densities increased to *c.* 1 m^{-2} by the 30-m mark (a subjective measure by which to define the beginning of the crab zone). Additionally, burrow densities in 2-m × 2-m contiguous increments were counted along the 30-m transects.

Crab exclusion experiment

To investigate whether crabs directly affect seedling densities and distributions, a randomized block design of 15 exclusion and control quadrats (25 m^2 each) was established within the crab zone. Quadrats were separated spatially throughout the crab zone into five blocks of three quadrats each. Each quadrat within a block was randomly assigned to one of three experimental treatments (fence-exclosure, fence-control and open-control) such that each block contained one quadrat for each treatment. The three quadrats in a given block were arranged at the points of an equilateral triangle with 5-m-long sides. The quadrats were symmetrically angled in towards the triangle's centre to standardize any potential inter-treatment effects. The five blocks were randomly spread along a 150-m line situated 400 m inland and parallel to the coast except that each block was separated from its nearest neighbour by >15 m. The fence-exclosure treatment was surrounded by a 0.5 m-high wire fence (mesh 2.5 cm × 1.25 cm) designed to exclude most herbivores larger than the mesh. Fencing material was buried at least 15 cm into the soil to deter crabs burrowing beneath. Crabs were removed from exclosure quadrats with Sherman live-traps and relocated > 200 m away. Exclosure quadrats were infiltrated by small numbers of crabs that climbed over the fencing requiring repeated trapping throughout the experiment. Thus, 'exclosures' actually represented regions of experimentally reduced crab densities rather than regions of zero crab density.

Two control treatments (fence-control and open-control) were used to account more effectively for potential effects of other forest animals (white-lipped and collared peccaries, tapir, agouti, coati, curosow, tinamou, rats etc.). 'Fence-control' quadrats excluded animals other than crabs by similarly fencing the quadrats; however, holes (20-cm × 20-cm) positioned every 60 cm along the perimeter permitted crabs to enter and leave. Crabs were not removed initially in this treatment. Open-control quadrats, also 25 m^2 in area and marked only with pinflags, had no fencing and were indistinguishable from natural forest. A 0.5-m side buffer-zone from which no data were collected was established on the inside perimeter of each quadrat to reduce any edge and fencing effects.

Within each 25-m^2 quadrat, the total number of seedlings and burrows from five randomly selected 1-m^2 subplots were repeatedly sampled from which a quadrat mean for each sampling date was calculated. Burrow densities for the complete quadrats were also estimated. These 1-m^2 subplots were chosen at the beginning of the 2-y experiment and were *not* re-randomized for each

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sampling date. I separated seedlings into three size classes (0–3.0 cm, 3.1–25 cm, and 25.1–50 cm) based on personal observations of crabs foraging upon medium-sized seedlings. Active burrows, defined by freshly excavated soil surrounding open entrances, were also counted. Burrow densities were assumed to represent crab densities. Due to logistical constraints, blocks 1–3 were established in July 1994 while the remaining two blocks (4–5) were established in June 1995 and data were combined to form the baseline measurements to which subsequent sampling periods, extending to July 1996, were compared.

Seedling preference experiments

To investigate whether land crabs might influence the presence or absence of particular species of seedlings within the crab zone, I tested for seedling preferences by crabs. Two trials were performed, the first in July 1995 and the second in July 2000. Each trial ran for 7 d with daily checks for seedling mortality. In the July 2000 trials, fourteen 1-m^2, circular, fenced enclosures were established within the crab zone (20 were established, six were lost due to crab escapes). From each enclosure, centred around a single active crab burrow, I removed all seedlings and plant litter (forage) to encourage the crabs to select among the presented seedlings (this experiment sought to reveal crab preferences and not consumption rates for seedlings.) Screen tops prevented falling leaves and most seeds from entering the enclosures. Three control plots were similarly set up except they contained no crab. Into each of the 17 enclosures, five seedlings were transplanted from the crab zone (‘local’) and five seedlings from the crabless zone forest (‘foreign’) in an alternating pattern circling the burrow entrance (or, for the controls, simply in a circle around the plot centre) for a total of 170 seedlings transplanted. Although I consistently alternated foreign and local seedlings, species order within each category was randomized. Foreign seedlings were collected from the beginning of the Danta Loops Trail off the Espavales Trail *c.* 2–3 km from the crab zone. Local seedlings were collected from within 100 m of the study site. Each seedling was transplanted equidistant from both its nearest neighbour and the burrow entrance or plot-centre.

