

Impacts of logging on density-dependent predation of dipterocarp seeds in a South East Asian rainforest

Robert Bagchi, Christopher D. Philipson, Eleanor M. Slade, Andy Hector, Sam Phillips, Jerome F. Villanueva, Owen T. Lewis, Christopher H. C. Lyal, Reuben Nilus, Adzley Madran, Julie D. Scholes and Malcolm C. Press

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Abstract

Much of the forest remaining in South East Asia has been selectively logged. The processes promoting species coexistence may be the key to the recovery and maintenance of diversity in these forests. One such process is the Janzen–Connell mechanism, where specialized natural enemies such as seed predators maintain diversity by inhibiting regeneration near conspecifics. In Neotropical forests, anthropogenic disturbance can disrupt the Janzen–Connell mechanism, but similar data are unavailable for South East Asia. We investigated the effects of conspecific density (two spatial scales) and distance from fruiting trees on seed and seedling survival of the canopy tree *Parashorea malaanonan* in unlogged and logged forests in Sabah, Malaysia. The production of mature seeds was higher in unlogged forest, perhaps because high adult densities facilitate pollination or satiate pre-dispersal predators. In both forest types, post-dispersal survival was reduced by small-scale (1 m^2) conspecific density, but not by proximity to the nearest fruiting tree. Large-scale conspecific density (seeds per fruiting tree) reduced predation, probably by satiating predators. Higher seed production in unlogged forest, in combination with slightly higher survival, meant that recruitment was almost entirely limited to unlogged forest. Thus, while logging might not affect the Janzen–Connell mechanism at this site, it may influence the recruitment of particular species.

1. Introduction

Tropical forests are being lost and degraded at an alarming rate¹². Forest loss has been particularly rapid in South East Asia, where less than half of the original forest cover remains³. While unexploited forest is now rare in the region, large areas of secondary forest remain⁴⁵ and their importance for conservation is increasingly recognized⁶⁷⁸. Commercial timber extraction has inevitable, dramatic impacts on the structure, diversity and community composition of these secondary forests⁹¹⁰, but they

¹ Curran L. M., Trigg S. N., McDonald A. K., Astiani D., Hardiono Y. M., Siregar P., Caniago I. & Kasischke E.. 2004 Lowland forest loss in protected areas of Indonesian Borneo. *Science* **303**, 1000–1003. doi:10.1126/science.1091714 ([doi:10.1126/science.1091714](https://doi.org/10.1126/science.1091714)). **Crossref, PubMed, Web of Science, Google Scholar**

² Achard F., Eva H. D., Stibig H. J., Mayaux P., Galleo J., Richards T. & Malingreau J.-P.. 2002 Determination of deforestation rates of the world's humid tropical forests. *Science* **297**, 999–1002. doi:10.1126/science.1070656 ([doi:10.1126/science.1070656](https://doi.org/10.1126/science.1070656)). **Crossref, PubMed, Web of Science, Google Scholar**

³ Sodhi N. S., Koh L. P., Brook B. W. & Ng P. K. L.. 2004 Southeast Asian biodiversity: an impending disaster. *Trends Ecol. Evol.* **19**, 654–660. doi:10.1016/j.tree.2004.09.006 ([doi:10.1016/j.tree.2004.09.006](https://doi.org/10.1016/j.tree.2004.09.006)). **Crossref, PubMed, Web of Science, Google Scholar**

⁴ McMorrow J. & Talip M. A.. 2001 Decline of forest area in Sabah, Malaysia: relationship to state policies, land code and land capability. *Global Environ. Chang.* **11**, 217–230. doi:10.1016/S0959-3780(00)00059-5 ([doi:10.1016/S0959-3780\(00\)00059-5](https://doi.org/10.1016/S0959-3780(00)00059-5)). **Crossref, Web of Science, Google Scholar**

⁵ Marsh C. W. & Greer A. G.. 1992 Forest-land use in Sabah, Malaysia: an introduction to Danum Valley. *Phil. Trans. R. Soc. Lond. B* **335**, 331–339. doi:10.1098/rstb.1992.0025 ([doi:10.1098/rstb.1992.0025](https://doi.org/10.1098/rstb.1992.0025)). **Link, Web of Science, Google Scholar**

⁶ Wright S. J. & Muller-Landau H. C.. 2006 The future of tropical forest species. *Biotropica* **38**, 287–301. doi:10.1111/j.1744-7429.2006.00154.x ([doi:10.1111/j.1744-7429.2006.00154.x](https://doi.org/10.1111/j.1744-7429.2006.00154.x)). **Crossref, Web of Science, Google Scholar**

⁷ Chazdon R. L., Peres C. A., Dent D., Sheil D., Lugo A. E., Lamb D., Stork N. E. & Miller S. E.. 2009 The potential for species conservation in tropical secondary forests. *Conserv. Biol.* **23**, 1406–1417. doi:10.1111/j.1523-1739.2009.01338.x ([doi:10.1111/j.1523-1739.2009.01338.x](https://doi.org/10.1111/j.1523-1739.2009.01338.x)). **Crossref, PubMed, Web of Science, Google Scholar**

⁸ Dent D. H. & Wright S. J.. 2009 The future of tropical species in secondary forests: a quantitative review. *Biol. Conserv.* **142**, 2833–2843. doi:10.1016/j.biocon.2009.05.035 ([doi:10.1016/j.biocon.2009.05.035](https://doi.org/10.1016/j.biocon.2009.05.035)). **Crossref, Web of Science, Google Scholar**

⁹ Foody G. M. & Cutler M. E. J.. 2003 Tree biodiversity in protected and logged Bornean tropical rain forests and its measurement by satellite remote sensing. *J. Biogeogr.* **30**, 1053–1066. doi:10.1046/j.1365-2699.2003.00887.x ([doi:10.1046/j.1365-2699.2003.00887.x](https://doi.org/10.1046/j.1365-2699.2003.00887.x)). **Crossref, Web of Science, Google Scholar**

¹⁰ Bischoff W., Newbery D. A., Lingenfelder M., Schnaegel R., Petol G. H., Madani L. & Ridsdale C.. 2005 Secondary succession and dipterocarp recruitment in Bornean rain forest after logging. *For-*

are still important reservoirs for biodiversity and provide crucial ecosystem services including provision of raw materials, soil protection, and sequestering and storing carbon¹¹¹²¹³¹⁴.

Despite the importance of secondary forests for species conservation, the consequences of human disturbance for the maintenance of diversity remain poorly understood¹⁵¹⁶. While there is an extensive literature on the effects of human disturbance on species richness and diversity (see recent reviews in¹⁷¹⁸), the effects on the structure and organization of ecological communities and associated ecological functions and processes have received less attention¹⁹²⁰. In particular, for forest biodiversity to recover and persist following disturbances such as logging, it is important that the processes re-

est Ecol. Manage. **218**, 174–192.doi:10.1016/j.foreco.2005.07.009 (doi:10.1016/j.foreco.2005.07.009). **Crossref, Web of Science, Google Scholar**

¹¹ Dent D. H.& Wright S. J.. 2009 The future of tropical species in secondary forests: a quantitative review. *Biol. Conserv.* **142**, 2833–2843.doi:10.1016/j.biocon.2009.05.035 (doi:10.1016/j.biocon.2009.05.035). **Crossref, Web of Science, Google Scholar**

¹² Foody G. M.& Cutler M. E. J.. 2003 Tree biodiversity in protected and logged Bornean tropical rain forests and its measurement by satellite remote sensing. *J. Biogeogr.* **30**, 1053–1066.doi:10.1046/j.1365-2699.2003.00887.x (doi:10.1046/j.1365-2699.2003.00887.x). **Crossref, Web of Science, Google Scholar**

¹³ Lugo A. E.. 2009 The emerging era of novel tropical forests. *Biotropica* **41**, 589–591.doi:10.1111/j.1744-7429.2009.00550.x (doi:10.1111/j.1744-7429.2009.00550.x). **Crossref, Web of Science, Google Scholar**

¹⁴ Berry N. J., et al. 2010 The high value of logged tropical forests: lessons from northern Borneo. *Biodivers. Conserv.* **19**, 985–997.doi:10.1007/s10531-010-9779-z (doi:10.1007/s10531-010-9779-z). **Crossref, Web of Science, Google Scholar**

¹⁵ Lewis O. T.& Gripenberg S.. 2008 Insect seed predators and environmental change. *J. Appl. Ecol.* **45**, 1593–1599.doi:10.1111/j.1365-2664.2008.01575.x (doi:10.1111/j.1365-2664.2008.01575.x). **Crossref, Web of Science, Google Scholar**

