Prevalent negative density dependence in later life stages in a species-rich subtropical forest, central China

By Guo Yili
Wuhan Botanical Garden

Presentation outline

- Introduction
- Materials and methods
- Results
- Discussion
- Acknowledgements

Introduction

- **Species coexist in natural communities, but the mechanisms by which they do so are poorly understood (Wright 2002). One of the most supported mechanisms is negative density dependence (NDD).**

- **Most previous studies have demonstrated that NDD regulated the demographics of tree species, both common species (Zhu *et al.* 2010; Bagchi *et al.* 2011) and rare species (Johnson *et al.* 2012). However, inconsistent results have been observed in some forests (Dovciak *et al.* 2001; Bin *et al.* 2011; Luo *et al.* 2012).**

- **Analysis approaches:**
  - **Mortality patterns: early life stages; short-term dynamic temporal data; may exaggerate the prevalence of NDD by density-independent factors.**
  - **Spatial distribution patterns: later life stages; DBH as potential life-span; conspecific clustering that declines with increasing size classes; appropriate null models.**

- **Confounding factors which can substantially influence the analysis of NDD are habitat heterogeneity (Zhu *et al.* 2010; Bagchi *et al.* 2011), timber harvesting or succession (Shmida and Wilson 1985).**

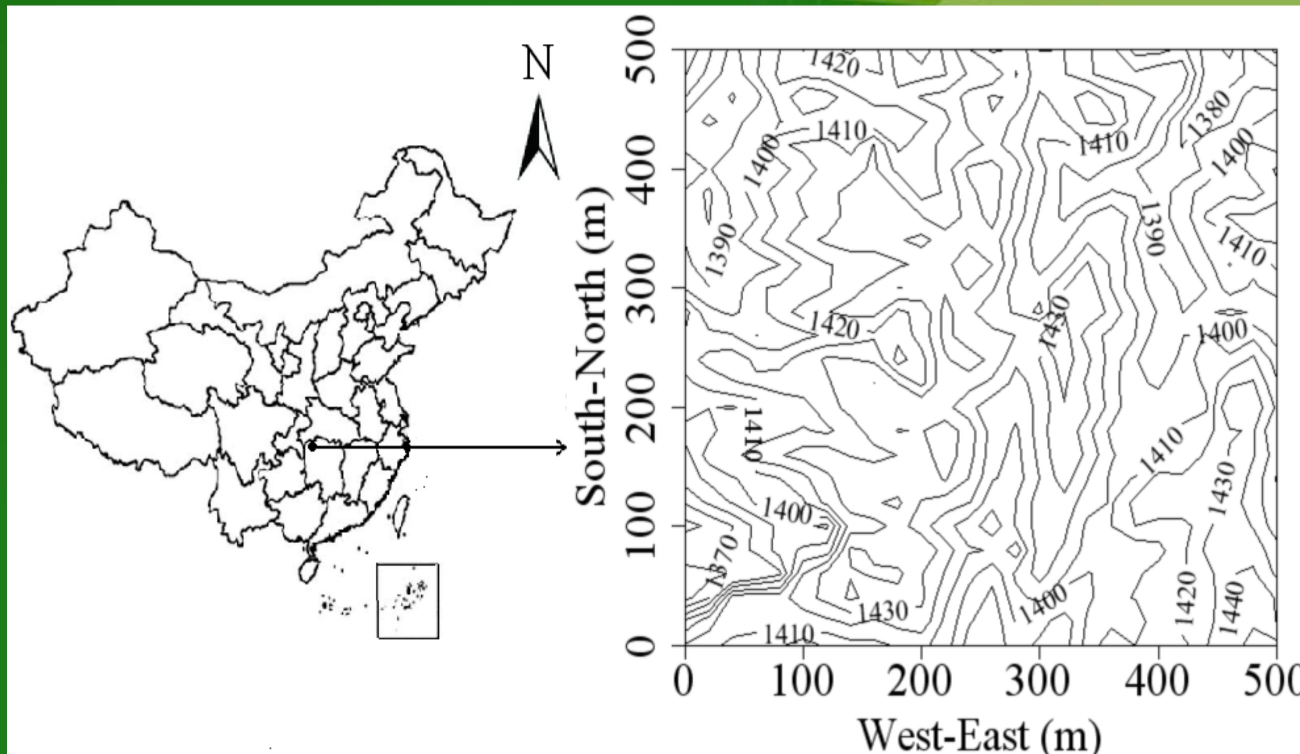
- **Species-level variations, such as shade tolerance, are important factors affecting spatial patterns of tree species (Wang *et al.* 2010). Species attributes are likely to confound the effects of NDD.**

