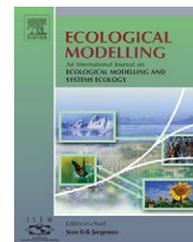


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## Reply to Letter to the Editor

# Achieving coexistence—Comment on “Modelling rain forest diversity: The role of competition” by Bampfylde et al. (2005)

### ARTICLE INFO

#### Keywords:

Competition  
Diversity  
Mathematical model  
Metapopulations  
Rain forests  
Seeding events

This Letter is the Reply to the Letter to the Editor by V.K. Arora and G.J. Boer, published in *Ecological Modelling*, issue 192 (1–2), pp. 322–324.

Arora and Boer (in press) propose a generalisation of the competition-colonisation model proposed by Tilman (1994), not of the model proposed by Bampfylde et al. (2005). They show that their model allows for species coexistence under a wide parameter regime. Specifically, they show that the inclusion of random mast fruiting events proposed by Bampfylde et al. (2005) is not a necessary condition for coexistence. Rather, they propose that a generalisation of the standard non-linear description of the species competition term allows for coexistence.

This general result complements the work of Bampfylde et al., who's model focuses on rain forest tree species dynamics, and is built around data collected over a 16 year period in Borneo. Arora and Boer's model may not be applicable in this ecosystem for two reasons. Firstly, their model allows competitive displacement of individuals of a subdominant species by those of a dominant species. This is an unrealistic scenario for undisturbed tropical rain forest where asymmetric competition (*sensu* Freckleton and Watkinson, 2001) predominates and where the competitive hierarchy is determined by individual size not species identity. This was our original criticism of Tilman's model. Secondly, Arora and Boer demonstrate that under the full interaction case (where their access exponent  $b=0$ ) equilibrium coexistence is possible and other random interaction mechanisms are unnecessary. However, full interaction assumes either ubiquitous seed

dispersal or an omnipresent seed bank, neither of which is biologically realistic in general in a tropical rain forest. Long distance dispersal could permit locally rare species to establish and seed or seedling banks allow for the short term possibility of absent species to colonise a site. These rare events could only occur under specific conditions at particular moments in time and space.

### REFERENCES

- Arora, V.K., Boer, G.J. Simulating competition and coexistence between plant functional types in a dynamic vegetation model, *Earth Interactions*, in press.
- Bampfylde, C.J., Brown, N.D., Gavaghan, D.J., Maini, P.K., 2005. Modelling rain forest diversity: the role of competition. *Ecol. Model.* 188 (2–4), 253–278.
- Freckleton, R.P., Watkinson, A.R., 2001. Asymmetric competition between plant species. *Functional Ecol.* 15 (5), 615–623.
- Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75, 2–16.

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14 October 2005

0304-3800/\$ – see front matter  
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doi:10.1016/j.ecolmodel.2006.01.001  
Published on line 15 February 2006