¹⁶ Lewis O. T.. 2009 Biodiversity change and ecosystem function in tropical forests. *Basic Appl. Ecol.* **10**, 97–102.doi:10.1016/j.baae.2008.08.010 (doi:10.1016/j.baae.2008.08.010). **Crossref, Web of Science, Google Scholar**

¹⁷ Chazdon R. L., Peres C. A., Dent D., Sheil D., Lugo A. E., Lamb D., Stork N. E.& Miller S. E.. 2009 The potential for species conservation in tropical secondary forests. *Conserv. Biol.* **23**, 1406–1417.doi:10.1111/j.1523-1739.2009.01338.x (doi:10.1111/j.1523-1739.2009.01338.x). **Crossref, PubMed, Web of Science, Google Scholar**

¹⁸ Dent D. H.& Wright S. J.. 2009 The future of tropical species in secondary forests: a quantitative review. *Biol. Conserv.* **142**, 2833–2843.doi:10.1016/j.biocon.2009.05.035 (doi:10.1016/j.biocon.2009.05.035). **Crossref, Web of Science, Google Scholar**

¹⁹ Lewis O. T.& Gripenberg S.. 2008 Insect seed predators and environmental change. *J. Appl. Ecol.* **45**, 1593–1599.doi:10.1111/j.1365-2664.2008.01575.x (doi:10.1111/j.1365-2664.2008.01575.x). **Crossref, Web of Science, Google Scholar**

²⁰ Lewis O. T.. 2009 Biodiversity change and ecosystem function in tropical forests. *Basic Appl. Ecol.* **10**, 97–102.doi:10.1016/j.baae.2008.08.010 (doi:10.1016/j.baae.2008.08.010). **Crossref, Web of Science, Google Scholar**

sponsible for maintaining diversity remain intact²¹. The mechanisms maintaining tree diversity have been extensively examined in the literature²², and these mechanisms could be potentially disrupted by disturbance²³. Reductions in tree diversity could have implications for diversity in other taxonomic groups because plant diversity, to some extent, sets the template for diversity at higher trophic levels^{24,25}. A particular concern is that, even when diversity is not severely reduced by exploitation itself, it might decline over time if these processes have been undermined.

Much research has tried to understand the processes involved in plant species coexistence, particularly in tropical forests²⁶. Among the most likely candidates is the Janzen–Connell mechanism^{27,28}, where seeds and seedlings near conspecific adults or in areas of high conspecific density suffer high mortality through the activity of specialized natural enemies. Consequently, locally rare species have an advantage, promoting species coexistence.

Support for the Janzen–Connell mechanism mainly comes from the Neotropics, and studies from Asia and Africa are rare²⁹. Of the small number of studies conducted in

²¹ Lewis O. T.. 2009 Biodiversity change and ecosystem function in tropical forests. *Basic Appl. Ecol.* **10**, 97–102.doi:10.1016/j.baae.2008.08.010 (doi:10.1016/j.baae.2008.08.010). **Crossref, Web of Science, Google Scholar**

²² Wright S. J.. 2002 Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**, 1–14. **Crossref, PubMed, Web of Science, Google Scholar**

²³ Lewis O. T.. 2009 Biodiversity change and ecosystem function in tropical forests. *Basic Appl. Ecol.* **10**, 97–102.doi:10.1016/j.baae.2008.08.010 (doi:10.1016/j.baae.2008.08.010). **Crossref, Web of Science, Google Scholar**

²⁴ Novotny V., Drozd P., Miller S. E., Kulfan M., Janda M., Basset Y.& Weiblen G. D.. 2006 Why are there so many species of herbivorous insects in tropical rainforests? *Science* **313**, 1115–1118.doi:10.1126/science.1129237 (doi:10.1126/science.1129237). **Crossref, PubMed, Web of Science, Google Scholar**

²⁵ Lewinsohn T.& Roslin T.. 2008 Four ways toward tropical herbivore megadiversity. *Ecol. Lett.* **11**, 398–416.doi:10.1111/j.1461-0248.2008.01155.x (doi:10.1111/j.1461-0248.2008.01155.x). **Crossref, PubMed, Web of Science, Google Scholar**

²⁶ Wright S. J.. 2002 Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**, 1–14. **Crossref, PubMed, Web of Science, Google Scholar**

²⁷ Janzen D. H.. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528.doi:10.1086/282687 (doi:10.1086/282687). **Crossref, Web of Science, Google Scholar**

²⁸ Connell J. H.. 1971 On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of numbers in populations* (eds , den Boer P. J.& Gradwell G. R.), pp. 298–312. Wageningen, The Netherlands: PUDOC. **Google Scholar**

²⁹ Carson W. P., Anderson J. T., Leigh E. G.& Schnitzer S. A.. 2008 Challenges associated with testing and falsifying the Janzen–Connell hypothesis: a review and critique. *Tropical forest community ecology* (eds , Carson W. P.& Schnitzer S. A.), pp. 210–241. Oxford, UK: Blackwell's. **Google Scholar**

Asia, several support the Janzen–Connell mechanism³⁰³¹³² but others do not and sometimes show patterns that run counter to its predictions³³³⁴. The ecology of South East Asian forests differs in several important regards from other tropical regions, and so we need to be cautious when generalizing from results obtained elsewhere. In particular, reproduction is typically highly episodic in these forests, occurring in supra-annual, community-wide mast fruiting events³⁵³⁶. Up to 88 per cent of canopy species can fruit at the same time and the most plausible explanation for this phenomenon is that it evolved to satiate seed predators³⁷³⁸. Predator satiation decreases mortality at the highest densities, directly opposing the Janzen–Connell mechanism. Indeed, Janzen³⁹ suggested that mast fruiting species were unlikely to be affected by the mechanism. However, while much of the literature on fruiting in South East Asian forests has concentrated on mast events, there is some evidence of successful recruitment outside

³⁰ Bagchi R., Press M. C. & Scholes J. D.. 2010 Evolutionary history and distance dependence control survival of dipterocarp seedlings. *Ecol. Lett.* **13**, 51–59. doi:10.1111/j.1461-0248.2009.01397.x (doi:10.1111/j.1461-0248.2009.01397.x). **Crossref, PubMed, Web of Science, Google Scholar**

³¹ Webb C. O. & Peart D. R.. 1999 Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* **80**, 2006–2017. doi:10.1890/0012-9658(1999)080[2006:SDDPCO]2.0.CO;2 (doi:10.1890/0012-9658(1999)080[2006:SDDPCO]2.0.CO;2). **Crossref, Web of Science, Google Scholar**

³² Blundell A. G. & Peart D. R.. 2004 Density-dependent population dynamics of a dominant rain forest canopy tree. *Ecology* **85**, 704–715. doi:10.1890/01-4101 (doi:10.1890/01-4101). **Crossref, Web of Science, Google Scholar**

³³ Itoh A., Yamakura T., Ogino K. & Lee H. S.. 1995 Survivorship and growth of seedlings of 4 dipterocarp species in a tropical rainforest of Sarawak, East Malaysia. *Ecol. Res.* **10**, 327–338. doi:10.1007/BF02347859 (doi:10.1007/BF02347859). **Crossref, Web of Science, Google Scholar**

³⁴ Maycock C. R., Thewlis R. N., Ghazoul J., Nilus R. & Burslem D. F. R. P.. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646. doi:10.1111/j.1654-1103.2005.tb02406.x (doi:10.1111/j.1654-1103.2005.tb02406.x). **Crossref, Web of Science, Google Scholar**

³⁵ Curran L. M., Caniago I., Paoli G. D., Astianti D., Kusneti M., Leighton M., Nirarita C. E. & Haeruman H.. 1999 Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* **286**, 2184–2188. doi:10.1126/science.286.5447.2184 (doi:10.1126/science.286.5447.2184). **Crossref, PubMed, Web of Science, Google Scholar**

³⁶ Curran L. M. & Leighton M.. 2000 Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* **70**, 101–128. doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2 (doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2). **Crossref, Web of Science, Google Scholar**

³⁷ Curran L. M. & Leighton M.. 2000 Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* **70**, 101–128. doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2 (doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2). **Crossref, Web of Science, Google Scholar**

³⁸ Janzen D. H.. 1974 Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica* **6**, 69–103. doi:10.2307/2989823 (doi:10.2307/2989823). **Crossref, Google Scholar**

³⁹ Janzen D. H.. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528. doi:10.1086/282687 (doi:10.1086/282687). **Crossref, Web of Science, Google Scholar**

mast events⁴⁰⁴¹. In these partial fruiting episodes, the chance of observing density dependence may be greater because fruiting trees are relatively isolated. Seed predators may be attracted to these trees, decreasing the survival of seeds close to their parent trees relative to those dispersed further away.