Seedlings considered common to the two zones and from 10–15 cm tall were transplanted. This size class was estimated from preliminary trials to be within the size range crabs consume. Seedling species were not chosen based upon knowledge of crab foraging preferences, simply whether they were located in and common in the foreign and local zones. Local seedlings used were *Capparis cynophallophora* L. and *C. discolor* Donn. Sm. (Capparidaceae), *Casearia corymbosa* Kunth (Flacourtiaceae), *Faramea occidentalis* (L.) A. Rich. (Rubiaceae) and *Maytenus guyanensis* Klotzsch ex Reissek (Celastraceae). Foreign seedlings chosen were *Inga alba* (Sw.) Willd. (Fabaceae–Mimosoideae), *Maripa nicaraguensis* Hemsl. (Convolvulaceae), *Mendoncia tonduzii* Turrill (Acanthaceae), *Otoba*

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novogranatensis Moldenke (Myristicaceae), and *Paullinia* sp. (Sapindaceae). Of these selected seedlings, each of the local seedlings were also found in the crabless zone transects whereas none of the foreign seedlings were found in the crab zone transects.

The July 1995 experiment was similar to the experiment described above except that I was unable, at that time, to identify (and therefore limit) the seedling species taken from the two zones (several hundreds of species exist as seedlings in Corcovado N. P.). Additionally, 20 enclosures were used instead of 14 such that a total of 100 local and 100 foreign seedlings were transplanted in this earlier experiment.

Survival of transplanted seedlings protected within the crab zone

As part of another experiment testing the effects of leaf litter on seedling survival run during June 1995, a 6-mo ad hoc control for the previously described seedling preference experiment was established. Local and foreign seedlings (without regard to seedling species) were transplanted into the crab zone and protected from crab predation. Forty fenced, covered exclosures (0.25 $m^2 \times 0.5$ m tall) were established. Into each, four local or four foreign seedlings were transplanted (n = 160 seedlings). Each seedling was numbered and monitored for 6 mo. Data on seedling survivorship were collected on 15 January 1996.

Statistical analysis

Transition zone transects. Paired-samples t-tests were used to compare densities of both plants and burrows in the first half (crabless zone side) and the second half (crab zone side) for the five transects. The transects were subdivided into sequential 2-m × 2-m sections within which the numbers of burrows and plants were determined and analysed using correlation.

Crab exclusion experiment. I used a repeated-measures two-way ANOVA within a randomized block design to analyse the effects of crab exclusion on seedling density over time. Time was incorporated as the within-treatment repeated-measures factor (July and October 1995; January, March and July 1996). In response to the long-standing and unresolved debate over the analysis of experiments involving blocking factors that are neither strictly random nor fixed effects (Newman *et al.* 1997), I follow the authors' suggestion and present two analyses that differ in their assumptions, risks of pseudoreplication, choice of residual error and null hypotheses tested. Model 1 is the conventional ANOVA output where the error term for the between-subjects analysis is the mean square of the treatment × block interaction and the error for the within-subjects analysis is the mean square of the date × treatment × block interaction. This analysis assumes that spatially separated blocks are randomly selected from a larger population of blocks and therefore recognizes the plausibility of treatment × block interactions. The null hypothesis tested by this

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analysis is that there is no treatment effect for any of the blocks. Use of Model 2 does not assume that blocks are random samples from a population of blocks such that treatment × block interactions are unlikely. The error term is the pooled mean square of the treatment × block, time × block and time × treatment × block interactions. The null hypothesis tested is that treatment effects may exist for individual blocks but average out to zero over all blocks.

Two-way ANOVAs with interactions between treatment and block were used to analyse seedling distribution patterns for baseline measurements and each subsequent repeated measure to clarify further the patterns over time of increasing treatment effects and decreasing block effects. A Bonferroni adjustment was used with these six ANOVAs and statistical significance reset to alpha = 0.0083. For seedling size classes of 1–3 cm and > 25 cm, data could not be transformed to conform to statistical assumptions necessary for repeated-measures analysis. Therefore, graphical analyses were used to reveal obvious patterns.

Seedling preference and survivorship. A paired samples t-test was used to test for differences in numbers of seedlings (local vs. foreign) consumed by each of the individually enclosed crabs. This t-test was also used for differences in numbers of seedlings (local vs. foreign) dying after transplantaton into crab exclosures.

Throughout the study (except where indicated) measures of variation are standard errors and statistical significance is accepted at alpha = 0.05. Departures from normality and homogeneity of variances were examined using the residuals from the repeated-measures ANOVA model, normal probability plots, Lilliefor's tests based on residuals, and skewness/kurtosis coefficients.

RESULTS

Vegetation density and diversity in the crabless zone

Despite a narrow transition region of less than 30 m, the crab and crabless zones of the Corcovado's coastal forest supported distinct plant communities. Transects from the crabless zone contained twice the density and diversity of dicotyledons, and three times the seedling density, than transects from the crab zone. Many of those species found in the crab zone were also found in the crabless zone but not vice versa.

