Disperson of Juveniles, Spatial Patterns of Plant Performance, and the Regulation of Density in Tropical Forest Trees

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Introduction

One important function of seed dispersal is to catapult young plants away from their parents, where high seedling density may otherwise have caused reductions in survival or growth. Thus, patterns of seed dispersal may be crucial in establishing the importance of density-dependence and intra-specific competition in a plant population, and ultimately in determining population density.

We are interested in understanding how recruitment, mortality, and growth of juveniles vary with local conspecific density, or with distance to the nearest adult, in tropical forest trees. In particular, we wish to assess the impact of such spatial patterns on density-dependent population regulation.

Studies of distance and density effects on plant performance are often called "neighborhood analyses", because intra-specific competition is presumed to operate only between close neighbors in plants. Most neighborhood analyses in plants have been carried out on herbaceous annuals growing in single-species stands, where competition occurs between immediate neighbors. In this setting, the carrying capacity set by intra-specific competition is simply the number of individual plants a particular plot of ground can support.

In species-rich tropical forests, the density of even the most abundant species is nowhere near the "self-thinning" density. Do populations of tropical trees ever reach densities where neighborhood interference can limit population growth and population density? We approach this question by calculating neighborhood effects on life table parameters — recruitment, growth, and survival — and by using population simulations to determine whether population growth might be affected by density.

Materials and Methods

The study was carried out in tropical moist forest on Barro Colorado Island in central Panamá. Two censuses of 50 ha of forest were carried out, first in 1982 and again in 1985. All free-standing, woody stems ≥ 1 cm diameter at breast height (dbh) were identified, tagged, and mapped.

Neighborhood effects. We examined neighborhood effects in two common understory trees, *Faramea occidentalis* (Rubiaceae) and *Desmopsis panamensis* (Annonaceae). Mortality rates were defined as the fraction of stems found in 1982 that had died by 1985. Growth was measured as the percent of plants that grew from one size class to the next between censuses, where size classes were defined as 1-2 cm dbh, 2-4 cm, 4-8 cm, 8-16 cm, and 16-32 cm. Recruitment was defined as the number of plants that appeared in the 1985 census that had not been counted in 1982.

Mortality rate, growth, and recruit density (number of recruits per hectare) were calculated in regions of the plot that differed in the local density of conspecifics in the following distance classes: 0-2 m, 2-4 m, 4-6 m, and 4-30 m. Chi-square tests were used to determine statistical significance. The smallest sample size in one category of a chi-square test was 219 for all size classes in *Faramea* and for all classes ≥ 8 cm dbh in *Desmopsis*. The 8-16 cm size class in *Desmopsis* had sample sizes as small as 15 for some categories.

Modeling. Life tables were constructed using observed transition probabilities between size classes. Density-dependence was incorporated as follows: In the model populations, we assumed that plants were randomly distributed, so that a poisson distribution could be used to calculate what fraction of forest had a given number of neighbors. Based on this fraction, various life table parameters were adjusted. Alterations in life table parameters were based on observed effects of local density on mortality, growth, and recruitment rates. Population growth was simulated using standard matrix projection techniques.

Results - Neighborhood Effects

Desmopsis **showed significant neighborhood effects on recruitment, but not on survival nor growth.** The number of neighbors within 0-2 m, 2-4 m, 4-6 m, and 4-30 m did not affect survival or growth of any size class above 1 cm dbh (Fig. 1, 2). There was, however, a sharp reduction in recruitment within 2 m of an adult *Desmopsis*. There were 21 *Desmopsis* recruits per hectare in regions within 2 m of an adult, and 41 recruits per hectare outside such regions.

Faramea **showed clear neighborhood effects on survival and growth.** Plants in the smaller size classes (up to 8 cm dbh) suffered significant reductions in survival and growth if they had neighbors within 4 m (Fig. 3). There was also an increase in mortality of juvenile *Faramea* as a function of the number of neighboring adults between 4 and 30 m, even after controlling for the number of neighbors within 4 m (Fig. 2). Larger size classes of *Faramea* were not effected by the presence of neighbors.

In areas within 1 m of adult *Faramea,* recruit density was significantly reduced, but only slightly (data not shown here).

Results Modeling

Simulations of *Desmopsis* populations using all parameters exactly as measured in the field were regulated at a density of about 6000 plants per hectare, or 30 times higher than the observed density (Fig. 4). Density-dependence in *Faramea* was not sufficient to regulate the population — even at infinite density, the population would still grow (simulation not shown).

But the carrying capacity calculated by these models was sensitive to estimates of density-independent mortality and growth (Fig. 4). The best way to assess the importance of density-dependence on population growth is to plot the population growth parameter (lambda) against total population density. This is because the decline in lambda happens at the same population density, regardless of the density-independent mortality and growth parameters (Fig. 5 and 6).