Deforestation and hunting may reduce seed predator populations, which may then be unable to constrain the recruitment of common species. Conversely, restricting predators to small forest fragments could prevent seeds of rare species from escaping in space, removing the rare species advantage. Both scenarios would weaken the Janzen–Connell mechanism. Studies in the Neotropics have suggested that human disturbance disrupts the Janzen–Connell mechanism. Hunting and forest fragmentation have both been linked to reduced density dependence and consequently plant diversity⁴²⁴³⁴⁴. However, similar data are lacking for South East Asian forests, although forest fragmentation and logging can reduce dipterocarp recruitment because low densities of dipterocarp trees are unable to produce enough seed to satiate seed predators (which are localized in remaining forest fragments)⁴⁵⁴⁶.

In this paper, we assess the distance from the nearest fruiting conspecific tree (which, in most cases will be the parent) and conspecific density effects on the survival of *Parashorea malaanonan* Merr (Dipterocarpaceae) seeds and germinating seedlings in both unlogged and logged forest in Sabah, North Borneo, during a non-mast year. We test the following three hypotheses:

⁴⁰ Maycock C. R., Thewlis R. N., Ghazoul J., Nilus R. & Burslem D. F. R. P.. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646. doi:10.1111/j.1654-1103.2005.tb02406.x (doi:10.1111/j.1654-1103.2005.tb02406.x). **Crossref, Web of Science, Google Scholar**

⁴¹ Bagchi R.. 2006 Factors influencing the diversity of trees in southeast Asian rain forests. PhD thesis, University of Sheffield., Sheffield, UK. **Google Scholar**

⁴² Wright S. J., Zeballos H., Dominguez I., Gallardo M. M., Moreno M. C. & Ibanez R.. 2000 Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conserv. Biol.* **14**, 227–239. doi:10.1046/j.1523-1739.2000.98333.x (doi:10.1046/j.1523-1739.2000.98333.x). **Crossref, Web of Science, Google Scholar**

⁴³ Wyatt J. L. & Silman M. R.. 2004 Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. *Oecologia* **140**, 26–35. doi:10.1007/s00442-004-1554-y (doi:10.1007/s00442-004-1554-y). **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁴ Dirzo R. & Miranda A.. 1991 Altered patterns of herbivory and diversity in the forest understorey: a case study of the possible consequences of contemporary defaunation. *Plant–animal interactions: evolutionary ecology in tropical and temperate regions* (eds , Price P. W., Lewinsohn T. M., Fernandes G. W. & Benson W. W.), pp. 273–287. New York, NY: John Wiley and Sons. **Google Scholar**

⁴⁵ Curran L. M., Caniago I., Paoli G. D., Astianti D., Kusneti M., Leighton M., Nirarita C. E. & Haeruman H.. 1999 Impact of El Nino and logging on canopy tree recruitment in Borneo. *Science* **286**, 2184–2188. doi:10.1126/science.286.5447.2184 (doi:10.1126/science.286.5447.2184). **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁶ Curran L. M. & Webb C. O.. 2000 Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* **70**, 129–148. doi:10.1890/0012-9615(2000)070[0129:ETOTSS]2.0.CO;2 (doi:10.1890/0012-9615(2000)070[0129:ETOTSS]2.0.CO;2). **Crossref, Web of Science, Google Scholar**

- seed and seedling survival will increase with distance from the nearest fruiting tree (distance dependence).
- seed and seedling survival will decrease with increased conspecific density (negative density dependence).
- the relationship between survival and distance and density will be stronger in the unlogged forest than in logged forest.

2. Methods

(a) Study site

The study was conducted around the Danum Valley Field Centre in Sabah, Malaysian Borneo (4°58′ N, 118°48′ E). Large areas of both logged and unlogged forest lie close to the field station. The Danum Valley Conservation Area (DVCA) contains 43 800 ha of unlogged, mostly lowland dipterocarp forest. The Yayasan Sabah Forest Management Area (YSFMA) is a logging concession of almost 1 million ha.

Logging in the YSFMA began in the mid-1970s and is ongoing. The areas included in this study were logged between 1970 and 1988. Timber was extracted using a combination of high lead on steep slopes and traditional tractor-based methods in other areas. Most of the healthy stems greater than 60 cm diameter at breast height (d.b.h.) were removed. Typical extraction rates were about 70 m³ ha⁻¹ although higher rates have been reported (see¹ for further site information).

(b) Study species

Parashorea malaanonan is among the commonest species in the YSFMA and more widely in Sabah². Permanent plots in the DVCA contain about 18.6 *P. malaanonan* stems ha⁻¹ (greater than 10 cm girth at breast height)³. Most of the forest in the YSFMA is classified as *P. malaanonan* (type A) forest, a category that includes much of the natural vegetation in the upper Segama region and coastal areas of Eastern Sabah⁴. *Parashorea malaanonan* is commercially harvested and its timber is classed

¹ Marsh C. W. & Greer A. G.. 1992 Forest-land use in Sabah, Malaysia: an introduction to Danum Valley. *Phil. Trans. R. Soc. Lond. B* **335**, 331–339. doi:10.1098/rstb.1992.0025 (doi:10.1098/rstb.1992.0025). [Link](#), [Web of Science](#), [Google Scholar](#)

² Marsh C. W. & Greer A. G.. 1992 Forest-land use in Sabah, Malaysia: an introduction to Danum Valley. *Phil. Trans. R. Soc. Lond. B* **335**, 331–339. doi:10.1098/rstb.1992.0025 (doi:10.1098/rstb.1992.0025). [Link](#), [Web of Science](#), [Google Scholar](#)

³ Stoll P. & Newbery D. M.. 2005 Evidence of species-specific neighborhood effects in the Dipterocarpaceae of a Bornean rain forest. *Ecology* **86**, 3048–3062. doi:10.1890/04-1540 (doi:10.1890/04-1540). [Crossref](#), [Web of Science](#), [Google Scholar](#)

⁴ Marsh C. W. & Greer A. G.. 1992 Forest-land use in Sabah, Malaysia: an introduction to Danum Valley. *Phil. Trans. R. Soc. Lond. B* **335**, 331–339. doi:10.1098/rstb.1992.0025 (doi:10.1098/rstb.1992.0025). [Link](#), [Web of Science](#), [Google Scholar](#)

as White *Serraya* Light Hardwood (timber density 0.52 g cm⁻¹⁵⁶). It is a relatively fast-growing dipterocarp and its seedlings perform better in gaps, and therefore it is considered relatively light demanding for a dipterocarp⁷. However, dipterocarps in general are very shade-tolerant and overall *P. malaanonan* has high survival⁸⁹ and growth rates¹⁰ in understorey conditions.

Parashorea malaanonan appears to fruit more often than other dipterocarps at the study site, and successfully set seed in 1996, 2000 and 2004 (the year of this study,¹¹). The winged seeds are dispersed by wind or gyration and mostly fall under the parent tree's canopy. Several vertebrates and invertebrates have been observed attacking seeds and seedlings of *P. malaanonan*, including bearded pigs *Sus babatus* (R. Bagchi 2004, personal observation), rodents¹² and insect seed predators and herbivores¹³¹⁴¹⁵.

