Tree seedling dynamics over 7 years in a subtropical rain forest, Taiwan

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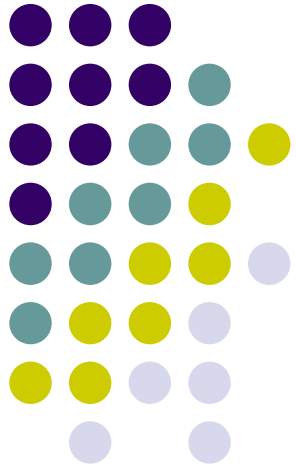


Outline

- General description of seedling dynamics in the Fushan forest

- Density dependence at new seedling stages

Introduction

- Seedling recruitment is a bottleneck in the life history of many tree species. (Swaine 1996)

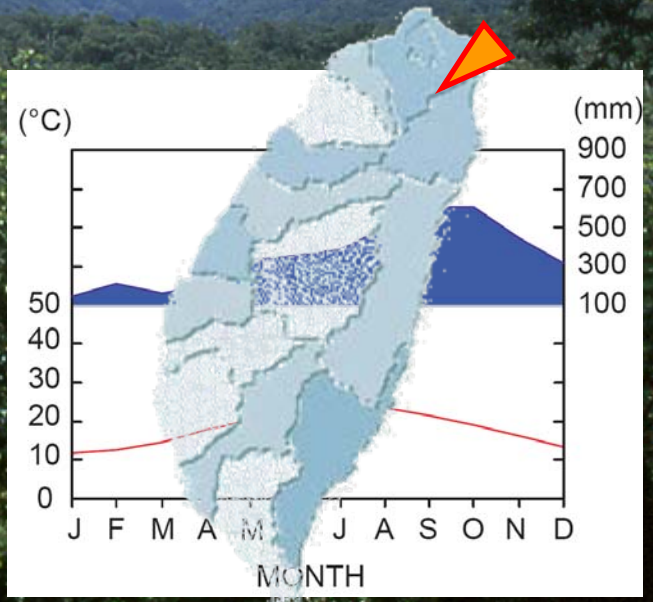
- Forest community structure and composition may be largely determined at early life history stages.

  (Augspurger 1984, De Steven 1991, Jones et al. 1994, Connell & Green. 2000)