In *Desmopsis* (Fig. 5), lambda was unaffected below a density of about 300 plants per hectare, which is above the currently observed density of 200 plants per hectare. Thus, **the current density of *Desmopsis* is too low to reduce the population's growth rate appreciably.**

In *Faramea,* (Fig. 6) lambda began to decline at a density of about 200-300 plants per hectare. Since this is below the currently observed density 500 plants per hectare, we can conclude that ***Faramea* is suffering a density-dependent reduction in population growth at its current population size.**

Discussion

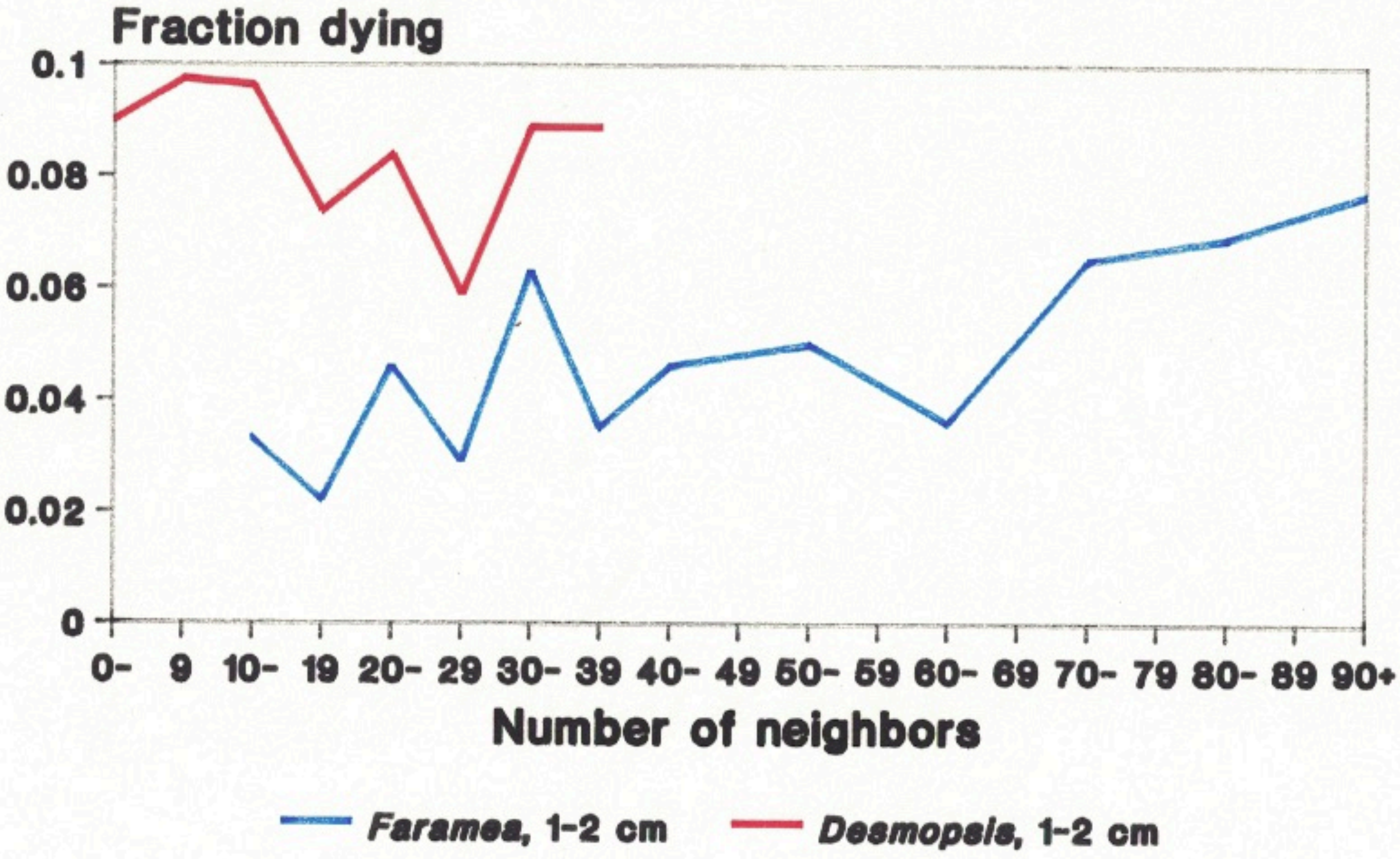
There was clear evidence for density-dependence in these two species of understory trees. In *Desmopsis,* neighborhood effects extended over 2 m, and plants above 1 cm dbh were unaffected. In *Faramea,* plants as large as 8 cm were adversely affected by the presence of conspecific neighbors, and the smallest plants were affected by neighbors as far as 30 m away. Such long-range effects are probably mediated by species-specific pathogens or herbivores, not competition for light or nutrients.