- **Questions:**
  - **Is NDD an important mechanism regulating plant population structure in later tree life stages in a subtropical mountain forest, central China?**
  - **After controlling for habitat heterogeneity, how does species-specific characteristics in shaping the strength of NDD in natural forests?**

- **Primary analyses:**
  - **Analysis 1: Spatial patterns of study objects.**
  - **Analysis 2: Variation in clustering of juveniles and adults.**
  - **Analysis 3: The prevalence of NDD.**
  - **Analysis 4: NDD and species attributes.**

Materials and methods

- **Study site**



- **A mid-subtropical, mid-elevation mountain evergreen and deciduous broad-leaved mixed forest in central China;**
- **53 families, 114 genera, 238 species, and 186 556 individuals;**
- **Mean annual precipitation: 2105.4 mm, ranges up to 2840.1 mm;**
- **Elevation: ranging from 1354.7 m to 1455.9 m a.s.l..**

- **Data collection:**
  - **Life stages: juveniles, adults (Bagchi *et al*. 2011).**
  - **Study objects: 88 species with ≥ 25 individuals at each stage.**
  - **Growth forms: canopy, understory, shrub.**
  - **Dispersal modes: animal, wind and gravity-dispersed (Seidler and Plotkin 2006).**
- **Null models:**
  - **Heterogeneous Poisson process (HPP): four environmental variables.**
  - **Bivariate random labeling (RL) (Wiegand 2004): case-control design.**

- **Statistical models:**
  - **HPP: pair correlation function g(r) (Analysis 1).**
  - **RL: adults as "control" (pattern 1).**
    - ➢ **$g_{dif} = g_{22}(r) - g_{11}(r)$ (Analysis 2).**
    - ➢ **$d(r) = g_{21}(r) - g_{22}(r)$ (Analysis 3).**
  - **Nonparametric methods: $d_{max}(r)$ (Analysis 4).**

Results

- **Spatial patterns of common species:**
  - **68 out of 88 showed aggregation at certain scale.**
  - **35 still showed aggregation at a scale of 30 m.**