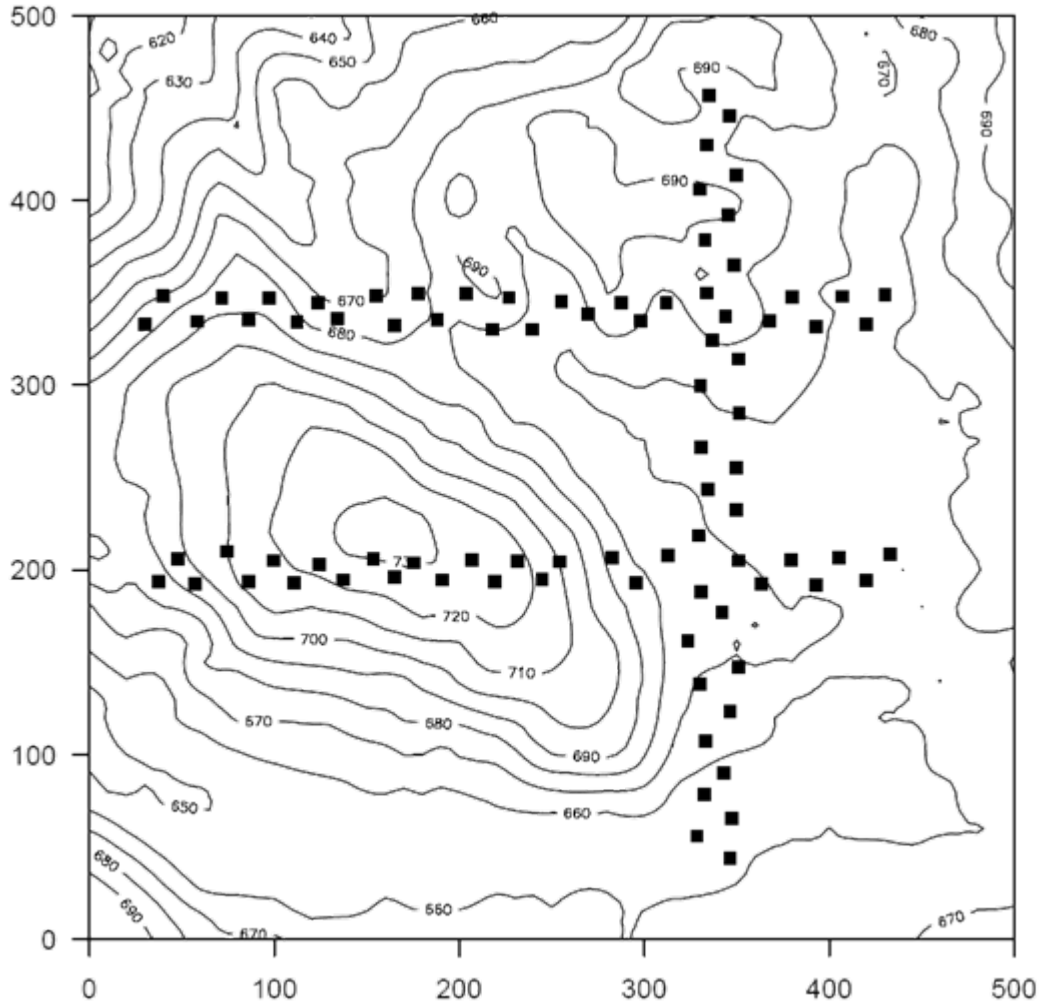
Fushan Forest Dynamics Plot

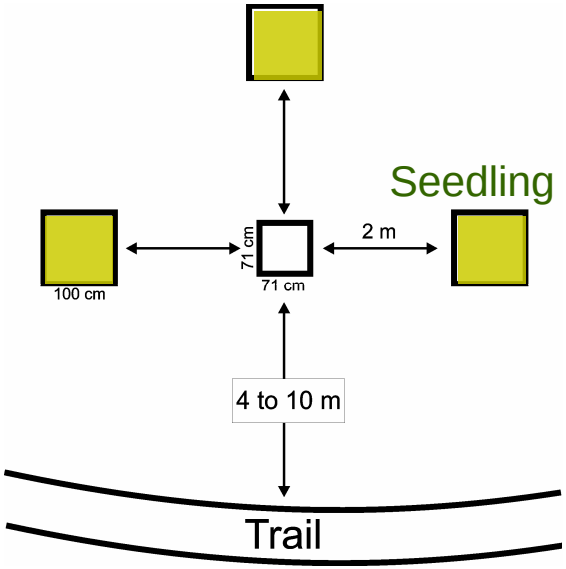
Area: 25 ha
Elevation: 650–733 m

Average temperature: 18.2 ℃
Annual precipitation: 4,271 mm
Typhoons: 1.4 / yr



Distribution of seed traps and seedling plots





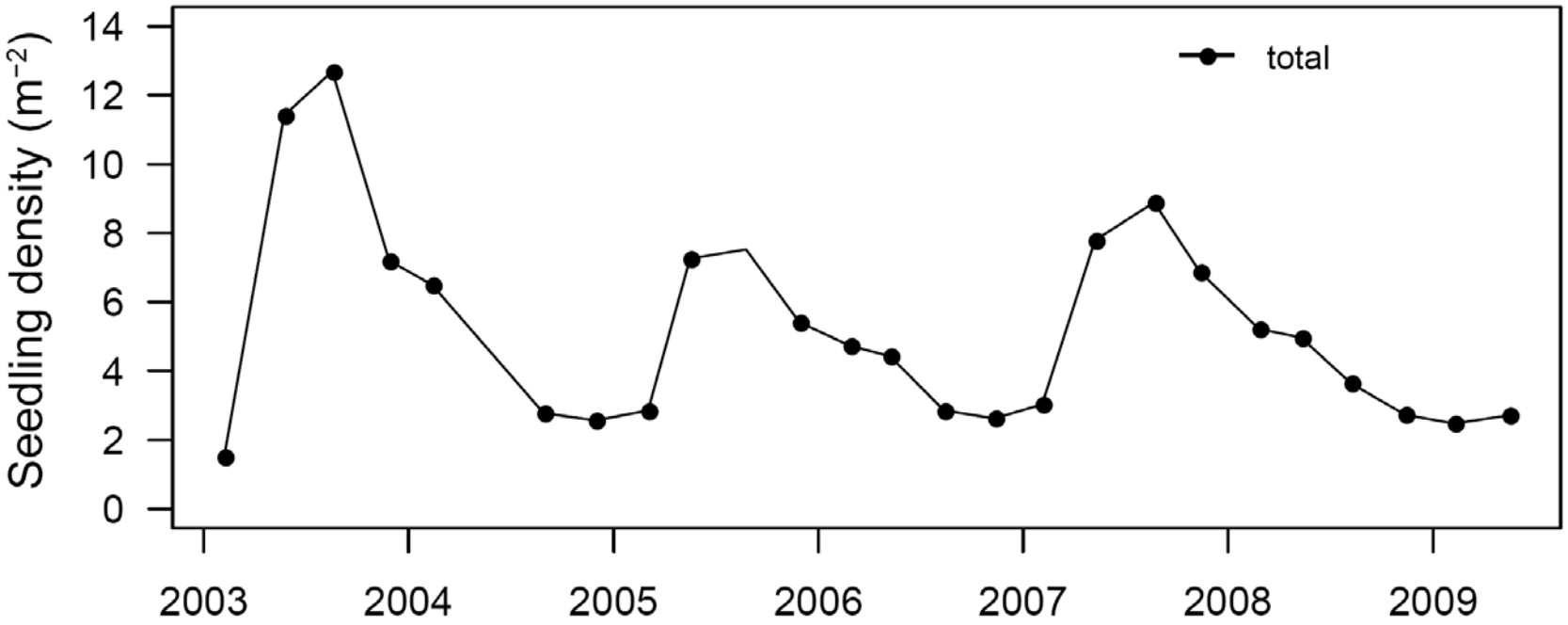
- 87 seed traps
- 261 seedling plots

Seedling census in Fushan FDP

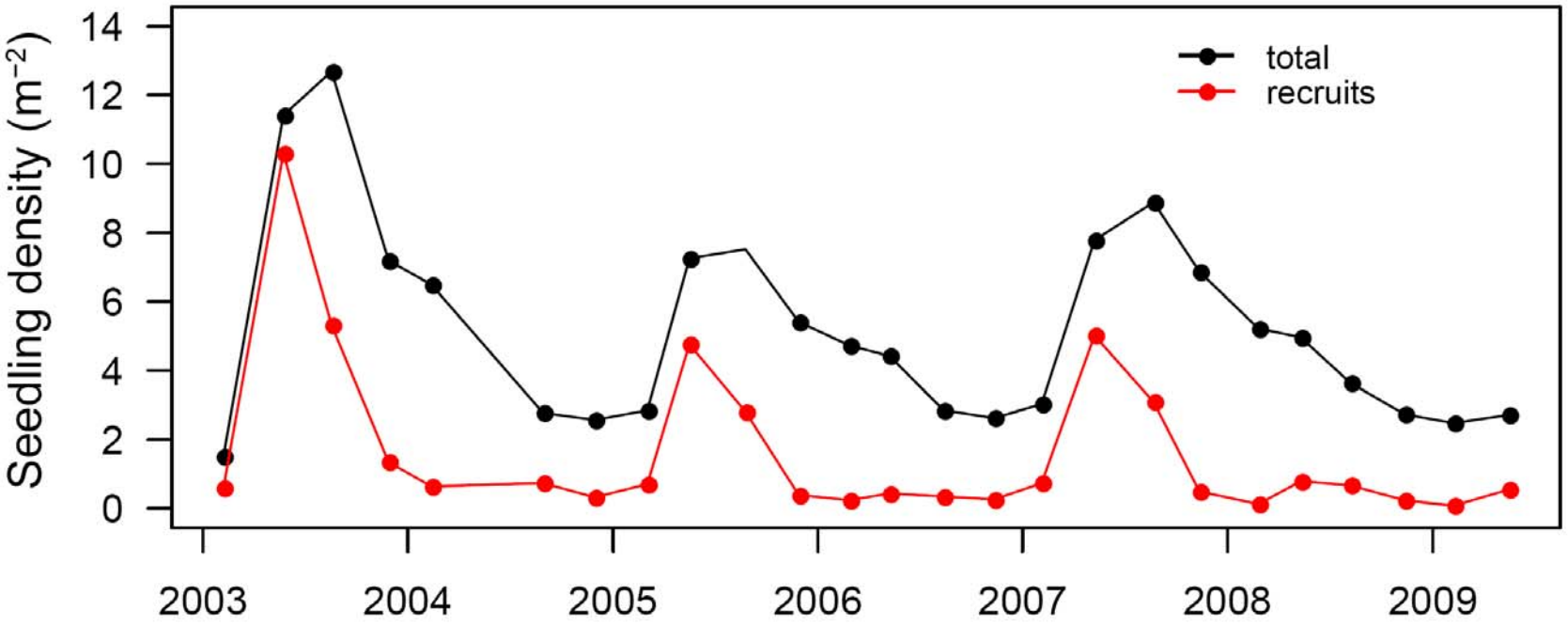
- 261 1-m^2 seedling plots
  - All tree species <1 cm DBH
  - First census: February, 2003
  - Recensus every 3 months

- Sample size (as of May 2009)
  - 25 censuses (census in May, 2004 was missed)
  - 10,932 seedlings
  - 36 species