The simulation models suggest that neighborhood effects of the magnitude we estimated could only regulate populations at densities above 200-300 per hectare. Thus, we conclude that *Desmopsis* cannot currently be suffering from intra-specific competition, but that *Faramea* may be since it is more abundant.

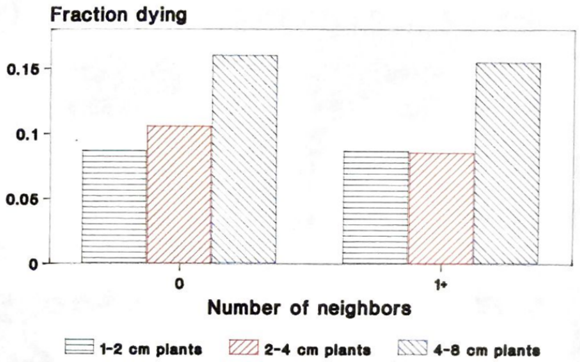
In a similar analysis of two canopy trees in the Barro Colorado plot (*Trichilia tuberculata* Meliaciae and *Quararibea asterolepis* Bombacaceae), we found parallel results. The abundant species (*Trichilia*) may currently have its population regulated by intra-specific competition, but *Quararibea* showed no evidence for neighborhood effects of any sort.

Our studies of density-dependence in tropical trees indicate that some of the more common species may indeed be regulated by intra-specific competition, probably mediated by species-specific herbivores and pathogens. Uncommon species are probably not so-regulated. We are extending these studies to include more species, and to examine the importance of inter-specific effects.

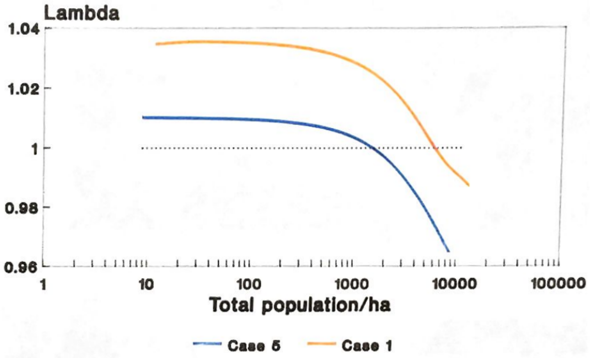
Neighborhood effects on mortality
Number of conspecific adults within 30 m



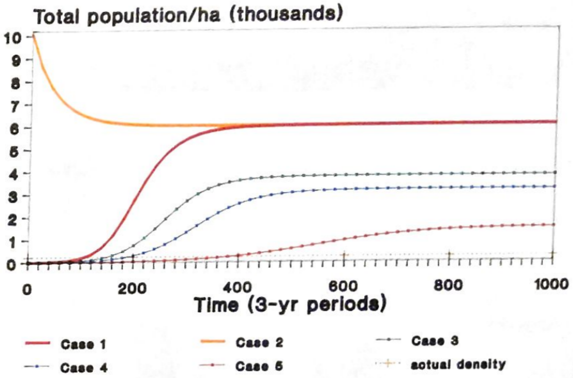
Neighborhood effects on mortality
number of adults within 2 m: *Desmopsis*



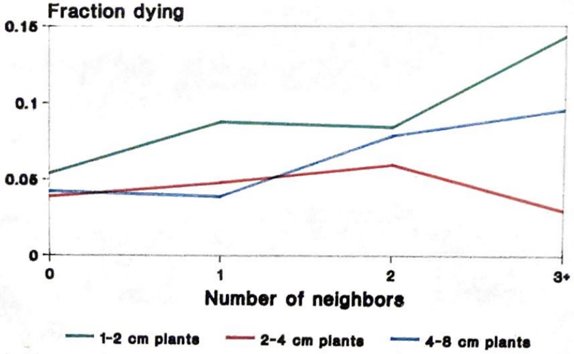
Simulations: population growth parameter
Desmopsis



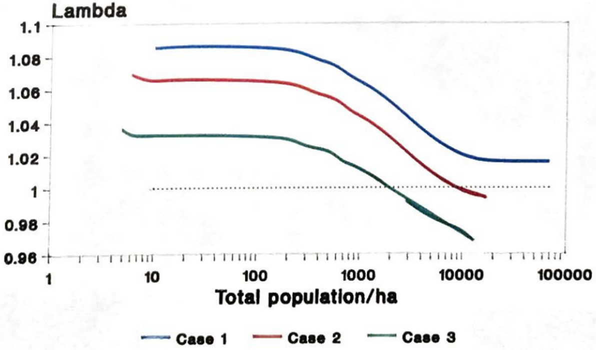
Simulation of *Desmopsis* population



Neighborhood effects on mortality
number of adults within 2 m: *Faramea*



Simulations: population growth parameter
Faramea



Simulations of *Faramea* population
lifetable parameters