One hundred and sixty-nine plants taller than 130 cm were counted from the four transects (240 m^2). From the 36 m^2 of seedling subplots, 675 seedlings (< 130 cm) were counted such that seedlings accounted for 80% of the 844 individual plants. These total stems represented 95 different species from 77 different genera and 42 different families of dicotyledonous plants. Although sampled from within 100 m of the crab zone, 72.6% of the species were unique to this zone (as were 70.1% of the genera and 47.6% of the families) suggesting that few of these species have successfully established within the adjacent crab zone.

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Vegetation density and diversity in the crab zone. The crab zone was distinct from the nearby crabless zone in both density and diversity of plants. A total of 358 dicotyledonous stems were counted in 240 m^2 of which 244 (57%) were seedlings representing only one third the number of seedlings counted in the crabless zone. The diversity of dicotyledons was also relatively low when compared to the crabless zone with only 46 species identified representing 38 genera and 25 families. In strong contrast to the distinctive species composition of the crabless zone, 56.2% of the species found in the crab zone were also recorded in the crabless zone as were 60.5% of the genera and 88% of the families. These data indicate a unilateral capacity for many plant species to establish and persist within the crabless zone.

The cumulative species–area relationships for the four sequentially sampled transects within each of the two zones are described by continuously climbing straight lines indicating that the two zones were not comprehensively sampled. The equations for the two lines from the crabless zone and crab zone transects are respectively described by $y = 18.1x + 22.5$ ($r^2 = 0.98$) and $y = 9.1x + 8.0$ ($r^2 = 0.97$) revealing a more strongly increasing slope for the crabless zone transects.

Patterns of vegetation and burrow density across the transition zone. The five 30-m × 2-m transects run perpendicular across the transition zone were located such that greater burrow densities were found in the second 15 m (11 burrows in the first half, 60 burrows in the second; paired $t = 7.0$, $df = 4$, $P = 0.02$.) *Piper reticulatum*, known from our floristic analyses to occur in both zones, was similarly dense in both halves of the transition zone (paired $t = 0.99$, $df = 4$, $P > 0.05$.) Additionally, no significant correlation was found between burrow density and density of *Piper reticulatum* ($y = 0.12x + 3.14$, $r^2 = 0.02$). In contrast, the first half of the transects supported over twice the density of the other four plant species than did the second half, but this trend was not statistically significant (53 vs. 22 individuals; paired $t = 2.4$, $df = 4$, $P = 0.06$.) A correlational analysis of burrow density and the densities of these four species explains *c.* 34% of the floristic distributional variation but is not statistically significant ($y = -0.6x + 6.53$; $n = 15$, $r^2 = 0.34$; $P > 0.05$).

Crab exclusion experiment

Two years of experimental exclusion of crabs from replicated regions of the crab zone produced consistent and significantly greater densities of seedlings when compared to adjacent controls.

Burrow densities. Before the start of the exclosure experiment, the mean (± SD) number of burrows in all 15 quadrats was 17.3 ± 7.4 burrows per 25 m^2 with no significant differences between the initial numbers of burrows among the three treatments ($F = 0.17$, $df = 2,8$; $P > 0.05$). The number of crab burrows per quadrat was variable with densities ranging from 6 to 32 burrows per 25 m^2.

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Throughout the experiment, crab densities were suppressed in the exclosure by repeated trapping and maintained at a mean of 3.8 ± 0.6 per 25-m^2 quadrat, a value significantly lower than the mean found in controls (17.3 ± 3.5; repeated measures ANOVA: $F = 4.45$, df = 2,8; $P < 0.05$). Quadrats randomly assigned to the open treatment supported fewer crab burrows throughout the study than did the fence-control treatment although not significantly so.

Changing seedling densities: (size class: 3–25 cm)

Baseline values. The only seedling size class that was significantly affected by crab exclusion was the medium-sized group from 3–25 cm high (Table 1). At the time of block establishment, before experimental treatments were imposed, exclosure quadrats contained approximately the same mean (± SE) density of seedlings (9.8 ± 3.5 m^{-2}) of the size class 3–25 cm as did open quadrats (10.2 ± 3.9 m^{-2}). Although fence-control quadrats contained fewer seedlings (5.4 ± 1.9 m^{-2}), the three treatments were not significantly different from one another ($F = 2.6$, df = 2,8; $P > 0.05$). When averaged, the two control treatments supported *c.* 70% of the exclosure seedling density for this size class. Baseline seedling densities did vary significantly, however, among the five blocks as one might expect in a spatially variable primary forest ($F = 9.9$, df = 4,8; $P < 0.01$).