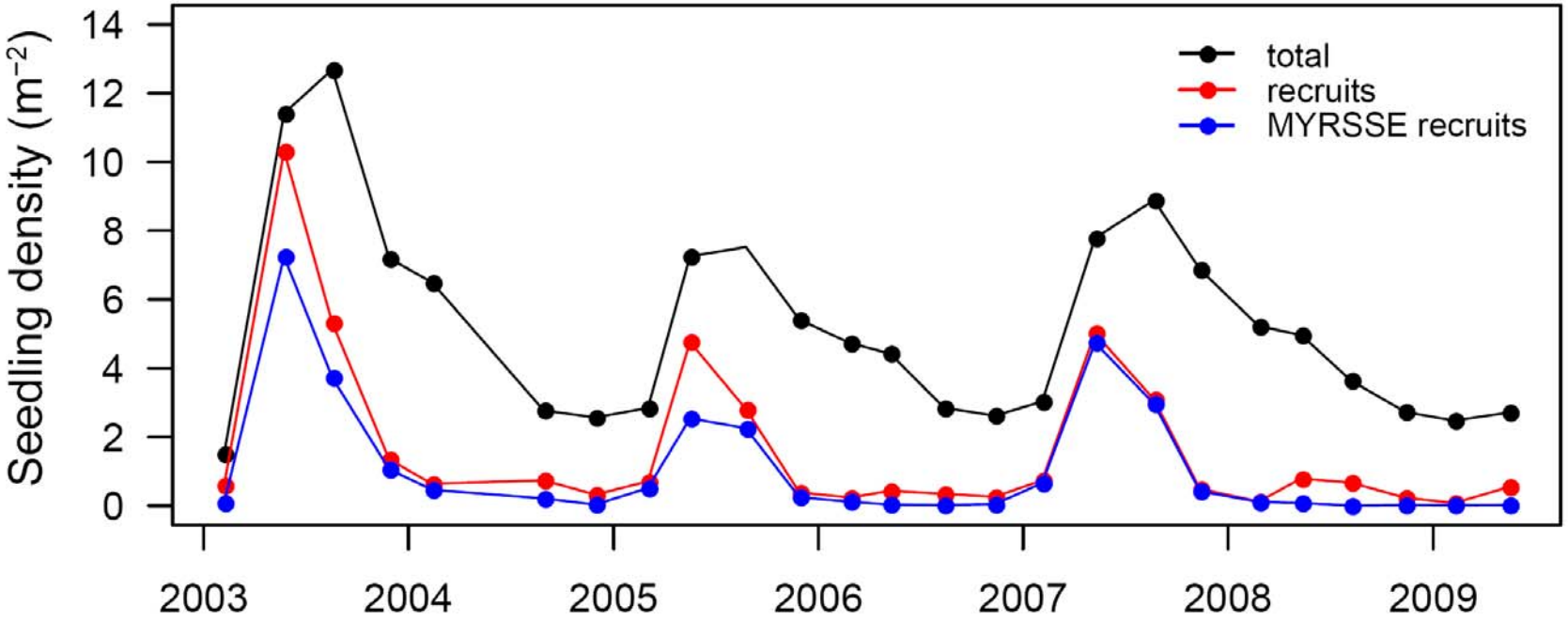
Interannual variation: Seedling density



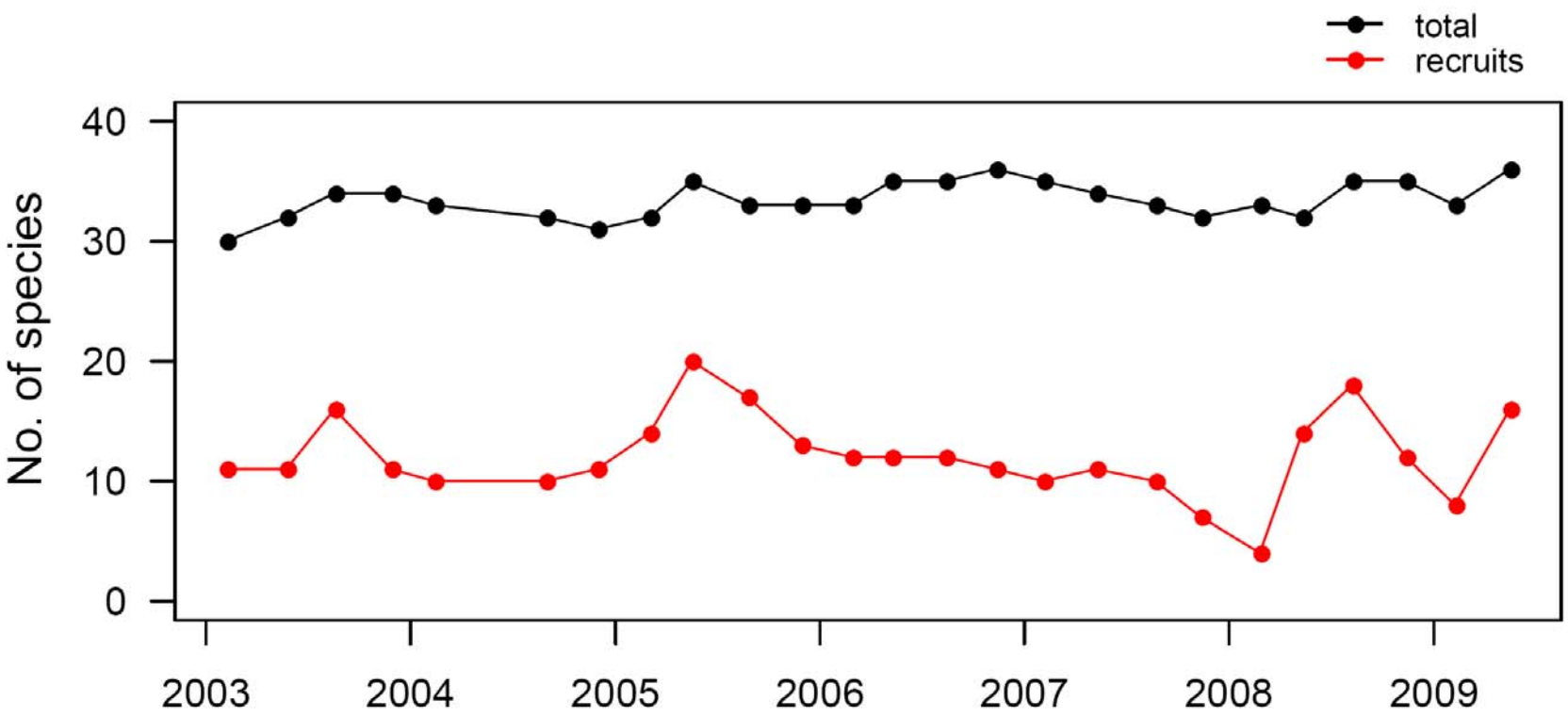
Interannual variation: Seedling density



Interannual variation: Seedling density

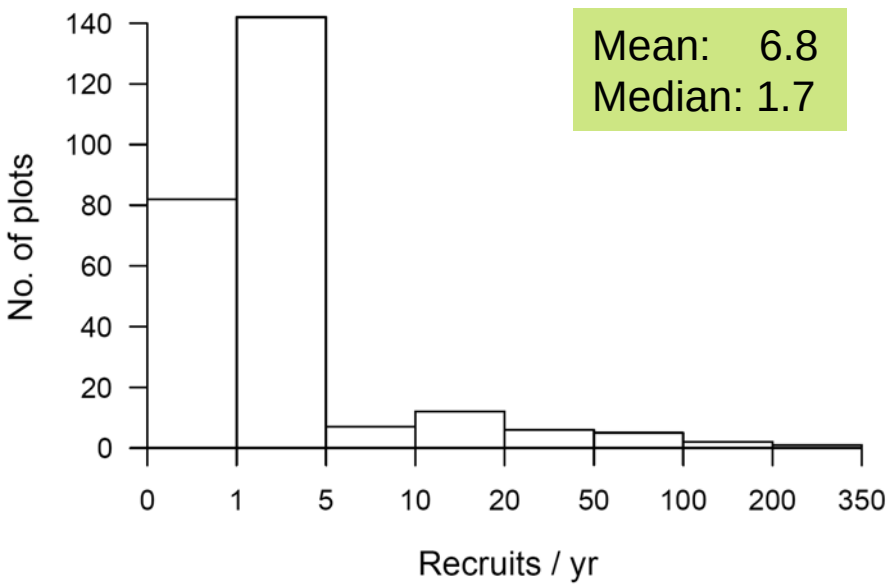


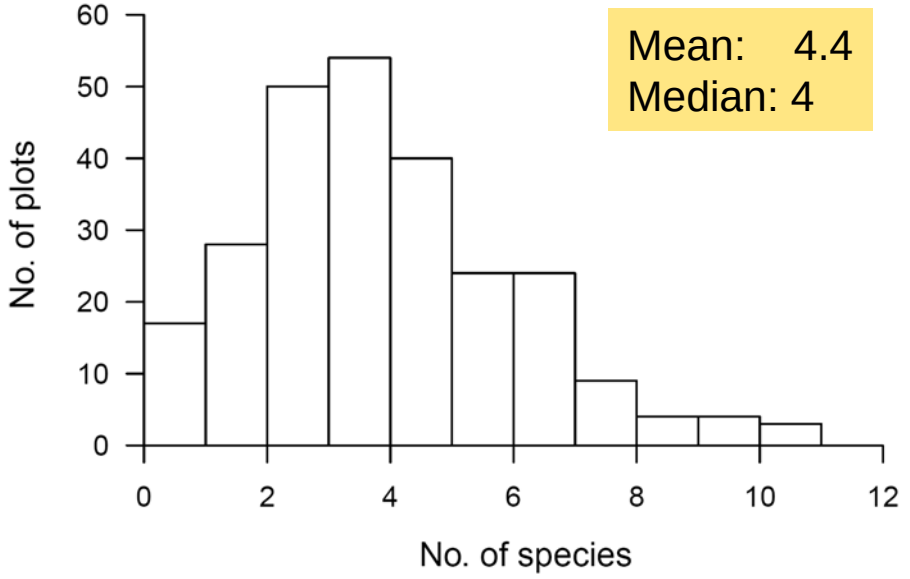
Interannual variation: Seedling species richness