⁵ Dirzo R.& Miranda A.. 1991 Altered patterns of herbivory and diversity in the forest understorey: a case study of the possible consequences of contemporary defaunation. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions* (eds , Price P. W., Lewinsohn T. M., Fernandes G. W.& Benson W. W.), pp. 273–287. New York, NY: John Wiley and Sons. **Google Scholar**

⁶ Burgess P. F.. 1966 *Timbers of Sabah*. Sandakan, Sabah: Forest Department of Malaysia. **Google Scholar**

⁷ Bebbler D. P., Brown N. D.& Speight M. R.. 2002 Drought and root herbivory in understorey *Parashorea* Kurz (Dipterocarpaceae) seedlings in Borneo. *J. Trop. Ecol.* **18**, 795–804.doi:10.1017/S0266467402002511 (doi:10.1017/S0266467402002511). **Crossref, Web of Science, Google Scholar**

⁸ Bagchi R., Press M. C.& Scholes J. D.. 2010 Evolutionary history and distance dependence control survival of dipterocarp seedlings. *Ecol. Lett.* **13**, 51–59.doi:10.1111/j.1461-0248.2009.01397.x (doi:10.1111/j.1461-0248.2009.01397.x). **Crossref, PubMed, Web of Science, Google Scholar**

⁹ Bebbler D. P., Brown N. D.& Speight M. R.. 2002 Drought and root herbivory in understorey *Parashorea* Kurz (Dipterocarpaceae) seedlings in Borneo. *J. Trop. Ecol.* **18**, 795–804.doi:10.1017/S0266467402002511 (doi:10.1017/S0266467402002511). **Crossref, Web of Science, Google Scholar**

¹⁰ Philipson C. D., et al. In press. Light-based regeneration niches: evidence from 21 dipterocarp species using size-specific RGRs. *Biotropica*. **Web of Science, Google Scholar**

¹¹ Bagchi R.. 2006 Factors influencing the diversity of trees in southeast Asian rain forests. PhD thesis, University of Sheffield., Sheffield, UK. **Google Scholar**

¹² Wells K.& Bagchi R.. 2005 Eat in or take away—seed predation and removal by rats (Muridae) during a fruiting event in a dipterocarp rainforest. *Raffles B Zool.* **53**, 125–130. **Web of Science, Google Scholar**

¹³ Bebbler D. P., Brown N. D.& Speight M. R.. 2002 Drought and root herbivory in understorey *Parashorea* Kurz (Dipterocarpaceae) seedlings in Borneo. *J. Trop. Ecol.* **18**, 795–804.doi:10.1017/S0266467402002511 (doi:10.1017/S0266467402002511). **Crossref, Web of Science, Google Scholar**

¹⁴ Whitmore T. C.& Brown N. D.. 1996 Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Phil. Tran. R. Soc. Lond. B* **351**, 1195–1203.doi:10.1098/rstb.1996.0102 (doi:10.1098/rstb.1996.0102). **Link, Web of Science, Google Scholar**

¹⁵ Slade E. M.. 2007 The effects of tropical forest management on biodiversity and ecosystem functioning. PhD thesis, University of Oxford, Oxford, UK. **Google Scholar**

(c) Site selection

In August 2004, fruiting *P. malaanonan* trees were located in the unlogged forest by searching along trails around the field station. The logged forest was surveyed from the logging roads. Ten trees were identified for the study in both forest types. Trees were considered suitable if they had a large fruit crop, were greater than 30 m away from roads and greater than 100 m from other fruiting trees included in the study. A 30 m transect was established starting at the base of each selected tree. The direction of this transect was constrained to avoid trails and other fruiting *P. malaanonan* trees but otherwise chosen at random (i.e. a restricted random design; see electronic supplementary material, figure S1).

(d) Seedfall traps

Traps were used to establish seedfall rates soon after the first seedfall was observed. Traps were deployed at 2, 10, 20 and 30 m along the transects. Each 1 × 1 m trap was constructed by suspending a piece of plastic mesh above the ground with string attached to suitable trees. Dipterocarp seeds are dispersed by gyration and generally land close to the parent tree¹⁶¹⁷¹⁸. Our experience is that few seeds disperse further than 30 m and this is supported by the data presented here (figure 1). Seeds were collected from the traps in both forests every 4 days between 23 September and 30 November 2004. In addition, at each census, we collected five seeds (if possible) from the ground at each distance interval, but avoided the immediate vicinity of the traps and plots. These seeds would have been exposed to both pre-dispersal and post-dispersal insect predators. The collected seeds (trap and ground) were brought back to the laboratory in order to rear out insect seed predators (see §2g).

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¹⁶ Osada N., Takeda H., Furukawa A. & Awang M.. 2001 Fruit dispersal of two dipterocarp species in a Malaysian rain forest. *J. Trop. Ecol.* **17**, 911–917. doi:10.1017/S0266467401001687 ([doi:10.1017/S0266467401001687](#)). [Crossref](#), [Web of Science](#), [Google Scholar](#)

¹⁷ Whitmore T. C.. 1984 *Tropical rainforests of the Far East*, 2nd edn. Oxford, UK: Oxford University Press. [Google Scholar](#)

¹⁸ Kettle C. J., Hollingsworth P. M., Burslem D. F. R. P., Maycock C. R., Khoo E. & Ghazoul J.. 2011 Determinants of fine-scale spatial genetic structure in three co-occurring rain forest canopy trees in Borneo. *Perspect. Plant Ecol. Evol. Syst.* **13**, 47–56. ([doi:10.1016/j.ppees.2010.11.002](#)). [Crossref](#), [Web of Science](#), [Google Scholar](#)

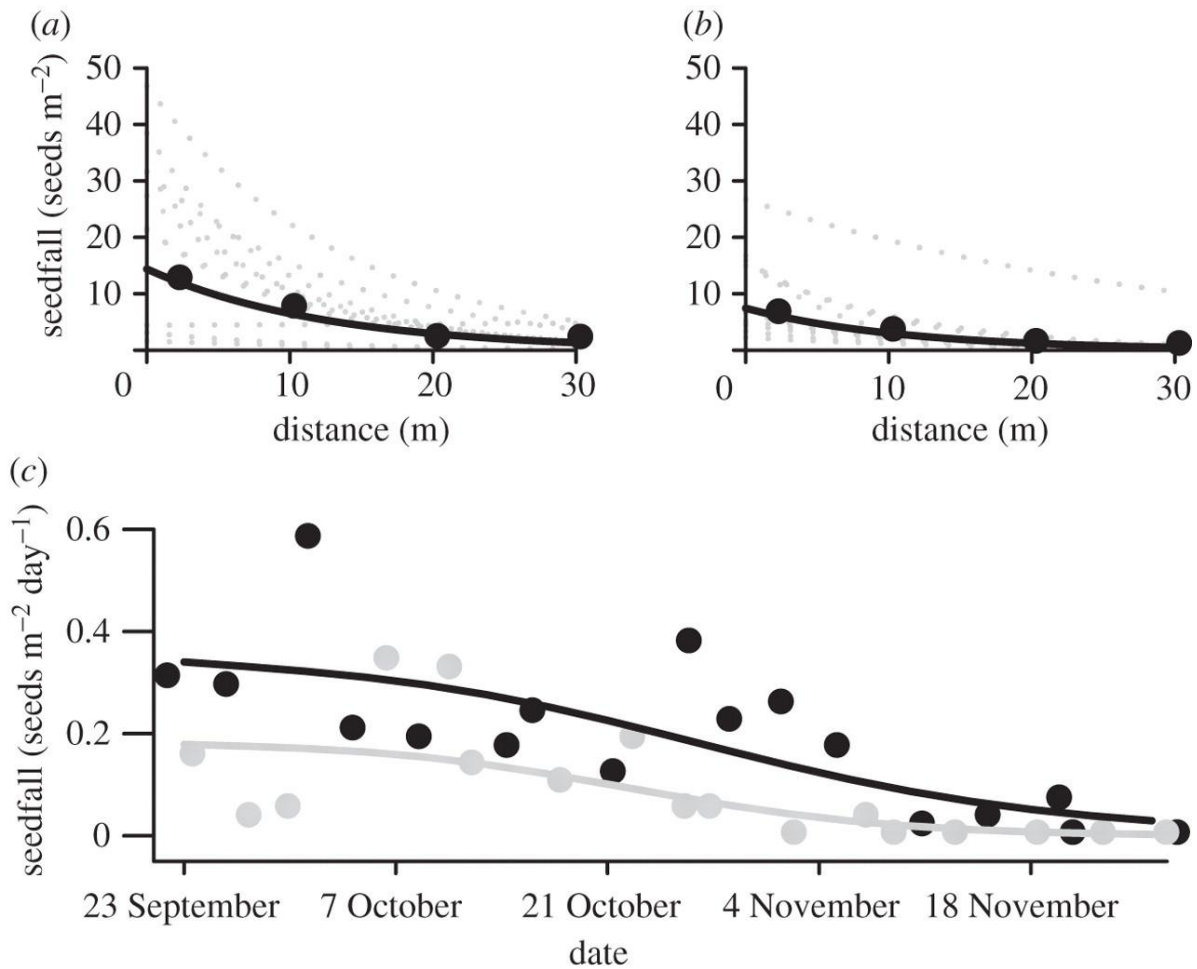


Figure 1. The relationship between *P. malaanonan* seedfall and distance from the nearest fruiting tree in (a) unlogged and (b) logged forest. Points are the mean number of seeds falling into 1 m² seed traps located at 2, 10, 20 and 30 m from 10 trees in each forest type. Solid lines represent the number of seeds predicted to fall at each distance by the model fitted to the data. Dotted lines represent the predictions for each of the 10 trees in each forest type. (c) The majority of seeds fell in the first six weeks of the study. Points are the mean number of seeds that fell in seed traps placed 2 m away from each tree and lines are the model predictions. Black line, unlogged; grey line, logged.

