

## TREE SIZE DISTRIBUTIONS, POPULATION TRENDS AND SHADE TOLERANCE

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## (MOST) TREE SIZE DISTRIBUTIONS CAN BE BROADLY CLASSIFIED INTO TWO GROUPS







# WHAT EXPLAINS THE SHAPE OF TREE SIZE DISTRIBUTIONS?

Two general types of explanations have been proposed.

 Population growth/decline: population increase or stasis → Reversed J population decline → Unimodal

2. Life history, specifically shade tolerance: shade tolerant species → Reversed J light demanding species → Unimodal (Wright et al. 2003)

## **MOTIVATION FOR THIS STUDY**

Unimodal size distributions are expected to be quite rare in old-growth forests, because declining species and light-demanding species are expected to be rare.

But in the forest at our study site, Dinghushan, a substantial minority of species show strongly unimodal size distributions.

What explains the unimodal size distributions at this site?

Specific aims:

- 1. To test for an association between size distribution and population growth.
- 2. To investigate the relationships of size distributions with life history and shade tolerance.

### STUDY SITE: DINGHUSHAN FOREST DYNAMICS PLOT



Climate: subtropical monsoon

Mean temperature: 20.9℃

Mean annual precipitation: 1929 mm

Vegetation type: Monsoon evergreen broadleaved forest

Forest age since last disturbance: 400 years

Plot area: 20 ha

Census dates: 2005 and 2010.

<u>Census methods</u>: All trees with diameter ≥ 1 cm are tagged, mapped, measured, and identified to species.

## The plot hosts 71,617 individuals, 210 species, 119 genera, 56 families.

Focal species: 31 species having ≥500 individuals.

## CLASSIFYING THE SHAPE OF TREE SIZE DISTRIBUTIONS

#### **Our method**

Peak **NOT** at the smallest size class

**Modal** (unimodal and multimodal) Peak was at the smallest size class

**Reversed J** (strictly non increasing)

**Significant peak** 

NON Significant peak

Modal

### INDIVIDUAL SPECIES SIZE DISTRIBUTIONS



8/31 species had unimodal distributions in 2005

23/31 species had reversed J distributions in 2005

# WAS THE SHAPE OF THE SIZE DISTRIBUTION RELATED TO POPULATION GROWTH?



$$N_t = N_o (1+\lambda)^{\Delta t}$$

 $\lambda$ = the per capita population growth rate

 $N_o$  = initial population size

 $N_t$  = the population size at time *t* (in 2010)

 $\Delta t$  = the time difference (5 years)

### **NO.** Annual population growth rates were NOT significantly different between reversed J and modal species.

(Wilcoxon Rank Sum test, W = 125, p = 0.1448)

# WAS THE SHAPE OF THE SIZE DISTRIBUTION RELATED TO SHADE TOLERANCE?



**NO** significant association between size distribution and shade tolerance.

(X-square = 0.7901, df = 2, p = 0.6737)

### WAS THE SHAPE OF THE SIZE DISTRIBUTION **RELATED TO MORTALITY RATES?**

$$A_t = N_0 (1-m)^{\Delta}$$

- **m**: annual per capita mortality rate
- $\times$  A<sub>t</sub>: No. of survivor at t=5
- $\times$  N<sub>o</sub>: No.of Ind. at t=0; delta t=5

No. There was no significant association between the shape of the size distribution and mortality rate.

(Wilcoxon Rank Sum Test W = 107, p= 0.5203)

## WAS THE SHAPE OF THE SIZE DISTRIBUTION RELATED TO THE RECRUITMENT RATE?

$$\lambda = r - m$$

Yes. Modal species had significantly lower recruitment rates than reversed-J species. (Wilcoxon rank sum test: W = 149, p = 0.00865)

#### WAS THE SHAPE OF THE SIZE DISTRIBUTION RELATED TO SIZE- DEPENDENT GROWTH AND MORTALITY?



Dips in mortality and growth curves were also found among reversed J species, but the co-occurence of dips in both mortality and absolute growth functions was rare among reversed J species (just 4 /23 species).

Size distributions of 2 of these 4 species were modal in 2010.

Yes. We observed that in modal species, the peak in the size distribution tended to correspond with a dip in mortality and a dip in growth.

## Methods for calculating expected size distributions from size-dependent growth and mortality

At demographic equilibrium

$$p(D) = \frac{R}{NG(D)} \exp\left(\int_{D_0}^{D} -\frac{M(D')}{G(D')}dD'\right)$$

(Kohyama 1991)

R = recruitment rate N = abundance in the initial census G(D)= absolute diameter growth as a function of diameter M(D) = mortality as a function of diameter  $D_0$  = the size of individuals upon recruitment



#### Test 1 – Is the general shape the same?

Of the 8 observed unimodal species

- 7 were predicted to be unimodal
   (4 statistically significantly so)
- × 1 was predicted reversed J

Of the 23 observed reversed J species

- × 18 were predicted reversed J
- 5 were predicted modal; 3 of these 5 had unimodal size distributions in 2010.

Yes in 25 (or 27) of 31 species.

#### Test 2 – Are size class abundances similar?

There were strong (r>0.5) and significant (p<0.05) correlations between observed and expected abundances per size class in 24 of 31 species (18 reversed J and 6 modal):.

Observed and expected size distribution had overlapping confidence intervals, i.e. not significantly different, in over 50% of size classes in 12 of 31 species (10 reversed J and 2 modal).

#### Mixed results.

#### **Test 3 – How do shape parameters compare?**



 $p(D) = \frac{1}{n} \exp(-\alpha D)$ 

They are correlated, but not well-predicted.

### THE PREDICTED EQUILIBRIUM SIZE DISTRIBUTIONS ARE FAR FROM CURRENT SIZE DISTRIBUTIONS.

Size distributions (and abundances) may still be changing over time, and far from equilibrium.

## CONCLUSIONS

- \* At this site, unimodal size distributions are not consistently associated with either population decline or shade-intolerance.
- Equilibrium size distributions predicted from sizedependent growth (G(D)) and size dependent mortality (M(D)) match current size distributions in some species but not others.
- Even though the forest at this site is 400 years old, it is not at equilibrium. Ongoing changes may reflect late succession, and/or responses to environmental change.

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