Table 1. Results from crab exclusion experiment documenting effects of land crabs on changing densities of seedling size class 3–25 cm. Repeated-measures ANOVA uses fixed treatment factor (exclosure, open-control and fenced-control), and random blocking factors over 2 y of sampling. Whether spatially separated blocks can be assumed to be arbitrarily defined, or to be part of a larger population of blocks, is debatable. Therefore, two models of ANOVA are presented (*sensu* Newman *et al.* 1997).
Model 1: Blocks are assumed to represent natural units and therefore effects of treatment × block interactions are plausible. The null hypothesis for this test is that there is no treatment effect for any block. The interaction term's mean squares are used for the denominator in the F calculations. Greenhouse–Geisser corrections are also presented.
Model 2: Blocks are assumed to be arbitrarily defined such that one can assume the absence of a treatment × block interaction. The null hypothesis tested is that potential treatment effects average to zero over all blocks. The error term used is the pooled mean squares of treatment × block, time × block and time × treatment × block.

	Source	df	MS	*F*	P	G-G
Model 1						
Between subjects	Treatment	2	1493	20.5	< 0.01	—
	Block	4	344	4.7	0.03	—
	Residual Error	8	73			
Within subjects	Time	4	10	1.5	ns	0.3
	Time × Treatment	8	31	4.4	0.001	0.027
	Time × Block	16	6	0.9	ns	0.5
	Residual Error	32	7			
Model 2						
Between subjects	Treatment	2	1493	92.4	< 0.01	
	Block	4	344	21.3	< 0.01	
Within subjects	Time	4	10	0.6	ns	
	Time × Treatment	8	31	1.9	ns	
	Time × Block	16	6	0.4	ns	
	Time × Treatment × Block	32	7	0.4		
	Residual Error	56	16.2			

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Effects of treatment, block and time. Over the 2-y period, seedling densities of the size class 3–25 cm significantly increased in crab exclosures but not in fence- and open-control quadrats (Figure 1, Table 1). At the end of the study, exclosures contained an estimated mean density of 23.9 ± 3.8 seedlings m^{-2} (598 ± 95 seedlings per 25 m^2) compared to pooled mean of 6.2 ± 1.1 seedlings m^{-2} for the controls. Final values represented a 144% increase over baseline for exclosures compared to a 29.4% and 3.7% decrease for open- and fence-control treatments, respectively. Although no significant treatment differences existed at the beginning of the experiment, by the end, exclosures supported from 3 to 4.5 times more seedlings than did open or fence-control quadrats, respectively (Figure 1). In contrast, over the duration of the experiment, seedling densities did not significantly differ between the two control treatments. The magnitude of the treatment effect strengthened over the 2-y study (from $P = 0.0034$ in July 1995 to $P = 0.0002$ in July 1996). Different repeated-measures ANOVAs, however, provide contradictory conclusions regarding the effects of time × treatment (Table 1).

In contrast to treatment effects, statistically significant blocking effects were found for the baseline conditions representing the natural spatial variation of the distributions of forest seedlings ($F = 9.9$, $df = 4,8$; $P = 0.003$; Bonferroni

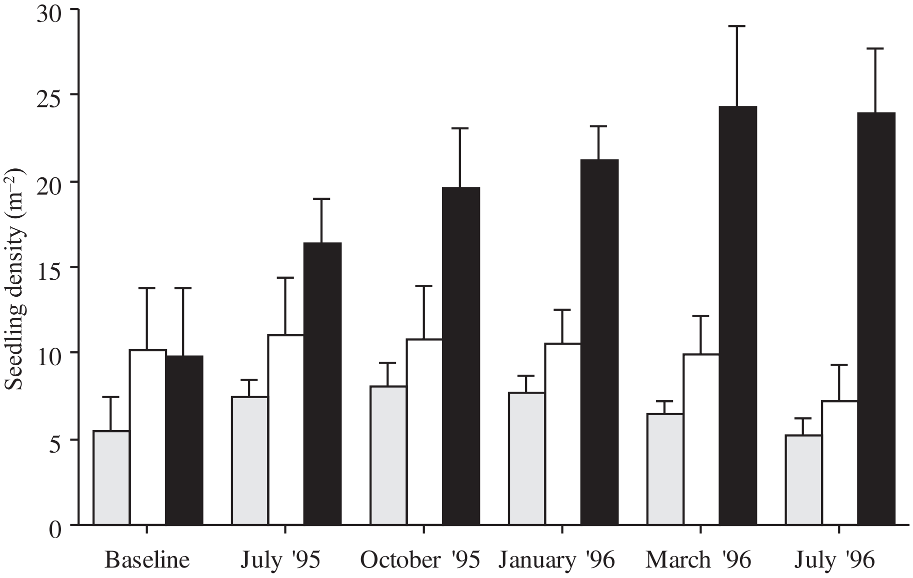

Figure 1. Changes in mean (± SE) seedling density m^{-2} (size class 3–25 cm) over time as a function of three different treatments: crab exclosure (black bars), fence-control (light grey bars), and open-control (unshaded bars). Each point graphed represents the average value from five replicate quadrats; each quadrat value represents a mean of five 1-m^2 sub-samples. Blocking effects were significant only for Baseline and July 1995 measurements and were insignificant thereafter. No significant treatment effects were found for Baseline data. Significant treatment effects begin in July 1995 and strengthen over the remainder of the experiment. Probability values from individual ANOVAs (Bonferroni adjusted), used to test treatment effects at a given time, changed over time as follows: July 1995 = 0.0034; October 1995 = 0.0022; January 1996 = 0.0063; March 1996 = 0.0023; July 1996 = 0.0002.