(e) Non-manipulated plots

A 1×1 m plot was established 2 m to the right of each seed trap. Seeds found in the plot were tagged with small numbered flags pinned to their wings. The presence and status of tagged seeds were checked at the same time as the seedfall traps, and new seeds were tagged and recorded. The status of each seed was recorded as potentially viable (intact seeds with no visible signs of fungal attack or insect exit holes), dead (decomposing or empty), germinated, fungus-infected, insect-predated (with exit holes), consumed by vertebrates (partially consumed seed remaining), seedling browsed by vertebrates or removed from the plot (presumed dead). Some of the removed seeds were possibly secondarily dispersed, but previous work on dipterocarp seed predation suggests that most are consumed^{19,20}. Note that these categories were not exclusive. The plots were monitored until 30 November 2004.

(f) Density manipulation plots

Parashorea malaanonan seeds were collected from the vicinity of additional fruiting trees. To manipulate density and distance independently, we established two further 1×1 m plots at distances of 2 and 30 m from each focal tree, adjacent to the existing traps, on 9 October 2004. At each distance we assigned plots to high- or low-density treatments at random. We placed 25 (high density) or four (low density) tagged seeds on a regular grid in the plots. The high-density treatment (25 seeds m^{-2}) corresponds to the highest density we found in the naturally dispersed seed plots. The low-density treatment (4 seeds m^{-2}) is at the low end of seed densities observed naturally and provides some within-plot replication. All naturally dispersed seeds were removed throughout the experiment. These plots were censused until 30 November 2004, at the same time as the traps and non-manipulated plots. Seeds were assigned to the same categories as those in the non-manipulated plots (see earlier text).

(g) Insect rearing

Seeds collected from the ground and traps in different censuses were stored separately for rearing insects, but we pooled the seeds from each distance. Any visible

¹⁹ Maycock C. R., Thewlis R. N., Ghazoul J., Nilus R. & Burslem D. F. R. P. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646. doi:10.1111/j.1654-1103.2005.tb02406.x (doi:10.1111/j.1654-1103.2005.tb02406.x). **Crossref, Web of Science, Google Scholar**

²⁰ Wells K. & Bagchi R. 2005 Eat in or take away—seed predation and removal by rats (Muridae) during a fruiting event in a dipterocarp rainforest. *Raffles B Zool.* **53**, 125–130. **Web of Science, Google Scholar**

signs of insect predation were recorded and then seeds were placed in ventilated rearing boxes lined with damp tissue paper. Seeds were examined every 3 days, and date of germination or emergence of seed predators or parasitoids recorded. Lepidopteran predators were pinned on emergence and dried. Emerged weevils and parasitoids were stored in 90 per cent ethanol in a freezer. After four months, all seeds were dissected, predation recorded and any larvae or adults still inside the seeds stored in alcohol. Specimens were mounted and identified at the Natural History Museum (London) and the Oxford University Museum of Natural History. Insects were classed as pre-dispersal or post-dispersal predators on the basis of the literature²¹²²²³.

(h) Statistical analysis

We used generalized linear mixed-effects models (GLMMs)²⁴²⁵ for all analyses. Seed-fall was modelled as a function of forest type and distance from the nearest fruiting tree, assuming a Poisson error distribution. The intercept and effect of distance were allowed to vary between trees as normally distributed random effects (random intercept and slope model).

Initial analyses suggested only small differences in survival between seeds in the manipulated and non-manipulated plots, so data were combined for analyses. Seeds recorded as dead, removed or eaten by vertebrates were categorized as ‘dead’, while seeds in other categories were regarded as survivors. Note that seeds in the ‘insect-predated’ and ‘fungus-infected’ categories were not initially counted as dead, but if the seed was determined to be dead on a subsequent visit, these agents were considered responsible for their death. For each plot, the number of seeds that died or survived during each census interval was recorded.

We modelled seed and seedling survival using GLMMs, assuming a binomial error distribution. We examined the effects of forest type, distance to the nearest fruiting tree, conspecific density at the start of the census interval and the two- and three-way interactions between these predictors. Total seedfall at each tree over the study

²¹ Chey V. K.. 2002 Dipterocarp seed predators. *Malaysian Nat.* **55**, 46–49. **Google Scholar**

²² Lyal C. H. C. & Curran L. M.. 2000 Seed-feeding beetles of the weevil tribe Mecysolobini (Insecta: Coleoptera: Curculionidae) developing in seeds of trees in the Dipterocarpaceae. *J. Nat. Hist.* **34**, 1743–1847. doi:10.1080/00222930050122165 (doi:10.1080/00222930050122165). **Crossref**, **Web of Science**, **Google Scholar**

²³ Lyal C. H. C., Robinson G. D., Intachat J., Bupabanpot J. & Curran L. M.. 2011. The Dipterocarp insect seed-predator host database. See <http://www.nhm.ac.uk/research-curation/research/projects/dipterocarps/seed-predation/index.html> (accessed January 2011). **Google Scholar**

²⁴ Gelman A. & Hill J.. 2007 *Data analysis using regression and multilevel/hierarchical models*. New York, NY: Cambridge University Press. **Google Scholar**

²⁵ Bolker B. M., Brooks M. E., Clark C. J., Geange S. W., Poulsen J. R., Stevens M. H. H. & White J.-S. S.. 2009 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135. doi:10.1016/j.tree.2008.10.008 (doi:10.1016/j.tree.2008.10.008). **Crossref**, **PubMed**, **Web of Science**, **Google Scholar**

was included as a measure of medium-scale seed density. Intercept terms for each census were included in the model as normally distributed, random effects. This allows the overall survival rate to change over time (for example, if older seeds or seedlings are less vulnerable), without making assumptions about the form of this relationship, similar to Cox proportional hazard models²⁶. Preliminary analyses suggested that the relationship between survival and time differed considerably between the two forest types; so we included an interaction between census and forest type as a random effect. Intercept terms for trees and plots were included as normally varying random effects. The relationship between survival and time was also allowed to vary between plots as a random effect (random intercept and slope model).

The probability of predation by insects of seeds kept in the laboratory was modelled as a function of forest type and the total seed crop at each tree using a GLMM with a binomial error distribution. In a separate model, we examined the effect of distance from the nearest fruiting conspecific, forest type and their interaction using only the seeds collected from the forest floor. Predation of seeds collected in the traps will be dominated by pre-dispersal predation, and testing the effect of distance on predation of these seeds may therefore be inappropriate. In both models, separate intercepts for trees were modelled as normally distributed random effects.

There is much debate about how to appropriately test hypotheses using GLMMs^{27,28}. We used the methodology recommended by Gelman & Hill²⁹ to construct 95% confidence intervals (CIs) for parameter estimates. We resampled 1000 times from the posterior distribution of the parameter estimates, and calculated the 2.5 and 97.5 per cent quantiles. An approximate, two-tailed, p -value was estimated as

where x is the number of samples greater than 0. We present these approximate p -values and the parameter estimates on the scale of the linear predictor with their 95% CI. Analyses were executed in R 2.11.1³⁰ using the add-on packages lme4 0.999375-34 and arm 1.3-05. The R-code used to fit the models is available in the electronic supplementary material.

²⁶ Egli P.& Schmid B.. 2001 The analysis of complex leaf survival data. *Basic Appl. Ecol.* **2**, 223–231.doi:10.1078/1439-1791-00048 (doi:10.1078/1439-1791-00048). **Crossref, Web of Science, Google Scholar**

²⁷ Gelman A.& Hill J.. 2007 *Data analysis using regression and multilevel/hierarchical models*. New York, NY: Cambridge University Press. **Google Scholar**

²⁸ Bolker B. M., Brooks M. E., Clark C. J., Geange S. W., Poulsen J. R., Stevens M. H. H.& White J.-S. S.. 2009 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135.doi:10.1016/j.tree.2008.10.008 (doi:10.1016/j.tree.2008.10.008). **Crossref, PubMed, Web of Science, Google Scholar**

²⁹ Gelman A.& Hill J.. 2007 *Data analysis using regression and multilevel/hierarchical models*. New York, NY: Cambridge University Press. **Google Scholar**

³⁰ R Development Core Team. 2010 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. **Google Scholar**

3. Results

(a) Seedfall

Overall, 353 seeds were collected from seed traps in the unlogged forest and 174 seeds in the logged forest (figure 1*a,b*, respectively). The difference was marginally non-significant (parameter estimate for the effect of logged forest, 95% CI = $-1.61-0.09$, $p = 0.076$), and there was substantial variation between trees within forest types. The number of seeds in traps declined sharply with distance from focal trees, consistent with local seed dispersal (figure 1, , 95% CI = -0.11 to -0.06 , $p < 0.001$). Seedfall was heavy during the first few weeks of the study and began to decline after the first month of the study. Almost all seeds fell before the end of the sixth week (figure 1*c*).