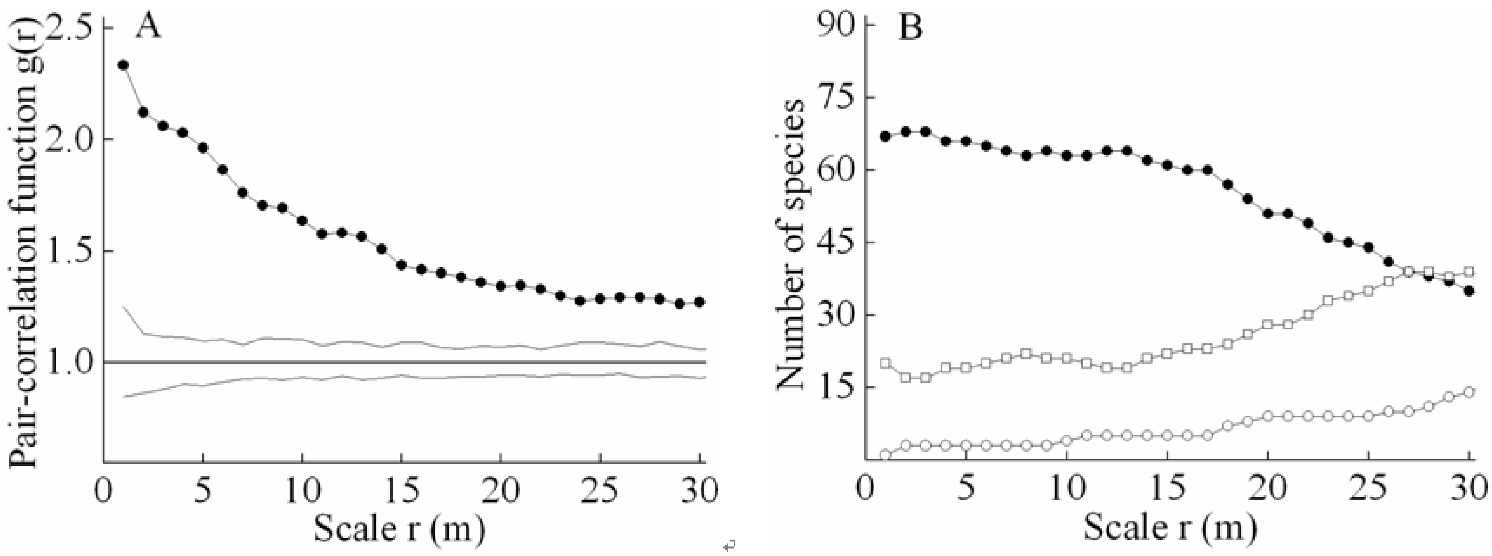


Fig. 2 Spatial patterns of common species. (A) *F. lucida* as an example. The simulation envelopes (dashed lines) were constructed using the 199 simulations of the HPP null model. The solid circles denote the g-functions of the observed data over scale r. (B) Number of species showing significant aggregation (solid circles), random (open squares) and regular patterns (open circles) over different scales in the BDGS plot.

- **Variation in clustering of juveniles and adults:**
  - **46 out of 88 showed a systematic decline in strength of clustering from juveniles to adults.**
  - **12 opposite tendency.**
  - **30 followed RL null model.**

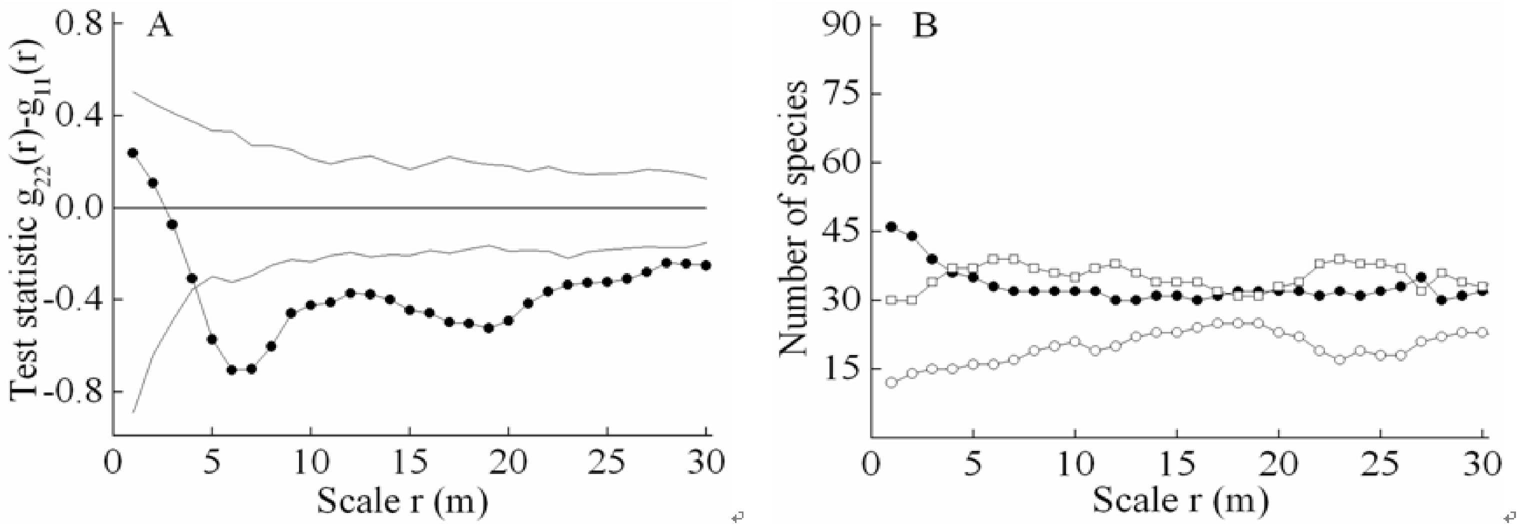


Fig. 3 Variation in clustering of juveniles and adults. (A) *F. lucida* as an example. The simulation envelopes (dashed lines) were constructed using the 199 simulations of the RL null model. Solid circles denote $g_{dif}(r) = g_{22}(r) - g_{11}(r)$ of the observed data over scale r. (B) Number of species showing $g_{dif} > 0$ (solid circles, i.e., class of juveniles more clumped than adults), $g_{dif} = 0$ (open squares, i.e., no significant shift between adults and juveniles) and $g_{dif} < 0$ (open circles, i.e., adults more clumped than juveniles) over different scales in the BDGS plot.