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adjusted P = 0.0083). Statistically significant blocking effects, however, continued only through the first sampling period of July 1995 (F = 7.9, df = 4,8; P = 0.007). For each consecutive sampling period thereafter, blocking effects were not significant and continuously weakened as treatment effects strengthened. The initial blocking effect, however, was sufficiently strong to affect the overall results from the repeated measures ANOVA (Table 1).

Shorter and taller seedling size classes

Based upon a priori observations of foraging crabs, data were also collected for seedlings of two other size classes chosen: the 'cotyledon stage' from 1–3 cm (Figure 2a) and taller seedlings from 26–50 cm (Figure 2b). Graphical analyses of these data, however, clearly reveal the lack of any significant treatment differences at any point during the study. For the March count taken at the end of the dry season, densities of the smallest seedlings were zero for most plots. For the 26–50 cm seedlings, the open treatment supported the highest absolute seedling densities for all dates except October but experimental crab exclusion failed to clearly affect densities of this size class.

Seedling preferences by crabs

Despite the equal access to both local and foreign species over 1 wk, crabs killed eight local seedlings (11.4%) and 43 foreign seedlings (61.4%; paired t = 8.6, df = 13, P << 0.001). Additionally, two other local and four other foreign seedlings were seriously damaged but not killed within the week. Among the eight local seedlings killed, four were *Faramea occidentalis* and two were *Capparis discolor*. Each of the five foreign species was killed although *Maripa nicaraguensis* accounted for 30.2% of killed foreign seedlings. *Mendoncia tonduzii*, *Paullinia* sp. and *Inga alba* together accounted for an additional 58.1% of the foreign mortalities with roughly equal numbers taken of each. Control exclosures lost no seedlings during the same period nor did their seedlings seem to experience any ill effects of transplantation, insect herbivory or fungal attack.

In the previously conducted experiment (1995), similar trends were found despite the fact that seedlings that were used were not taxonomically identified prior to or after their selection. The data supported the hypothesis that any seedling taken from the crabless zone would be more likely to be killed by crabs than any seedling taken from the crab zone. After 1 wk, 17% of the 100 transplanted local seedlings were killed whilst 53% of the 100 foreign seedlings were killed (paired t = 5.6, df = 19, P < 0.001). These data also suggest a strong preference by crabs for novel seedlings.

In the other experiment from 1995, 80 foreign and 80 local seedlings (again, unidentified) were transplanted into protective 0.25-m^2 fenced exclosures located in the crab zone < 25 m from the seedling preference trials; 82.5% of the foreign and 70% of the local seedlings survived 6 mo demonstrating the capacity of foreign seedlings to survive transplantation if protected from crabs.

