Juvenile Success Close to Adults in Tropical Forests: Does It Explain High Species Diversity?

I. Introduction

A. Thanks for inviting me here, John in particular

B. My work -- population biology and genetics of tropical forests.

1. I came to Hubbell lab because of interest in forest demography, tropics, and conservation biology. Work I mention here does not have immediate conservation effect, but any information is important, and I am also interested in more applied problems like demography of forest regeneration in tropics.

2. I will describe demographic work that I have completed, and at the end, mention briefly how I hope to use genetic information to further investigate this question. Hubbell and I have decided to commit a substantial amount of time to establishing DNA techniques that will allow us to identify parents in a natural population of trees. Worked hasn't progressed enough to give you any interesting results, but as time permits I'll summarize what we are trying.

C. Great question of tropical forests is diversity. Temperate ecology has built ideas of equilibrial communities, each species having a "place" which assures it's maintenance. But tropical forests consist of remarkable number of species of plants, all probably limited by sunlight. Single habitats with more or less uniform conditions of moisture, soil, etc., seem to contain more species than could be explained by niche partitioning.

D. The "Janzen hypothesis" (my term) is a solid theoretical concept that could help solve this "paradox of the plankton". It's old (1970) yet still popular, judging from recent theoretical confirmations (Armstrong), and virtually untested. Connell has been a supporter, and has provided support from Australia.

E. The work I describe is the most thorough and convincing test of the hypothesis available. This is a survey of 85 species in one forest to see if the most important predictions of the Janzen hypothesis are met.

II. What is the Janzen hypothesis? This is my name, and refers to Janzen's original idea plus subsequent work clarifying and extending it. A quick explanation:

A. Predators and pathogens of seeds and seedlings conspicuous in tropics, and often specific to one or a few species. Janzen was impressed with how effective these could be at destroying seed crops (eg Bruchid beetles). He noticed that in some cases, numerical response of predators was so extreme, that the entire crop close to adult was destroyed. Seeds dispersed far from parent were (sometimes) protected. Thus, an adult could inhibit its own reproduction in its immediate vicinity. (SLIDE from Janzen)

B. This can create a frequency dependent reproductive success among species, as follows

1. Consider a model forest with two species. Both cover half forest, and completely prevent their reproduction beneath canopy of any conspecific. A can only reproduce under B, and B under A. Half the forest is available to each. If a third species invades the forest (also suffering Janzen effect), when it is rare, it can reproduce anywhere. It thus has a two-fold advantage and will increase in abundance relative to A and B. After C enters, then species D can invade, initially having a 33% advantage. Note that the 100th species has only a 1% advantage. Note though that if Janzen effect extended to larger area, eg 10X canopy dimension, then 100th species can have 10% advantage.

2. An alternative view is to focus on one species and ask what prevents it from taking over forest. Even if it is competitively dominant, if it suffers Janzen effect, then it opens up a region beneath it where other species have an advantage. (SLIDE of model forest). It provides another "niche" for other species to persist, but a niche that moves around with adults.

C. What we should see if this is an important effect is

1. Increased mortality beneath canopy.

2. Fewer recruits of species A near adults than recruits of other species.

III. The test

A. Primary moist forest in Panama on BCI, operated by Smithsonian. (SLIDES of BCI)

B. Two censuses of a 50 ha. region (1982 and 1985), providing very large sample sizes for several species organized by S. Hubbell and R. Foster. Can calculate mortality and growth of juveniles under adults and far from adults. And can determine whether RS, as measured by new recruits into the population on second census, avoid adults. 306 species, 240,000 individuals

omit mortality

C. SLIDE of Anaxagorea to show topography; mention ANAP as an aside

D. SLIDE of Hybanthus showing swamp

IV. The answer, part I, mortality and growth 1 cm and above. Sample sizes sufficient for 35 species (at least 10 juveniles in region within 1 canopy radius of adults. Many shrubs were left out because juveniles are <1cm, the minimum size of census

A. Define canopy distance

B. Two sets of numbers -- I forgot slide -- for TRI3: mortality within 5m of adult is 18.4%, further, 11.2%; growth 10.5% near adults, 16.5% far

(N=152 near, 6664 far). We'll hear more about TRI3 later. CROB (small tree): 77.6% die near adults, 42.7% far (N=49, 281).

omit

C. SLIDE of number of species showing various patterns; few species show "Janzen effect"

V. But survival and growth is only part of the story; the real answer is the actual distribution of reproduction; my estimate is to use recruits into 1cm class (define)

A. Tally number of recruits at varying distances from nearest adult (since I don't know parents); I count only nearest neighbor, ignore second nearest

B. Compare to recruit distribution of rest of the forest; explain how this is computed

C. Illustrations

1. SLIDES of CORB; first graph then map
2. SLIDES of OCOS; only graph, not map
3. SLIDES of BEIP ; remove map
4. SLIDES of TRI3; compare to mortality results
5. SLIDES of EUGO -- clearer than TRI3

pull out BEIP map

pull out EUGO chart

D. What this means--if observed greater than expected, that species has advantage in that region over other species; explain that although BEIP shows "Janzen effect", it is not sufficient to maintain diversity

E. Tally of different patterns--SLIDE for total, SLIDE by growth form

F. Bias for large trees--maybe more than it appears are suffering Janzen effect, but this would apply only to rare ones; in fact, many rare species may be rare because of Janzen effect, but can't be tested