- **The prevalence of NDD:**
  - **66 out of 88 exhibited greater aggregation relative to adults.**
  - **35 of 66 showed density dependent thinning even up to 30m.**

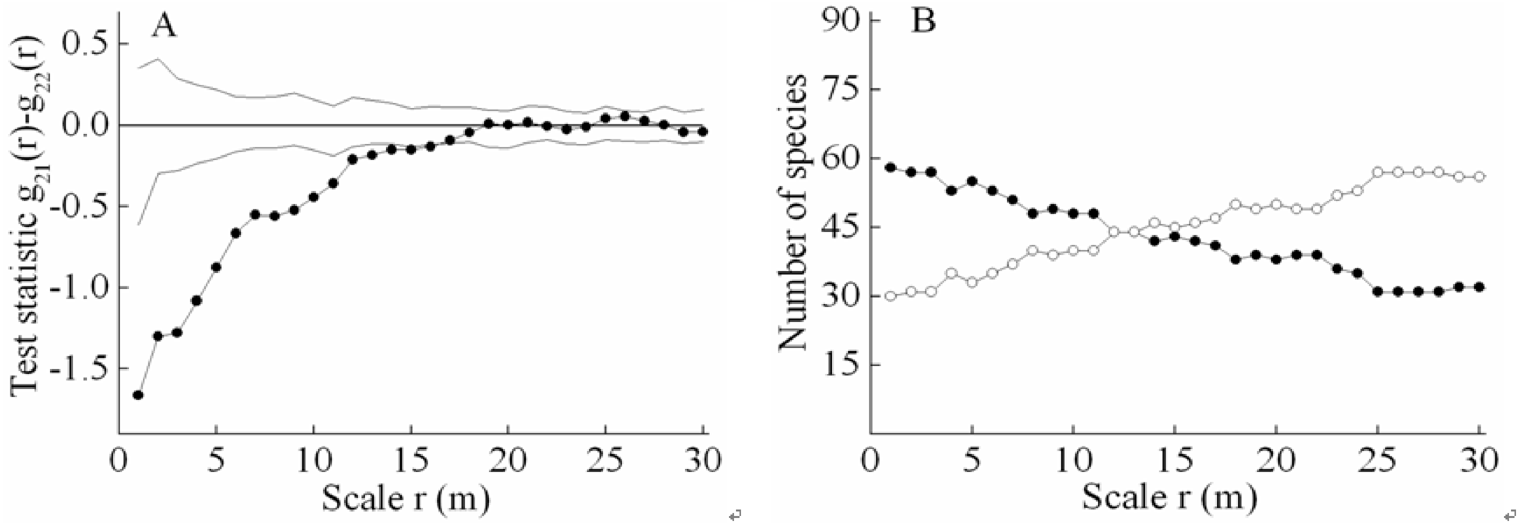
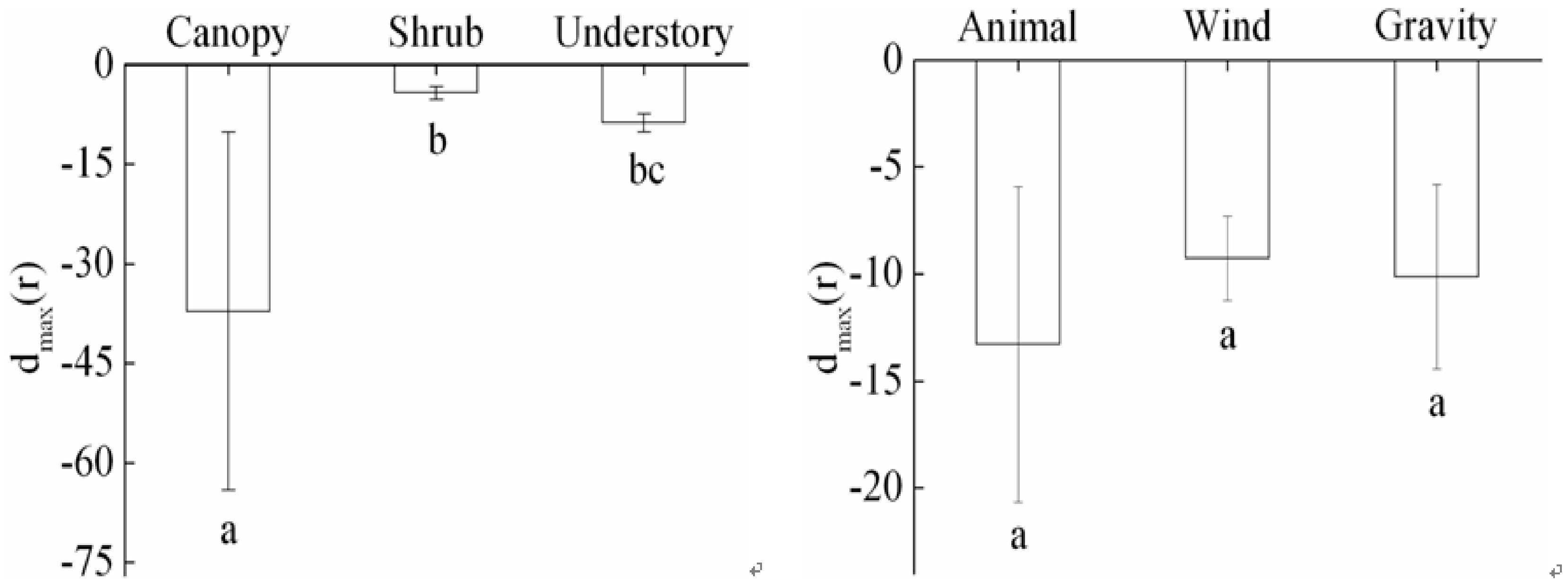