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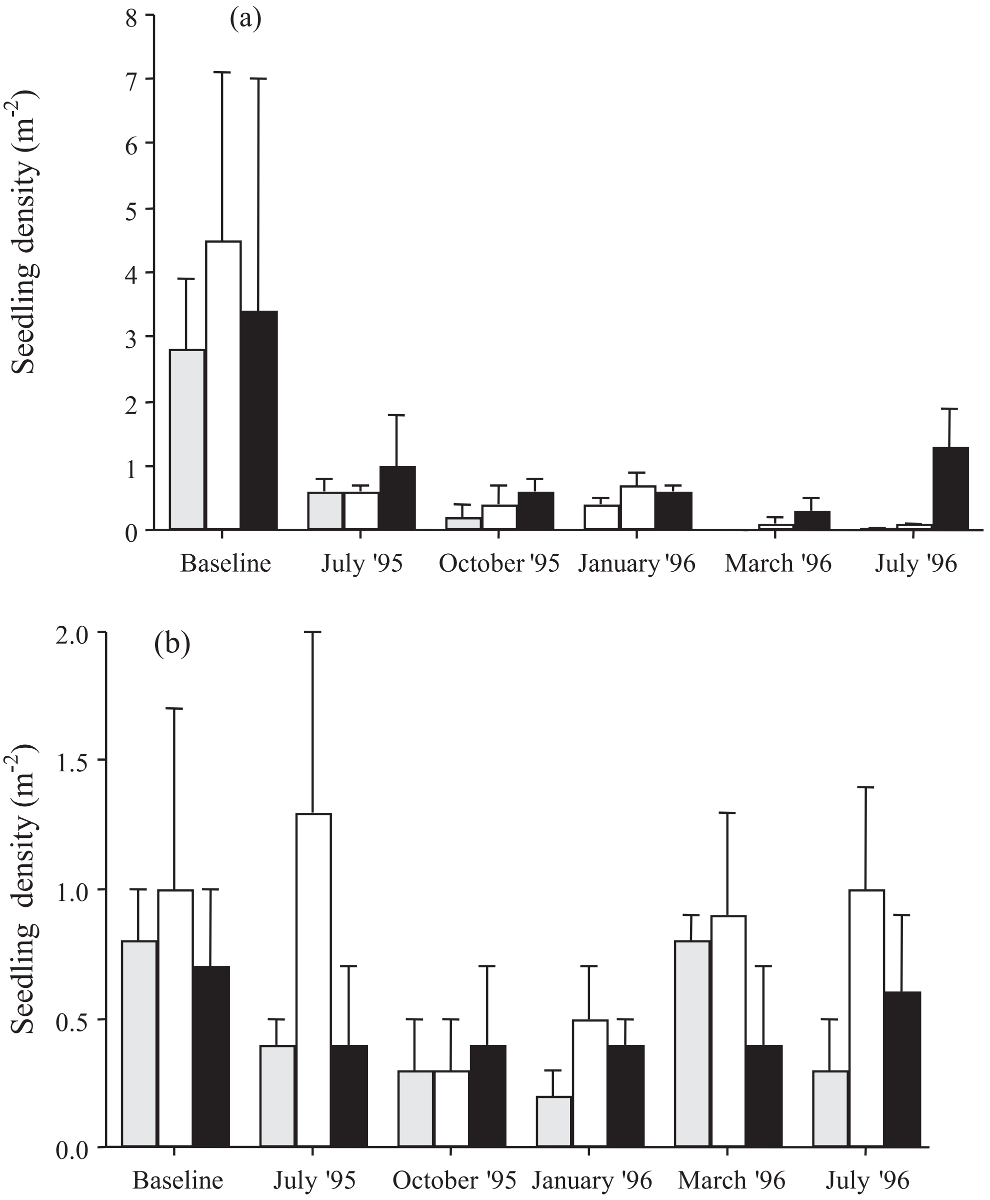

Figure 2. Changes in mean (± SE) seedling density m^{-2} over time for (a) seedling size classes 1–3 cm and (b) 26–50 cm, as a function of three different treatments: crab exclosure (black bars), fence-control (light grey bars), and open-control (unshaded bars). No significant treatment effects were found for either size class.

DISCUSSION

Data presented suggest that dense populations of herbivorous *Gecarcinus quadratus* significantly reduced the density and diversity of medium-sized seedlings within coastal forests of Corcovado National Park. Transects run through the

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coastal crab zone and the adjacent crabless zone clearly revealed an abrupt diversity gradient for dicotyledonous plants with less than half the plant density and diversity recorded where crabs live. The two forest zones are further distinguished by their distinct compositions as 43.8% of the crab zone's species and 72.6% of the crabless zone's species were unique to their respective sides. Experimental manipulations of crab densities and seedling preference tests suggest that this floristic distinction between the two zones results primarily from the selective consumption of seedlings by land crabs inhabiting the crab zone. There are, however, alternative hypotheses.

Potential sampling error in the four transects run per zone must be considered. Species–area curves of the sequentially run transects indicate that additional sampling would be required to describe fully the floristic diversity of the two zones. However, the species–area curve from the crabless zone is twice as steep as that from the crab zone suggesting that further sampling in the two zones would result in both higher absolute numbers of species and even greater zonal divergence in species richness.

There may be ecological mechanism(s) that could produce such a steep gradient in species richness that do not directly involve land crabs. It is possible, for example, that seeds from the crabless zone are unable to infiltrate the crab zone because of the prevailing winds that blow inland from the coast. However, most of the species found in these two zones, as in many neotropical rain forests, are dispersed by animals (O. Vargas and R. Aguilar, *pers. comm.*; Janson 1983, Willson *et al.* 1989). It therefore seems unlikely over ecologically relevant time periods, that only a small fraction of seeds from the crabless zone could recruit into the small band of coastal forest inhabited by crabs. Seed deposition would likely be comparable in both zones and data from currently running experiments testing this hypothesis are forthcoming. Rather, it seems more likely that plant species are entering the crab zone as seeds but failing to establish themselves. Micro-climatic differences between the two zones may be influential.