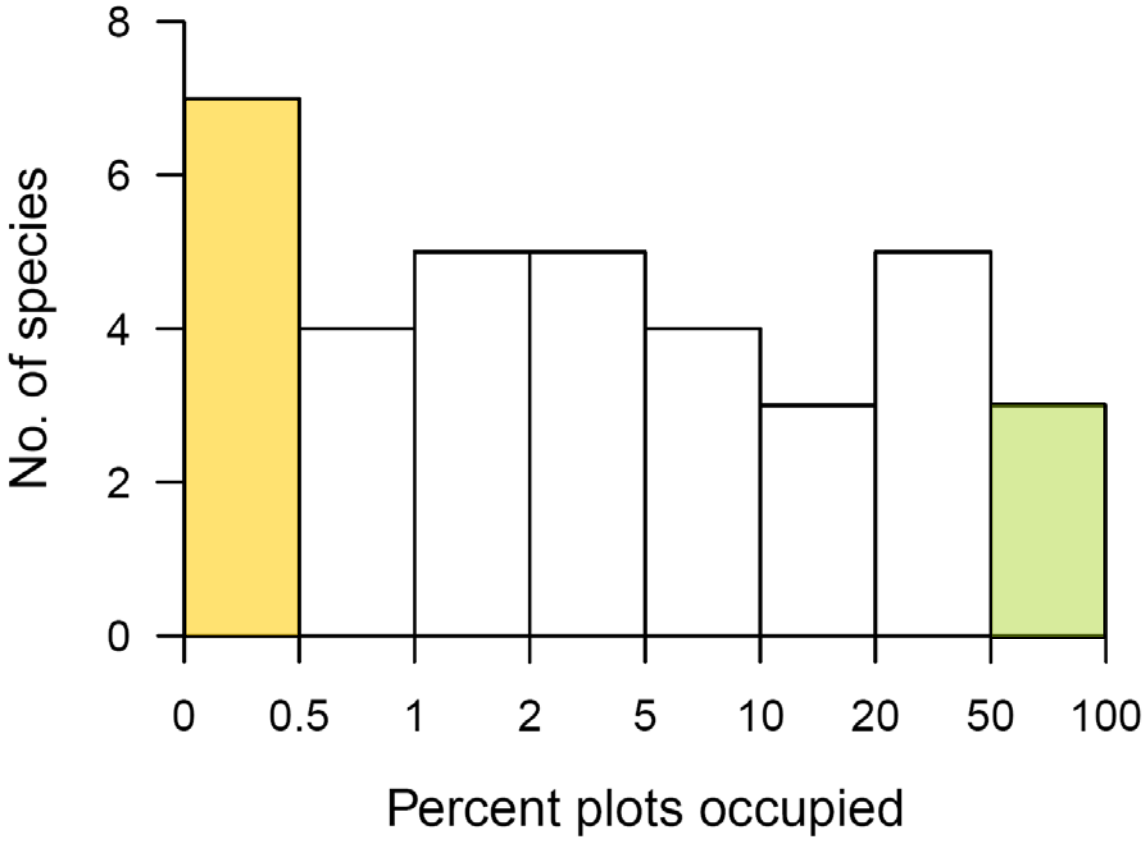
Spatial variation:

Seedling density & species richness



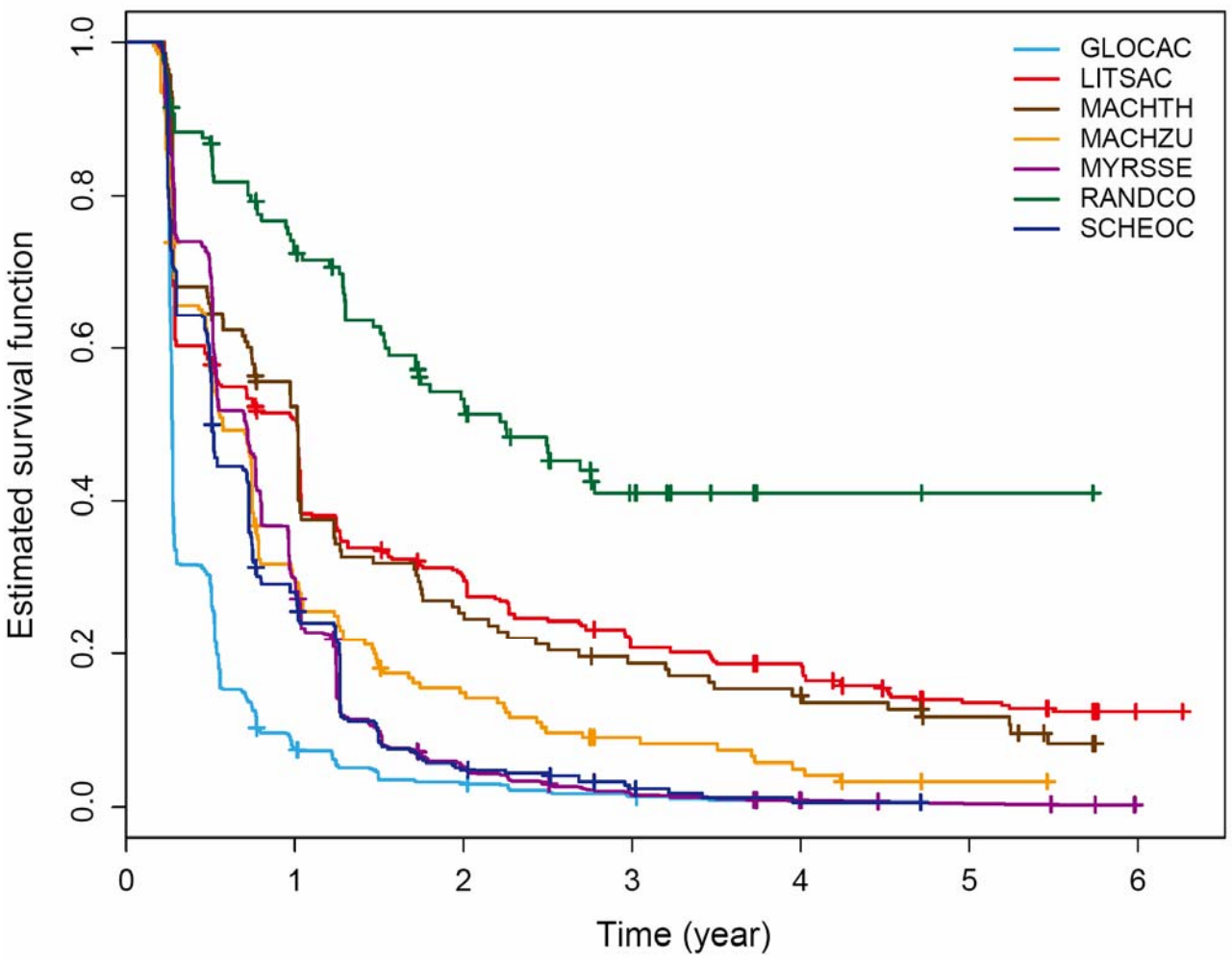


Seedling spatial distribution

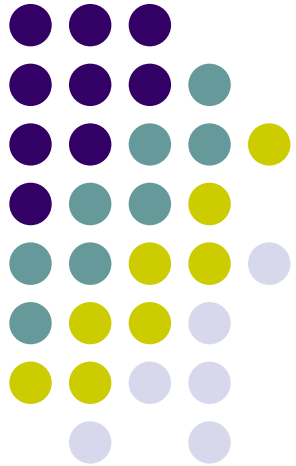


Seedling survival

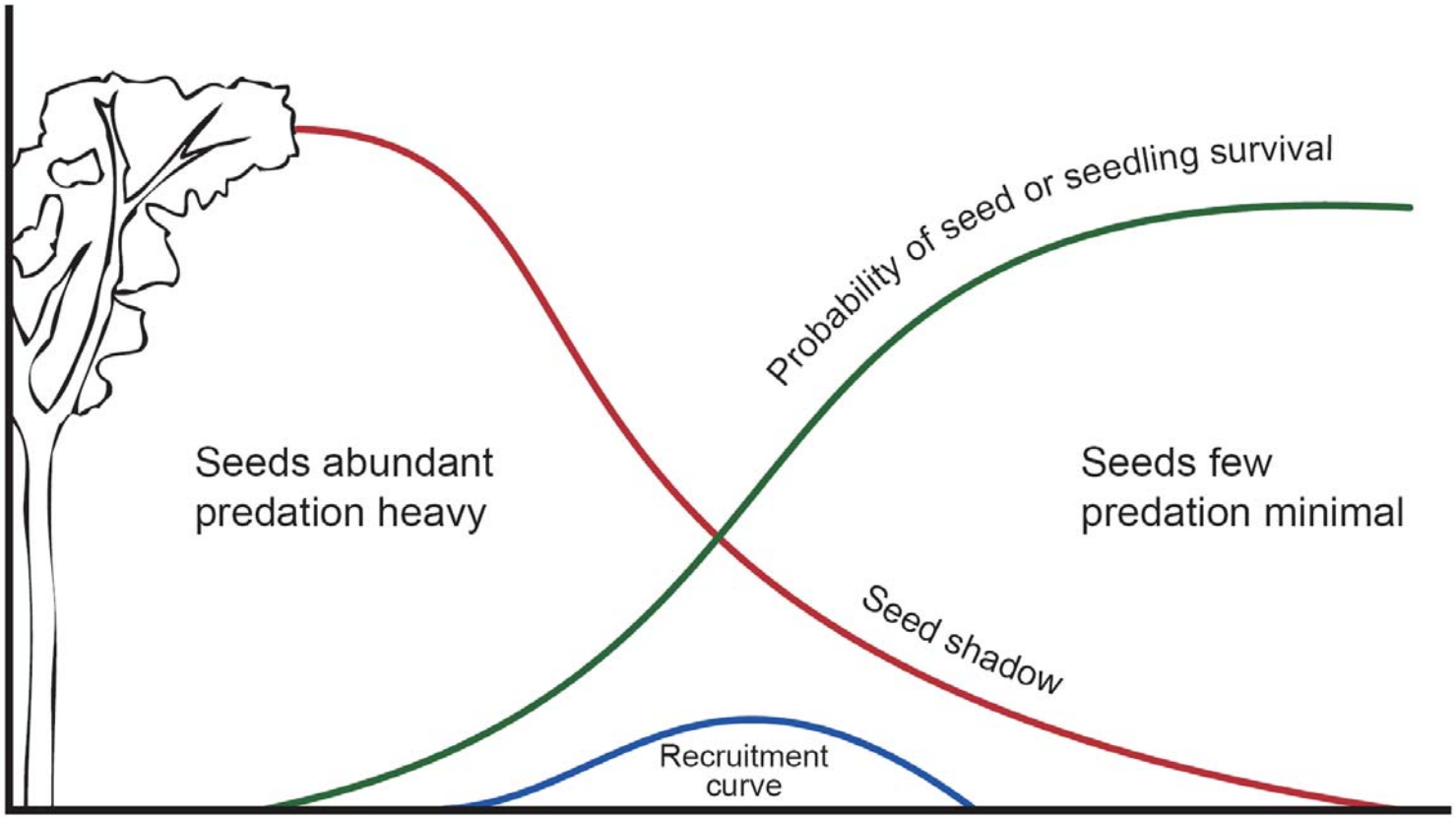
Product limit (Kaplan-Meier) estimator



Density-dependent effects at young seedling stages



Janzen-Connell hypothesis



(Janzen 1970, Connell 1971)

- Density-dependent seedling recruitment and mortality in tropical forests (Webb & Peart 1999, Harms et al. 2000, Hille Ris Lambers et al. 2002)
- Negative density dependence is thought to be strongest for young seedlings. (Clark & Clark 1985)
- Hurricanes can alter the processes that may determine the seedling dynamics. (Walker & Neris 1993, Walker et al. 2003)
- Hurricanes may lead to weaker density-dependent effects of adults on seedling survival. (Vanermeer et al. 1996)

Objects

- Does density dependence occur at new seedling stages of Fushan tree species?
  - Recruitment (seed-to-seedling transition)
  - Survival
  - Growth

Seed-to-seedling transition

- 8 tree species with >50 new seedlings
- Model fitted by maximum likelihood

$$R_{it} = aS_{it}^{\ b}$$

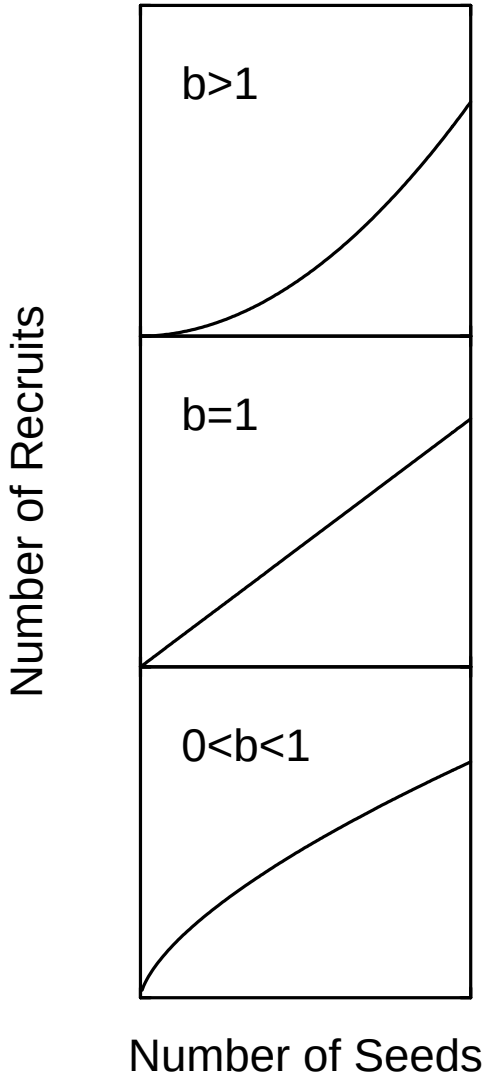
- Definitions:

  $R_{it} \equiv$ recruit density for station i in year t

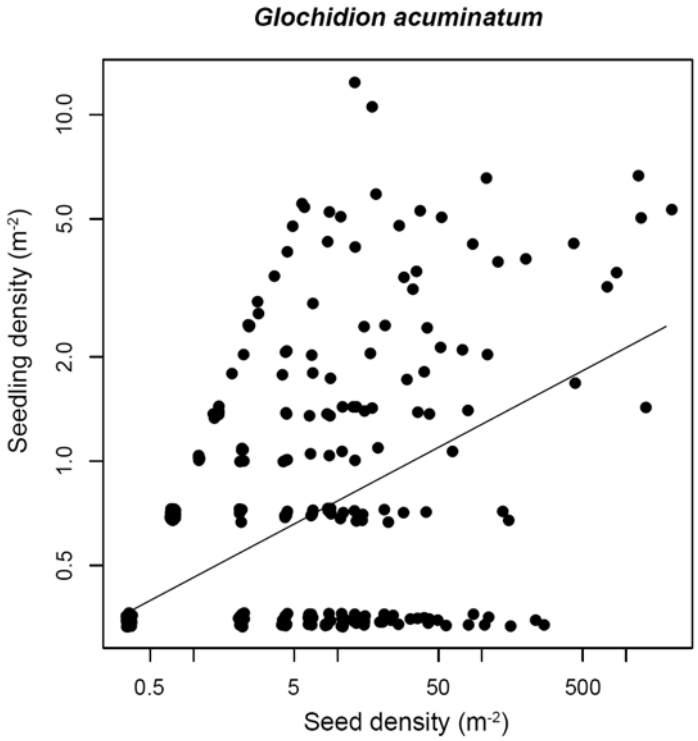
  $S_{it} \equiv$ seed density for station i in year t

  $a, b \equiv$ fitted parameters

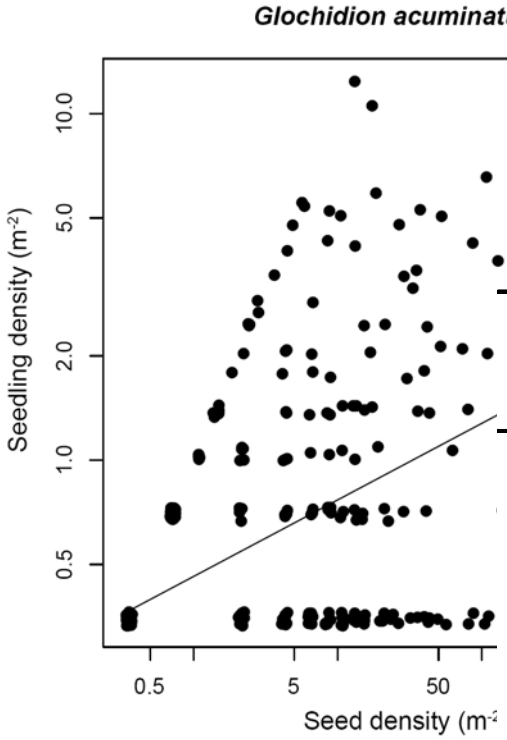
- Asymptotic 2-unit support limits (analogs of 95% CIs)