(b) Seed survival

Over two months, 332 seeds were naturally dispersed into the non-manipulated plots (217, 5.4 seeds m^{-2} , in unlogged forest, 115, 2.9 seeds m^{-2} , in logged forest). A further 1160 seeds were added to the 80 density manipulation plots (evenly distributed between the two forest types). No seeds fell into 23 of the non-manipulated plots, so the analyses are based on the remaining 57 non-manipulated and 80 manipulated plots.

Of these seeds, 304 (38% of the non-manipulated and experimental seeds combined) survived to the end of the experiment in the unlogged forest compared with 117 (17%) in the logged forest. However, this difference was not significant (, 95% CI = $-2.13-1.50$, $p = 0.746$) because of the considerable variation in seed survival among trees (figure 2*a*). Only seven seeds (0.2 seeds m^{-2}) remained in the non-manipulated plots in logged forest at the end of the study compared with 75 in the unlogged forest (1.9 seeds m^{-2}). Total seedfall at a tree had a slight positive effect on seed survival (, 95% CI = $-0.002-0.053$, $p = 0.072$,figure 2*b*). There was a strong negative relationship between small-scale density and survival in both forest types (, 95% CI = -1.31 to -0.55 , $p < 0.001$,figure 3). The strength of this relationship was unaffected by forest type (, 95% CI = $-0.67-0.39$, $p = 0.574$). Distance from the nearest fruiting tree did not affect seed survival significantly, and the interaction between distance and density was also non-significant (figure 2).

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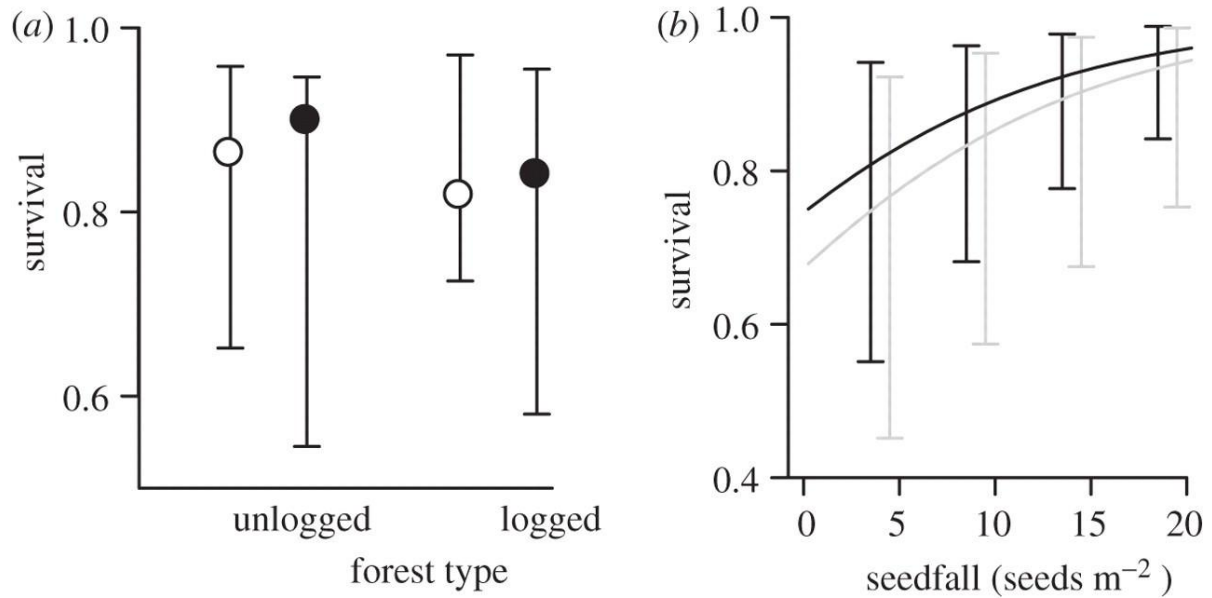


Figure 2. (a) Survival of *P. malaanonan* seeds and seedlings in both unlogged and logged forest. Seed and seedling survival were not significantly affected by either forest type or distance from the nearest fruiting trees. Open circles, 2 m; filled circles, 30 m. (b) The effect of seed production at each tree on seed and seedling survival. Data are the mean survival rates (\pm s.e.), taking into account the variation between plots and focal trees. Black line, unlogged; grey line, logged.

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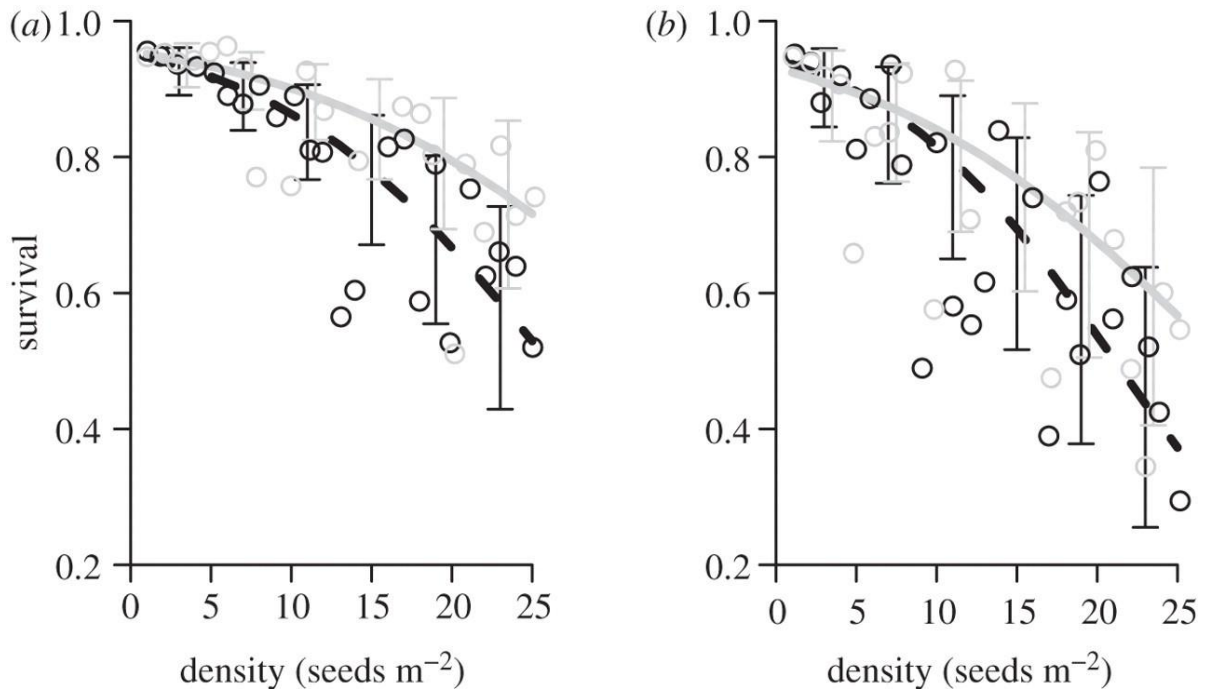


Figure 3. Survival of *P. malaanonan* seedlings declined with conspecific seed and seedling density in both (a) unlogged and (b) logged forest. Distance from nearest fruiting tree did not affect survival. Points are the observed proportion of seeds that survived through 4 day census intervals in 1 m² plots at each density at 2 and 30 m from the focal trees. Lines represent the expectations of the model fitted to the data and error bars represent the standard errors. Black dashed line, 2 m; grey solid line, 30 m.

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(c) Causes of mortality

Most seed mortality appeared to be due to vertebrate seed predators, with seeds either missing or found partially eaten in the vicinity of the plots (figure 4). A large proportion of individuals also died soon after germinating and subsequently being browsed by mammals. Insects and fungi contributed little to the overall mortality between them. This pattern was similar in both forest types (figure 4).