G. But what of the common ones? Their importance is they "threaten" to take over the forest

1. TRI3, ALSB clearly under
TET2 no effect but almost under, no mortality effect
2. PROT, PRIC clearly over
QUA1 no effect (but almost over)
3. BEIP no effect
4. GUAD, POUA, and VIR1 don't have enough to say strongly, but show no effect

H. SLIDE of repel distances

I. SLIDE of attraction distances

SLIDE of number of species showing mort & growth effect

add mortality section if there's time eg > 20 min left

VI. Summary conclusions

A. Summary--few species inhibited after they reach 1cm, but this misses seed and seedling stages; shrubs usually strongly attracted, but about half of tree species show some indication of repulsion out to 5-15m

B. What causes the recruit patterns

1. Favor attraction

a. Limited dispersal probably most important

b. Habitat preferences, eg, show map of OCOS; not apparently important here but difficult to test

c. Adults could condition habitat to favor their offspring--mycorhizae

d. Asexual reproduction, perhaps important in shrubs

2. Repulsion

a. Pathogens, according to the Janzen effect

b. Death of adults--some recruits may have been right next to their now deceased mother

C. Conclusion regarding Janzen hypothesis is not favorable; it does not appear that the effects are of the right range, or strong enough, to account for the large number of species in forest; that is, although 2-3 of 7 most common canopy trees may have reached a level of density dependent population regulation, this cannot account for the long list of rare species, none of which I have named (there are 11 species in the plot with one individual in the 50 ha)

D. The non-equilibrium hypothesis--no forces maintaining the species mixture; some will drift out, others drift in; it can take a very long time, eg 1000 or more years, for a species that got abundant due to different conditions long ago to finally disappear

E. Future needs and plans

1. Adult density and reproduction, not just nearest neighbor

2. Follow to larger sizes

3. Modeling to determine if TRI3, eg, is restricting its own abundance now

4. Modeling to examine effect of overabundance of recruits near adults, as in OCOS; pose question, if OCOS were inferior competitor, does it persist longer by flooding immediate neighborhood with recruits?

VII. Genetics and population studies

A. I've spent majority of time recently with tree DNA hoping to identify regions that would allow fairly rapid determination of parentage, eg "DNA fingerprinting

advantage of HF plot for this work

B. Obvious extension to this study would be to examine recruit distance to actual parents, not nearest adult; sample sizes would be small, but we would start by looking at seedling stage for effect of parent's proximity; it would be most interesting to determine whether parents have affect on juveniles that other conspecifics don't--genotype specific pathogens

B½. Look at RS of rice species

C. There are several types of loci that show promise of being highly variable within a population; all are classes of repetitive DNA

1. Fingerprinting probes are 15-30bp repeats
2. 3bp repeats have proven useful in humans, not tried in plants
3. Most promising to me now are 2bp repeats, which are ubiquitous (10^6 loci of $(AC)_n$ in humans), found in all plants I have checked so far, and quite variable in humans; probaby selectively neutral, might prove to be a useful gauge of genetic variation in all species, as well as providing a generalized technique, avialable for any species, for doing parentage; 7-10 such loci needed; use of PCR so need little DNA

D. So I'm rather excited about prospects of this technology, and will check back with you in about a year to document their success

Density dependent population growth in the 10 commonest canopy trees

Species	Difference in lambda values between regions of		Critical difference value
	low and high adult density	low and high subadult density	
Alseis blackiana	**0.074**	0.025	0.044
Beilschmiedia pendula	-0.056	-0.017	0.060
Guatteria dumetorum	0.024	-0.037	0.081
Poulsenia armata	-0.026	-0.065	0.092
Prioria copaifera	-0.018	0.014	0.070
Proteum tenuifolium	0.023	0.016	0.038
Quararibea asterolepis	0.030	-0.004	0.050
Tetragastris panamensis	0.038	0.001	0.079
Trichilia turberculata	**0.109**	0.040	0.056
Virola sebifera	0.039	-0.011	0.060

Multiple regression analysis of survival versus density in *Trichilia turberculata*

1 dependent variable -- survival (takes value 0 or 1)
9 independent variables -- number of neighbors in three size classes at three distance classes
significant effects boldface in parentheses

Effect of conspecific density within 5 m	1-4 cm DBH	4-16 cm DBH	16+ cm DBH
On survival of			
1-2 cm	+	**(– –)**	**(– –)**
2-4 cm	-	-	**(– –)**
4-8 cm	+	-	-
8-16 cm	+	+	-
16-32 cm	+	+	-
32+ cm	**(+)**	+	+

Effect of conspecific density at 5-10 m	1-4 cm DBH	4-16 cm DBH	16+ cm DBH
On survival of			
1-2 cm	**(+)**	-	-
2-4 cm	+	-	-
4-8 cm	**(+)**	-	**(–)**
8-16 cm	-	+	+
16-32 cm	+	+	**(–)**
32+ cm	+	+	-

Effect of conspecific density at 10-15 m	1-4 cm DBH	4-16 cm DBH	16+ cm DBH
On survival of			
1-2 cm	+	-	-
2-4 cm	+	-	**(–)**
4-8 cm	-	-	+
8-16 cm	+	-	**(–)**
16-32 cm	+	+	-
32+ cm	-	-	-