Negatively density dependent recruitment

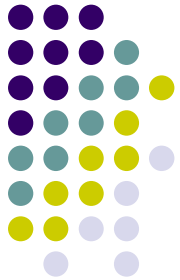


Negatively density dependent recruitment



Species	Estimated parameters			
	a	2-unit SL	*b*	2-unit SL
Elaeocarpus japonicus	0.78	(0.52, 1.25)	0.39	(0.21, 0.60)
Engelhardtia roxburghiana	0.58	(0.44, 0.79)	0.17	(0.09, 0.25)
Glochidion acuminatum	1.07	(0.93, 1.23)	0.23	(0.19, 0.27)
Litsea acuminata	0.83	(0.68, 1.01)	0.42	(0.35, 0.50)
Machilus thunbergii	0.94	(0.75, 1.19)	0.12	(0.03, 0.20)
Machilus zuihoensis	0.96	(0.82, 1.10)	0.02	(0.0002, 0.09)
Prunus phaeosticta	0.73	(0.56, 0.97)	0.02	(0.000007, 0.12)
Schefflera octophylla	0.73	(0.56, 0.94)	0.48	(0.42, 0.54)

Density-dependent effects on new seedling **survival**



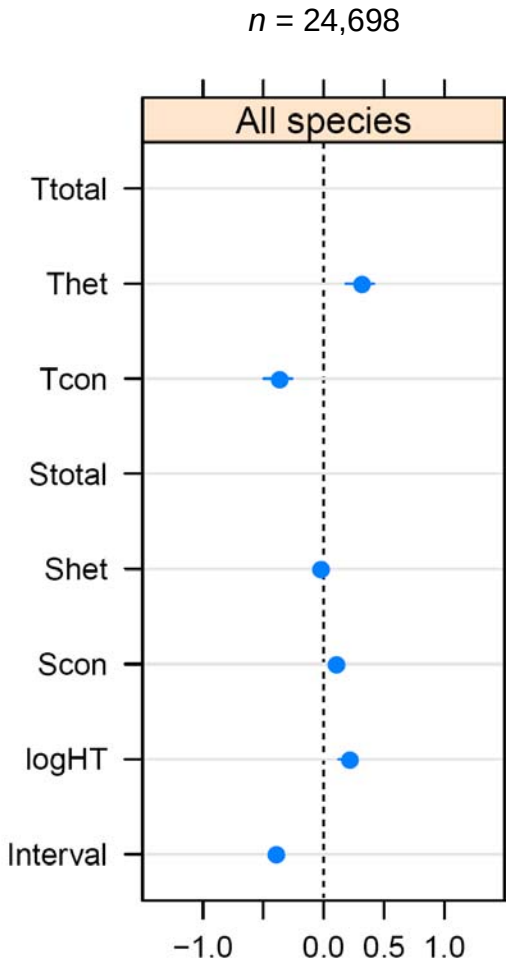
- Generalized linear mixed-effects models (GLMM) with binomial errors
- Explanatory variables (Fixed effects)
  - Census interval
  - log(Initial height)
  - Seedling density in the same 1-m^2 seedling plot
    - Total, conspecific, & heterospecific seedling neighbors
  - Adult stem number within 10 m
    - Total, conspecific, & heterospecific adult neighbors
- Random effects
  - Individuals, species, station/plot

Seedling survival models

Model type	Model	Variables included
Density independent	0	$a + b\ \mathrm{INT} + c\ \mathrm{HT}$
Effect of conspecific density = effect of heterospecific density	1	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d\ \mathrm{S_{total}}$
	2	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + f\ \mathrm{T_{total}}$
	3	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d\ \mathrm{S_{total}} + f\ \mathrm{T_{total}}$
Effect of conspecific density ≠ effect of heterospecific density	4	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d_1\ \mathrm{S_{con}} + d_2\ \mathrm{S_{het}}$
	5	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + f_1\ \mathrm{T_{con}} + f_2\ \mathrm{T_{het}}$
	6	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d_1\ \mathrm{S_{con}} + d_2\ \mathrm{S_{het}} + f\ \mathrm{T_{total}}$
	7	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d\ \mathrm{S_{total}} + f_1\ \mathrm{T_{con}} + f_2\ \mathrm{T_{het}}$
	8	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d_1\ \mathrm{S_{con}} + d_2\ \mathrm{S_{het}} + f_1\ \mathrm{T_{con}} + f_2\ \mathrm{T_{het}}$

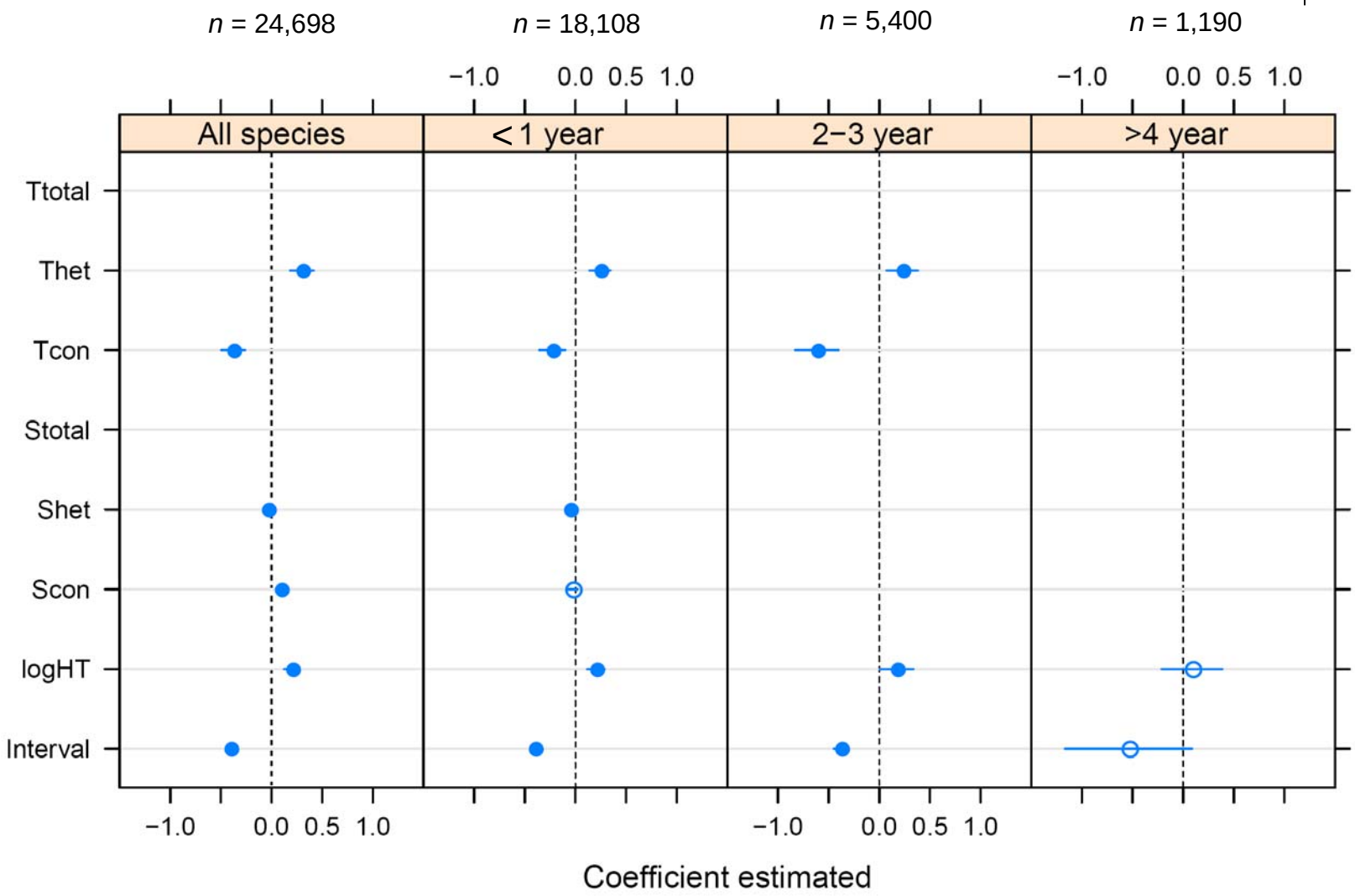
- Model selection: Akaike's Information Criterion (AIC)
- 2 different scales: community level, species level