Fig. 4 Analysis of density dependent thinning at each scale. (A) *F. lucida* as an example. The simulation envelopes (dashed lines) were constructed using the 199 simulations of the RL null model. The solid circles denote $g_{21}(r) - g_{22}(r)$ of the observed data over scale r. (B) Number of species showing density dependent thinning at each scale. The solid circles denote $d(r) < 0$ (i.e., juveniles more clumped than adults) of the observed data over scale r. The open circles denote $d(r) = 0$ (i.e., no significant shift between adults and juveniles).

- **NDD and species attributes:**
  - d_{max} increased with species abundance.
  - d_{max} decreased with species mean and maximum DBH.
  - Varied for different growth forms.
  - No difference among the three dispersal modes.



Difference analysis of density dependent intensity among growth forms (left) and dispersal modes (right). (Kruskal-Wallis test and Wilcoxon sign rank test)

Discussion

- **From pattern to process:**
  - **Using patterns to detect formative processes is a classical approach in ecological research (Watt 1947; Chave 2013).**
  - **Spatial pattern analysis is an effective statistical approach for detecting NDD when using sophisticated analytical methods (e.g., appropriate null models; Getzin *et al.* 2008; Bagchi *et al.* 2011).**

- **Aggregation should disappear well below 30 m, or the assumption of separation of scales may not hold (Wiegand *et al*. 2007). Large-scale habitat heterogeneity still exhibited (analysis 1).**

- **46 species for this self-thinning effect were detected using, especially at small scales (analysis 2). Only 15% of tested species in Condit *et al.* (2000).**

- **The prevalence of NDD:**
  - **NDD is a prevalent mechanism for regulating the population spatial structure of most tree species (66 of 88) in later life stages in BDGS plot. Proportion (86.5%) is higher than Zhu *et al.* (2010, 83.0%).**
  - **Most species showed maximal intensity of NDD at a scale of 1 m, and the intensity decreased with increasing scales r (i.e., scale-dependent effects, Zhu *et al.* 2010).**

- **NDD and species attributes:**
  - **Canopy layer showed significantly greater intensity of NDD than the shrub layer. The range in size, and hence age, that may be greater in canopy species** (Bagchi *et al.* 2011) **.**
  - **No discrepancy among three dispersal modes :**
    - **Dispersal mode categories were too coarse;**
    - **Secondary dispersal** (Vander Wall *et al*. 2005) **.**
  - **Although rare species show a stronger intensity of NDD than abundant species, NDD certainly occurs in abundant species (abundant 96.3%, common 73.3%, rare species 58.1%).**

- **Conclusions:**
  - **NDD is a prevalent mechanism regulating the spatial structure of tree species at later life stages in BDGS plot.**
  - **NDD is influenced by habitat heterogeneity and species attributes.**
  - **We recommend appropriate null models to take habitat heterogeneity, or other environmental factors and species-level variations into account in future studies.**

Acknowledgements

- Chinese Forest Biodiversity Monitoring Network (29200931131101919) and National Natural Science Foundation of China (Grant no. 31070465 and 31200329).
- The Administration Bureau of the Badagongshan National Nature Reserve.
- Many field workers.


Please give me your advice.