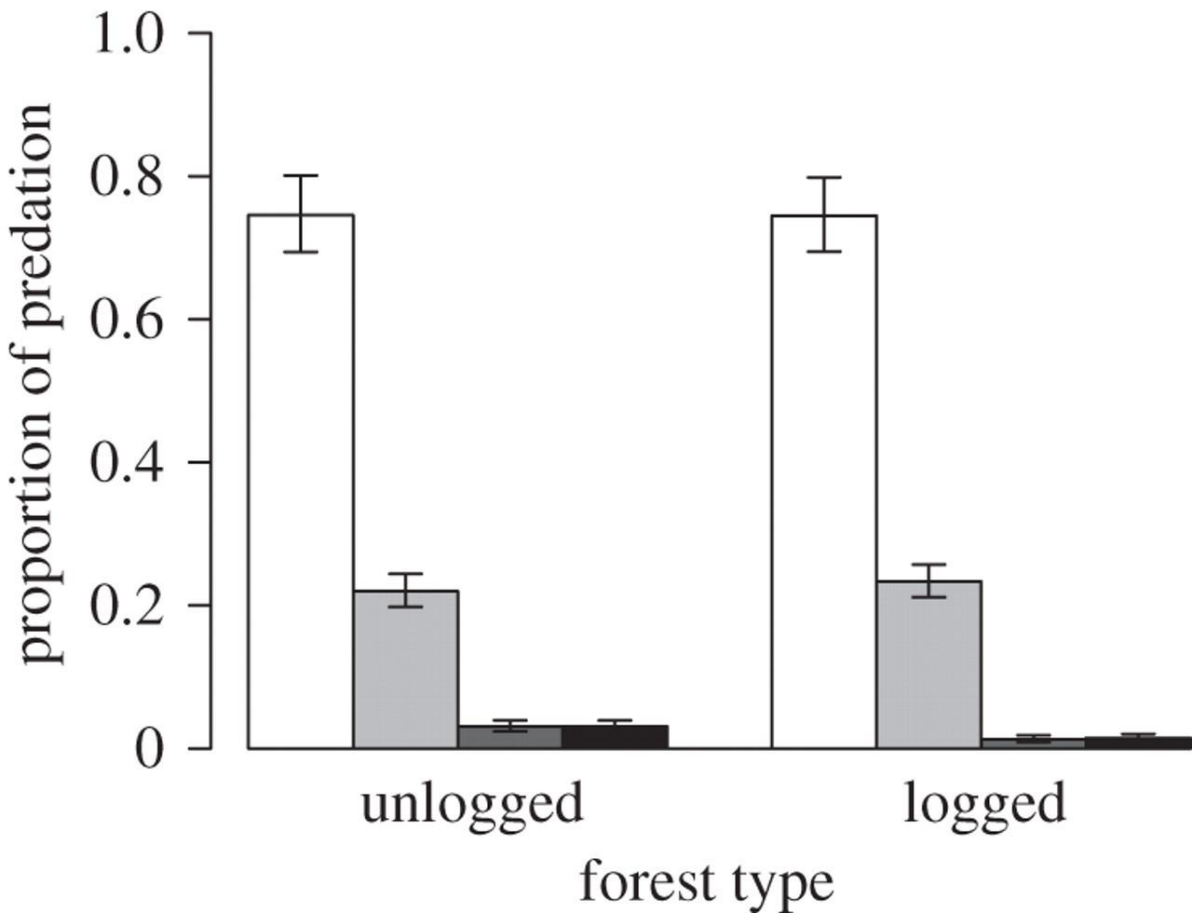


Figure 4. The causes of mortality of *P. malaanonan* seeds and seedlings in unlogged and logged forest. Data are the mean (\pm s.e.) proportion of deaths in which the mortality agent was implicated. Note that more than one agent could contribute to death; so the proportions can add up to greater than 1. Open bars, vertebrate predators; light grey bars, vertebrate browsers; dark grey bars, fungi; black bars, insects.

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(d) Insect predation

A total of 2337 seeds were collected from the traps (566 seeds) and the ground (1771 seeds) and brought back to the laboratory. Insects (moths, weevils or parasitoids) were reared from 210 (9%) of these seeds. A higher proportion of seeds in the unlogged forest were predated (, 95% CI = -1.16 to -0.34 , $p < 0.001$, figure 5a). Predation was reduced at trees with large seed crops (, 95% CI = -0.019 to -0.002 , $p = 0.012$, figure 5a). There was no effect of distance on predation by insects of seeds collected from the forest floor.

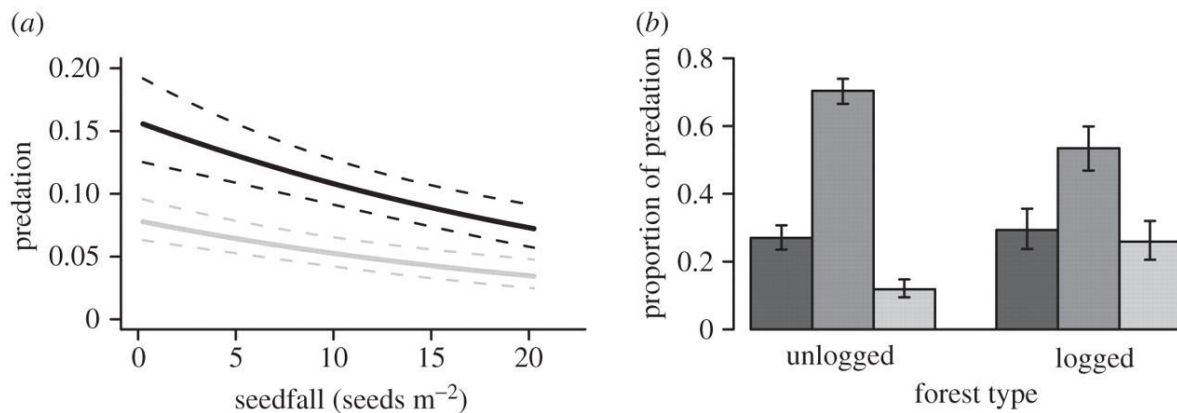


Figure 5. (a) Insect predation on *P. malaanonan* seeds collected in traps or from the forest floor nearby was higher in logged forest than unlogged forest and at trees that produced fewer seeds. Lines are the predictions of the models fitted to the data (\pm s.e.). Black line, unlogged; grey line, logged. (b) The proportion of predated seeds attacked by different predators. Bars represent the mean (\pm s.e.) proportion of seed predators within three different categories and the proportion of predators that had been parasitized. Dark grey bars, moths; mid-grey bars, weevils; light grey bars, parasitoids.

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The most important insect seed predators of *P. malaanonan* seeds were weevils of the Anthribidae and Curculionidae (figure 5*b*; electronic supplementary material, table S1). A micro-moth from the Tortricidae (probably *Andrioplecta shoreae* Komai; K. Tuck 2005, personal communication) was also an important pre-dispersal seed predator, accounting for all but two moths that emerged (see electronic supplementary material, table S1). When the seeds were dissected at the end of the experiment, several seeds contained dead larvae of weevils from the families Curculionidae (probably *Alcidodes* sp.) and Anthribidae (probably *Araecerus* sp.). However, no adult *Alcidodes* were successfully reared from the seeds, although a few adult *Araecerus* were. Parasitoids were reared from 18 per cent of predated seeds and were primarily of the families Braconidae and Ichneumonidae (figure 5*b*; electronic supplementary material, table S1). We assumed that seeds with parasitoids must have been attacked by seed predators first, and these were therefore counted as predated.

There were 41 seeds from the traps that had insect exit holes on collection, but no insects emerged from 22 of them. It is possible that these seeds had been predated by weevils of the family Nanophyidae, such as *Nanophyes* species, which often leave the seed before it falls from the tree¹.

¹ Toy R. J., Marshall A. G. & Pong T. Y.. 1992 Fruiting phenology and the survival of insect fruit predators—a case-study from the South-East Asian Dipterocarpaceae. *Phil. Trans. R. Soc. Lond. B* **335**, 417–423. doi:10.1098/rstb.1992.0033 (doi:10.1098/rstb.1992.0033). [Link](#), [Web of Science](#), [Google Scholar](#)

4. Discussion

(a) Effects of logging on the Janzen–Connell mechanism

We found strong negative effects of small-scale (1 m²) conspecific density on the survival of *P. malaanonan* seeds and germinating seedlings in both unlogged and logged tropical forest. The strength of this density dependence was independent of logging history. This suggests either that logging has not affected seed-predator-mediated density dependence or this process has recovered within 15–35 years after logging.