Seedling survival model at **community level** **(All species combined)**

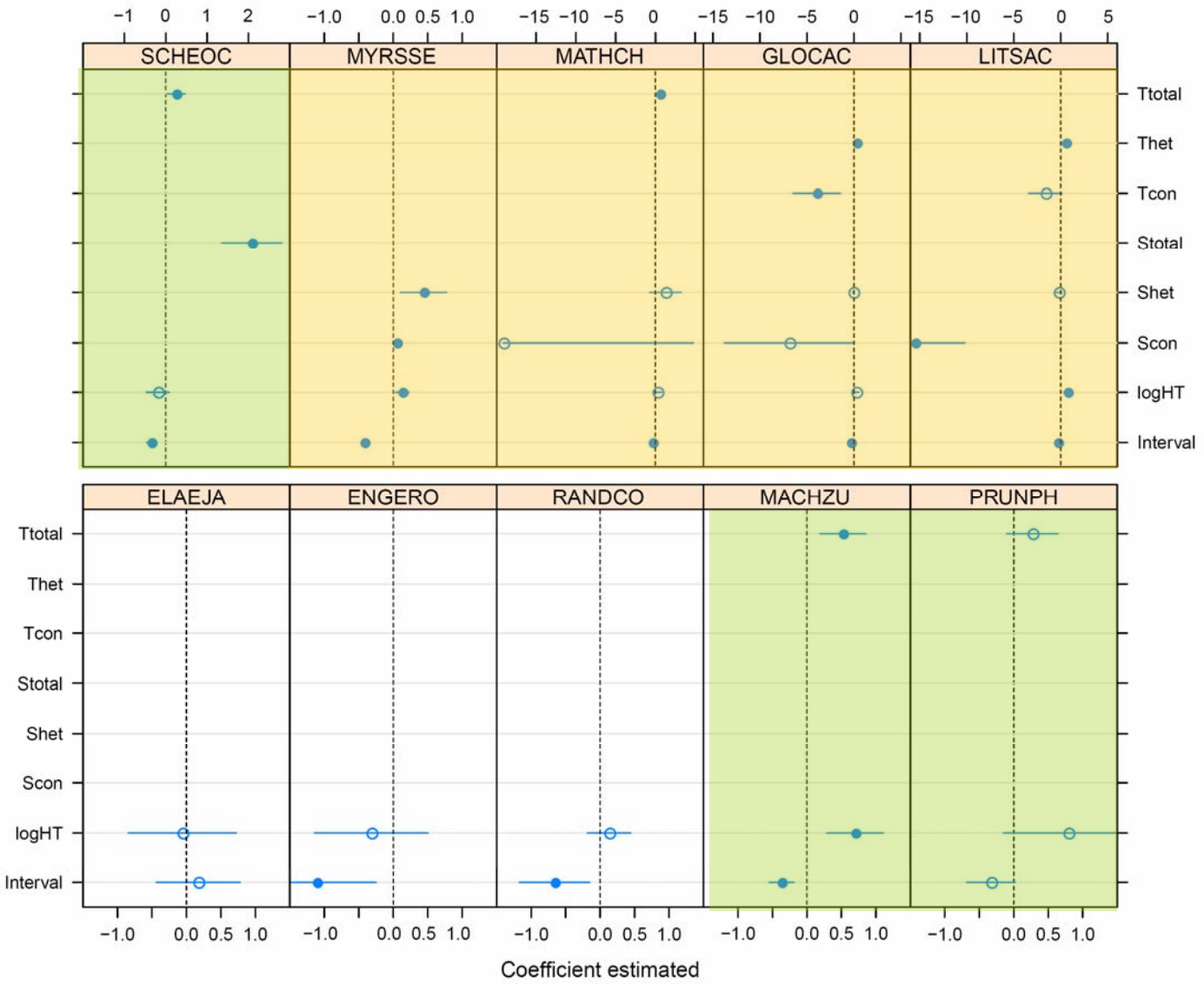


- Best model: 8
- Effects of conspecific density $\neq$ effects of heterospecific density

Seedling survival models at **community level** (All species combined)



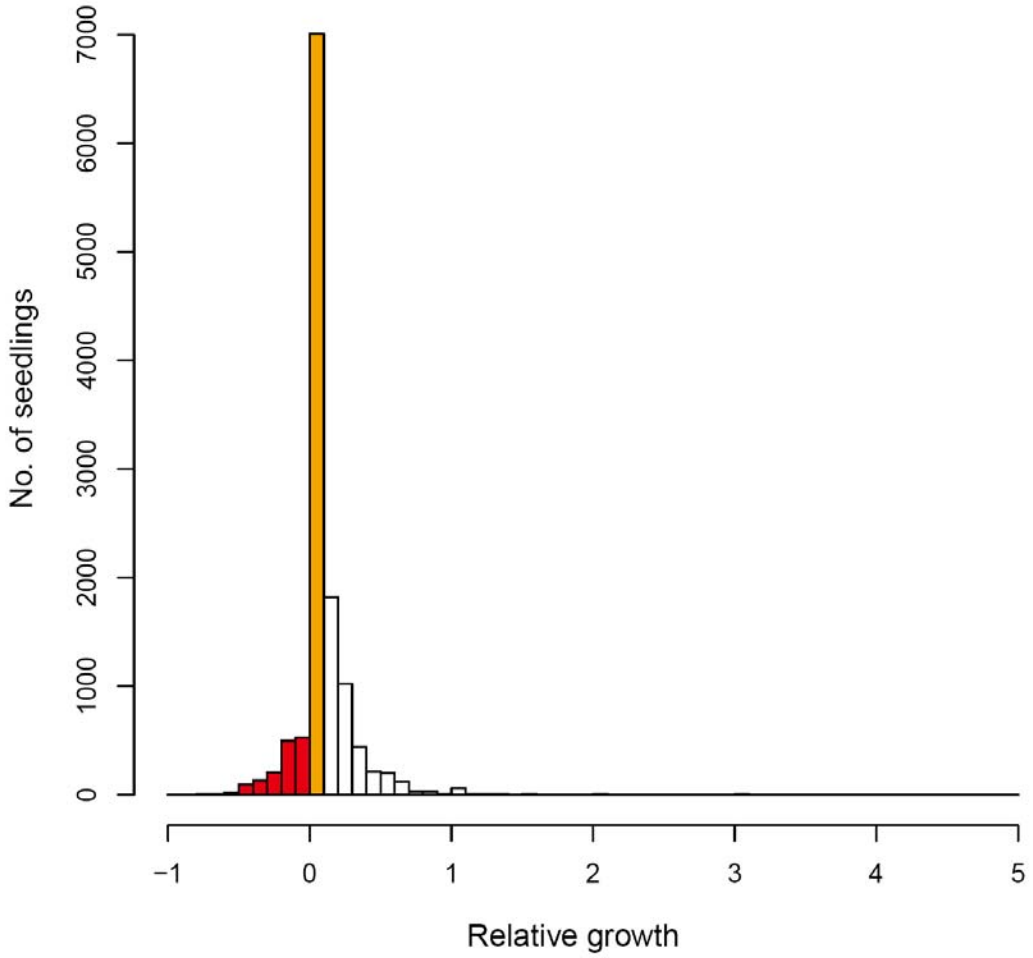
Seedling survival models at **species level** (Species with >100 recruits)



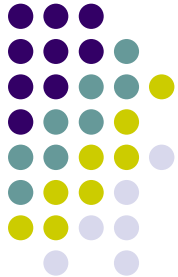
Density-dependent effects on new seedling **growth**