Seeds and seedlings entering and inhabiting the two zones must contend with very different micro-climatic conditions. The transition region is a sharp and brief intermixing area between the two zones but the crabless zone supports a ubiquitous and thick leaf-litter layer (> 15 cm) that accumulates throughout the year. In stark contrast, on the coastal side there is a near lack of accumulated leaf litter upon the forest floor – the topsoil is largely bare and litter patchily distributed. While seeds and young seedlings may find protection from selection pressures within the organic matter of the crabless zone, the bare-soil conditions of the crab zone can expose plant propagules to various stresses. Such stresses may involve the increased fluctuations in soil moisture and temperature associated with bare soils, increased exposure to herbivory and predation, altered competitive dynamics between seedlings and the absence of litter invertebrate assemblages (see reviews by Facelli & Pickett

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1991, Green *et al.* 1999, Howe & Smallwood 1982, Molofsky & Augspurger 1992). The absence of a leaf litter layer may also lead to a reversal in soil nutrient profiles such that higher nutrient levels are found deeper in the soils rather than in the top soils (Sherman 1997).

The absence of a leaf litter layer in the crab zone, however, is not coincidental to the presence of land crabs. Rather, data from Sirena (Sherman 1997) and evidence from other ecosystems influenced by Gecarcinidae (Delfosse 1990, Green *et al.* 1999, Kellman & Delfosse 1993, O'Dowd & Lake 1989) and additional crab families (Emmerson & McGwynne 1992, Robertson 1986, 1991; Robertson & Daniel 1989) clearly implicate crabs as the cause of this leaf-litter reduction. In Sirena, land crabs have been shown to selectively relocate as much as 85% of the leaf-litter from the forest floor to their 0.5-m deep burrows (Sherman 1997). The resulting patchy distribution of leaf litter is characteristic of the crab zone. It is possible, therefore, that the primary influence of land crabs on seedling distributions may not be their selective consumption of seeds and seedlings but rather their selective relocation of the leaf-litter layer to burrow chambers.

Importantly, the distinction between the crab and crabless zones extends beyond the mere presence or absence of crabs and the biomass of accumulated leaf-litter. The soils of Corcovado's crabless zone are clay while the crab zone's are sandy. Foreign seedlings may, therefore, fail to recruit into the sandy soils of the crab zone due to unsuitability of the substrate; the presence or absence of land crabs may be coincidental. Whilst fossorial crabs themselves may be restricted by the hard, dense clay substrate that supports a thick rooting mat, the unanswered question remains: are seedlings restricted by sandy soils? Long-term exclosure plots currently capturing and protecting seeds falling into the crab-zone will help address this uncertainty. However, the results described here indicate that soil differences are not, at least over 6 mo, a prohibitive factor for seedling establishment in the crab zone. Sixty-six of 80 foreign seedlings (82.5%) transplanted into the crab zone and protected from herbivory survived and grew over 6 mo. Similarly transplanted seedlings from the crab zone survived less well (70%). Unfortunately, that study ended when the dry season began so the seedlings were not more severely stressed. Further work is required.

Using fencing to exclude crabs experimentally from forest within the crab zone produced unequivocal results. After 2 y of crab exclusion, exclosure densities of medium-sized seedlings (3–25 cm) had increased 144% from baseline values whereas seedling densities from the control treatments decreased during the same period. Although initial seedling densities were not significantly different among the three treatments, final densities in exclosures were nearly four times those of the two control treatments that remained similar to one another. Densities of shorter and taller seedlings within the experimental blocks, however, did not respond to crab exclusion presumably reflecting a

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preference by foraging crabs for medium-sized seedlings. I did expect, however, to find increasing numbers of taller size-class seedlings in exclosures resulting from growth of medium-sized seedlings, but it seems that 2 y of growth was insufficient time in the deep shade of 30 m of multiple canopy layers.

Seedling consumption by *Gecarcinus quadratus* in Corcovado National Park appears to be species, as well as size, selective. In preference tests comparing seedlings collected from the crabless zone (foreign) and crab zone (local), *G. quadratus* preferred foreign seedlings five-to-one. In the case of *Maripa nicaraguensis* (the most favoured of the transplanted seedlings), 13 of the 14 seedlings transplanted were killed by crabs within 7 d. Even though the enclosure design accentuated the effects of foraging crabs, these data suggest that some of the local seedlings survive, in part, because they are not chosen by selectively foraging crabs. It seems likely that tree species from the crabless zone cannot successfully recruit by seed into the crab zone unless the propagules are unpalatable to, or somehow protected from, crabs.