- Binary growth data
  - RG >0: 1
  - RG $\leqslant$0: 0

$$\text{Relative Growth (RG)} = \frac{H_T}{H_0}$$



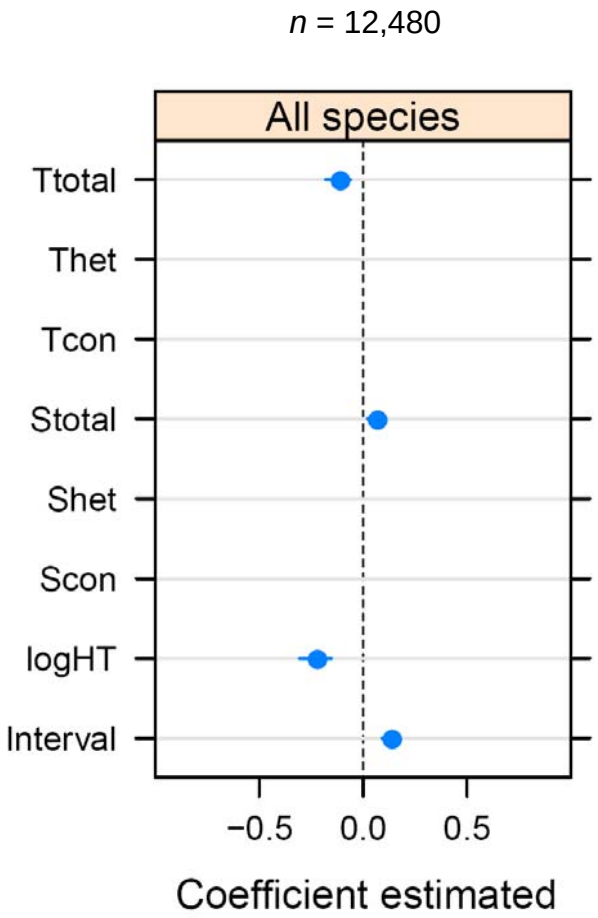
Density-dependent effects on new seedling growth



- Binary growth data
  - RG >0: 1
  - RG $\leqslant$0: 0

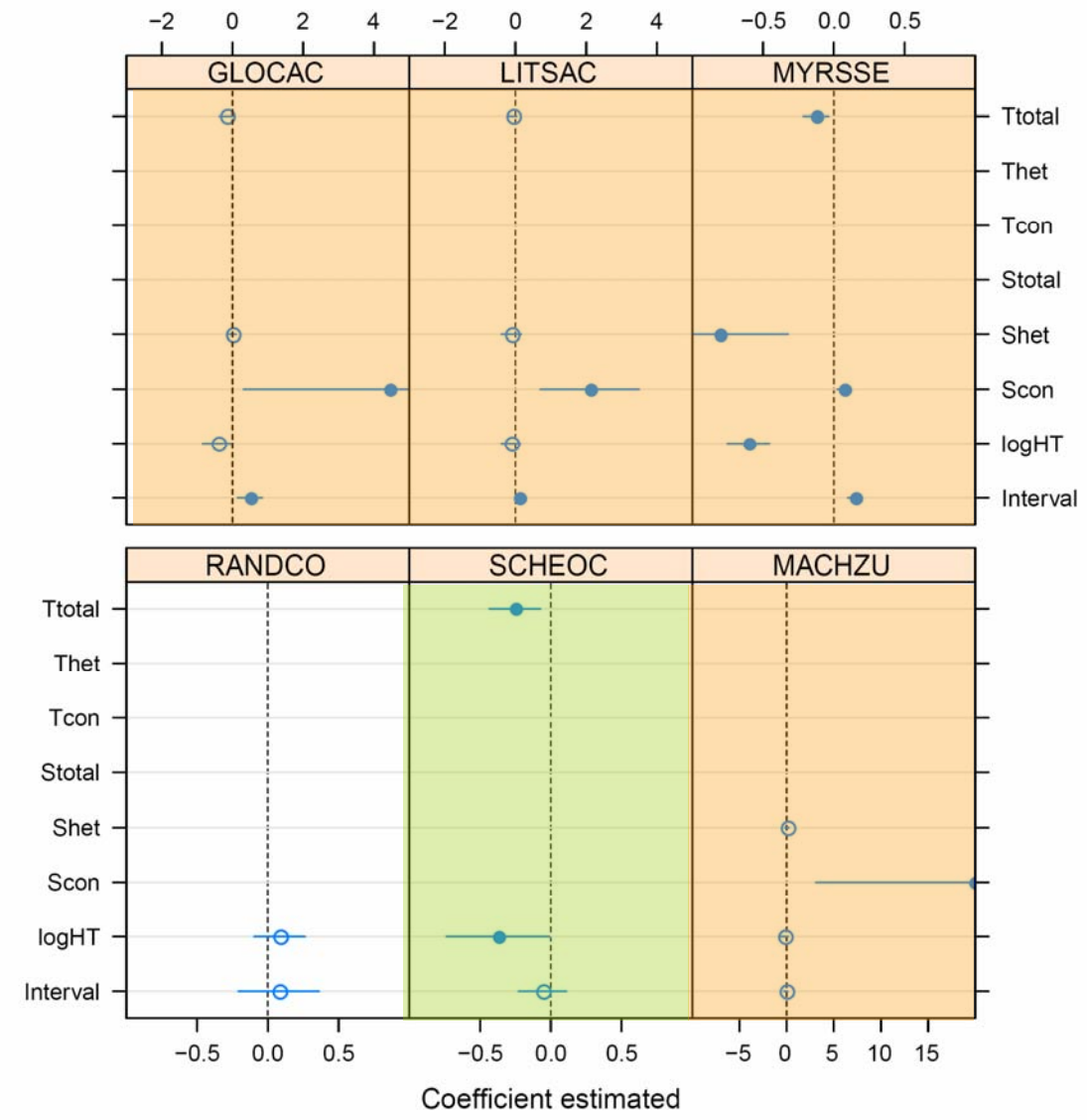
- Generalized linear mixed-effects models (GLMM) with binomial errors
  - Fixed effects
    - Interval, log(HT), seedling and adult density
  - Random effects
    - Individuals, species, station/plot

Seedling growth model at **community level** **(All species combined)**



- Best model: 3
- Effects of conspecific density = effects of heterospecific density

Seedling growth models at **species level** (Species with >100 recruits)

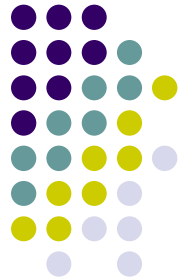


Summary

- Density dependence characterized the seedling recruitment, mortality, and growth.
  - Negatively density-dependent recruitment were observed for all species examined.
  - At community level, seedling and adult density were significant drivers of seedling mortality and growth.
  - Individual species-level analyses showed considerable variation among species.

Acknowledgements

- Funding
  - Taiwan Forestry Research Institute
  - Taiwan Forestry Bureau
- Logistical support
  - Fushan Research Center, TFRI
  - National Taiwan University
  - Tunghai University
- Sheng-Hsin Su (TFRI)
- Census team of Fushan FDP
- Students from many schools



Explanatory variables in new seedling survival and growth models

Parameter	Data		
	Range	Mean	Median
Census interval (days)	59 - 210	93.60	92
Initial height (cm)	0.3 - 38	6.05	4
Seedling density (m^{-2})			
Total	1 - 1049	36.84	12
Conspecific	1 - 1041	26.17	5
Heterospecific	0 - 1048	10.67	3
Adult stem number within 10 m			
Total	21 - 448	212.60	230
Conspecific	0 - 81	20.21	8
Heterospecific	20 - 447	192.40	207

Seedling survival models (Species with >100 recruits)

Model type	Model	Variables included	No. species
Density independent	0	$a + b\ \mathrm{INT} + c\ \mathrm{HT}$	3
Effect of conspecific density = effect of heterospecific density	1	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d\ S_{total}$	0
	2	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + f\ T_{total}$	2
	3	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d\ S_{total} + f\ T_{total}$	1
Effect of conspecific density $\neq$ effect of heterospecific density	4	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d_1\ S_{con} + d_2\ S_{het}$	1
	5	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + f_1\ T_{con} + f_2\ T_{het}$	0
	6	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d_1\ S_{con} + d_2\ S_{het} + f\ T_{total}$	1
	7	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d\ S_{total} + f_1\ T_{con} + f_2\ T_{het}$	0
	8	$a + b\ \mathrm{INT} + c\ \mathrm{HT} + d_1\ S_{con} + d_2\ S_{het} + f_1\ T_{con} + f_2\ T_{het}$	2