Seedlings may be able to escape in time or space from the intense predation pressure of crabs within the crab zone. Seedling densities do increase in the crab zone during the dry-season months when land crabs are essentially inactive (Sherman 1997). Whether this increase relates to the inactivity of the land crabs at this time, increased solar radiation infiltrating the thinning canopy, increased accumulation of leaf litter, or some other factor is still unknown. Data suggest, however, that if seedlings can grow beyond a height of *c*. 25 cm, crabs will not consume them. Corcovado's 3–4 mo dry season, however, is probably insufficiently long to allow most species of seedlings to establish themselves and grow beyond this height. Longer dry seasons may be necessary and tree recruitment may rely upon rare, episodic droughts that could extend crab inactivity thereby providing temporal windows of opportunity for some drought-resistant seedlings.

Seedlings may escape crab predation in space as well. Light gaps can increase the growth rates of seedlings (*sensu* Brandani *et al.* 1988, Howe 1990, Raich & Gong 1990) while locally reducing crab activity because crabs are known to avoid areas and times of low humidity (Green 1997). However, the only published attempt to covary crab access with varying light regimes was unable to detect differential seedling recruitment in exclosures under high light vs. shade conditions (Green *et al.* 1997). Counter-intuitively, these authors found that exclosures in crab zone light gaps supported fewer individuals of many of the seedling species relative to nearby understorey regions. In Corcovado, light gaps may well influence rates of seedling establishment and growth for some pioneer plant species but they are unlikely to affect the nocturnally active *Gecarcinus quadratus* and, therefore, are unlikely to alter significantly the crab–seedling interactions. In short, light gaps do not protect seedlings from crabs in Corcovado.

Seedlings may be able to escape predation spatially because crab burrow

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densities are variable throughout the crab zone. Densities range widely from an average of 0.7 to over 6 burrows m^{-2}. Whilst for unknown reasons, some areas have few if any burrows, crabs do congregate at the base of trees and buttress roots. Over the four crab zone transects (60 m^2 each) designed for the sampling of trees, burrow densities sequentially, and coincidentally, decreased from 66, 47, 22 to 16 burrows. Therefore, the ever-increasing species–area curve found in the crab zone and discussed previously, may simply represent the negative relationship between seedling species and crab densities suggested by the transitional zone transects. Perhaps seedlings can escape crab predation and successfully recruit into pockets within the crab zone where burrow densities fall below some threshold. If the distribution of active burrows ebbs and flows with time, it is possible that seedlings can take advantage of this heterogeneity (Sherman 1997).

Together, these data thus far suggest that: (a) two adjacent forest zones support different dicotyledonous communities, (b) a pattern of plant species distributions exists between the two zones such that a majority of those plants that live in the crabless zone cannot live in the crab zone but most of the crab zone species successfully recruit to the crabless zone, (c) crabs forage selectively for seedlings based upon size and species of seedlings, (d) seedlings found in the crab zone most likely represent those species less preferred by crabs presumably because preferred seedlings have previously been eaten, (e) foreign seedlings may be able to establish and survive in the crab zone only if protected from crab predation, and (f) crabs may ultimately represent an important selective force controlling plant diversity.

My findings from Corcovado National Park corroborate those of the other published experimental studies addressing the effects of Gecarcinidae on the seedling communities of Christmas Island in the Indian Ocean (Green *et al.* 1997, O'Dowd & Lake 1990). These authors report that *Gecarcoidea natalis* killed nearly 100% of certain seedlings in open forest quadrats where fewer than 15 seedling recruits could be found in 25 m^2. In contrast, adjacent crab exclosures supported from 100 to 600 seedlings 25 m^2 representing several species. Seedling densities from 25-m^2 quadrats in Corcovado showed similar patterns but at higher densities. Control quadrats supported 155 ± 28 medium-sized seedlings while exclosures supported an average of 598 ± 95 medium-sized seedlings.

Corcovado National Park, Costa Rica, contains considerably greater plant and animal species diversity than most other island and mainland systems, and, therefore, one might expect the relative impact of land crabs on forest ecology to be accordingly less pronounced. With over 2500 recorded plant species (Quesada *et al.* 1997), I expected to find higher densities and diversities of seedlings than reported from the relatively species-poor Christmas Island. Additionally, crab activities are strictly limited to nocturnal foraging, largely by palpation, perhaps because predation pressures on the crabs themselves can

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be periodically intense when families of 50+ coati feed in the crab zone during the day. In contrast, the crabs of Christmas Island, dominate the island where large indigenous fauna are limited in both biomass and diversity. Nevertheless, many of the clear findings from Christmas Island, and the impressive and similar influence of other families of crabs in mangrove systems (Camilleri 1989, Clarke & Myerscough 1993, Emmerson & McGwynne 1992, McIvor & Smith 1995, Micheli 1993, Robertson 1986, 1991; Robertson & Daniel 1989, Smith 1987a; Smith *et al.* 1989), are repeated by *G. quadratus* in Sirena. With further work, I suspect that we will discover that land crabs play important ecological roles in coastal forest systems pantropically.

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