Similar work in the Neotropics has generally found strong effects of human disturbance on density dependence of tree survival¹²³. It is likely that this disparity with our data is due to differences in the type of disturbance to which the forests were subjected. While logging operations in the YSFMA extract large volumes of timber, hunting pressure on wildlife is relatively low⁴. The Neotropical studies compared forests subjected to intense hunting and missing key seed predators to relatively undisturbed ones. Indeed, hunting was identified as the major cause of the reduced density de-

¹ Wright S. J., Zeballos H., Dominguez I., Gallardo M. M., Moreno M. C. & Ibanez R.. 2000 Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conserv. Biol.* **14**, 227–239. doi:10.1046/j.1523-1739.2000.98333.x (doi:10.1046/j.1523-1739.2000.98333.x). **Crossref, Web of Science, Google Scholar**

² Wyatt J. L. & Silman M. R.. 2004 Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. *Oecologia* **140**, 26–35. doi:10.1007/s00442-004-1554-y (doi:10.1007/s00442-004-1554-y). **Crossref, PubMed, Web of Science, Google Scholar**

³ Dirzo R. & Miranda A.. 1991 Altered patterns of herbivory and diversity in the forest understorey: a case study of the possible consequences of contemporary defaunation. *Plant–animal interactions: evolutionary ecology in tropical and temperate regions* (eds Price P. W., Lewinsohn T. M., Fernandes G. W. & Benson W. W.), pp. 273–287. New York, NY: John Wiley and Sons. **Google Scholar**

⁴ Marsh C. W. & Greer A. G.. 1992 Forest-land use in Sabah, Malaysia: an introduction to Danum Valley. *Phil. Trans. R. Soc. Lond. B* **335**, 331–339. doi:10.1098/rstb.1992.0025 (doi:10.1098/rstb.1992.0025). **Link, Web of Science, Google Scholar**

pendence in each case⁵⁶⁷. Furthermore, the Dipterocarpaceae are mainly abiotically dispersed⁸ in contrast to many Neotropical species that will have lost dispersers as well as seed predators. Because our data are the first from South East Asia to compare density-dependent effects between unlogged and logged forests, it would be premature to conclude that hunting pressure, rather than regional differences, explains the differences between our results and those of previous studies. However, it provides the most likely explanation. The vertebrate faunas in many forests in the region suffer severely from hunting⁹, so data comparable to those reported here could be collected from other South-East Asian forests.

While high conspecific density at very small scales increased mortality, seed predation in the field and by insects reared in the laboratory was lower at trees with large seed crops. Such positive effects of seed density are unsurprising because both pre-dispersal insect¹⁰ and post-dispersal vertebrate¹¹ seed predators are likely to be satiated by large amounts of seeds. One explanation for the different response of post-dispersal predators to density at small and large scales is that while large seed crops eventually satiate them, they concentrate their foraging in areas of the seed shadow with the largest seed density. Seed predation by both insects and vertebrates was independent of proximity to the nearest fruiting adult, possibly because the disadvantages of being close to fruiting trees are offset by the ability of large amounts of seeds to satiate seed predators locally. The independence of insect seed predation to distance might reflect that a large proportion of the reared insects were pre-dispersal seed predators, even in the seeds collected from the forest floor.

⁵ Wright S. J., Zeballos H., Dominguez I., Gallardo M. M., Moreno M. C. & Ibanez R.. 2000 Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conserv. Biol.* **14**, 227–239. doi:10.1046/j.1523-1739.2000.98333.x (doi:10.1046/j.1523-1739.2000.98333.x). **Crossref, Web of Science, Google Scholar**

⁶ Wyatt J. L. & Silman M. R.. 2004 Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. *Oecologia* **140**, 26–35. doi:10.1007/s00442-004-1554-y (doi:10.1007/s00442-004-1554-y). **Crossref, PubMed, Web of Science, Google Scholar**

⁷ Dirzo R. & Miranda A.. 1991 Altered patterns of herbivory and diversity in the forest understorey: a case study of the possible consequences of contemporary defaunation. *Plant–animal interactions: evolutionary ecology in tropical and temperate regions* (eds Price P. W., Lewinsohn T. M., Fernandes G. W. & Benson W. W.), pp. 273–287. New York, NY: John Wiley and Sons. **Google Scholar**

⁸ Whitmore T. C.. 1984 *Tropical rainforests of the Far East*, 2nd edn. Oxford, UK: Oxford University Press. **Google Scholar**

⁹ Sodhi N. S., Koh L. P., Brook B. W. & Ng P. K. L.. 2004 Southeast Asian biodiversity: an impending disaster. *Trends Ecol. Evol.* **19**, 654–660. doi:10.1016/j.tree.2004.09.006 (doi:10.1016/j.tree.2004.09.006). **Crossref, PubMed, Web of Science, Google Scholar**

¹⁰ Lewis O. T. & Gripenberg S.. 2008 Insect seed predators and environmental change. *J. Appl. Ecol.* **45**, 1593–1599. doi:10.1111/j.1365-2664.2008.01575.x (doi:10.1111/j.1365-2664.2008.01575.x). **Crossref, Web of Science, Google Scholar**

¹¹ Schupp E. W.. 1992 The Janzen–Connell model for tropical tree diversity—population implications and the importance of spatial scale. *Am. Nat.* **140**, 526–530. doi:10.1086/285426 (doi:10.1086/285426). **Crossref, PubMed, Web of Science, Google Scholar**

While the strength of density dependence was very similar in unlogged and logged forests, seedfall and survival rates were less so. Mean seedfall and survival were both twice as high in the unlogged forest as the logged forest. Although the differences between forest types in both seedfall and survival were non-significant, this reflects the large amount of variation between focal trees within forest types rather than similar averages. Logging, inevitably, reduces the number of adults of timber species and this may explain reduced seed production in the logged forest. Increasing the distance of dipterocarps to the nearest flowering conspecific reduces cross-pollination and subsequently decreases seed set¹²¹³¹⁴. Logging has been observed to reduce seed production in previous work¹⁵¹⁶. The seed crop in logged forest may therefore be reduced at the scale of the individual tree by high proportions of unpollinated and self-pollinated flowers, and at the landscape scale by a decrease in the number of adult trees. Combined with the trend for survival to be highest at trees with large seed crops, this led nearly all surviving seeds to be in unlogged forest. Only seven seeds remained in the non-manipulated plots in logged forest at the end of the study compared with 75 seeds in the unlogged forest. Thus, natural regeneration in the logged forest was practically non-existent. It should be noted that even in the unlogged forest, seedling densities were very low at the end of the experiment (less than 2 seed m⁻²), and may therefore make little contribution to the recruitment of this species.

One caveat applies to all our comparisons between unlogged and logged forest. While one of this study's strengths is that the forest types were relatively similar in composition prior to logging¹⁷, we considered only one area each of unlogged and logged forest.

¹² Maycock C. R., Thewlis R. N., Ghazoul J., Nilus R. & Burslem D. F. R. P.. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646. doi:10.1111/j.1654-1103.2005.tb02406.x (doi:10.1111/j.1654-1103.2005.tb02406.x). **Crossref, Web of Science, Google Scholar**

¹³ Murawski D. A., Gunatilleke I. & Bawa K. S.. 1994 The effects of selective logging on inbreeding in *Shorea megistophylla* (Dipterocarpaceae) from Sri Lanka. *Conserv. Biol.* **8**, 997–1002. doi:10.1046/j.1523-1739.1994.08040997.x (doi:10.1046/j.1523-1739.1994.08040997.x). **Crossref, Web of Science, Google Scholar**

¹⁴ Ghazoul J., Liston K. A. & Boyle T. J. B.. 1998 Disturbance-induced density-dependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. *J. Ecol.* **86**, 462–473. doi:10.1046/j.1365-2745.1998.00270.x (doi:10.1046/j.1365-2745.1998.00270.x). **Crossref, Web of Science, Google Scholar**

¹⁵ Murawski D. A., Gunatilleke I. & Bawa K. S.. 1994 The effects of selective logging on inbreeding in *Shorea megistophylla* (Dipterocarpaceae) from Sri Lanka. *Conserv. Biol.* **8**, 997–1002. doi:10.1046/j.1523-1739.1994.08040997.x (doi:10.1046/j.1523-1739.1994.08040997.x). **Crossref, Web of Science, Google Scholar**

¹⁶ Ghazoul J., Liston K. A. & Boyle T. J. B.. 1998 Disturbance-induced density-dependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. *J. Ecol.* **86**, 462–473. doi:10.1046/j.1365-2745.1998.00270.x (doi:10.1046/j.1365-2745.1998.00270.x). **Crossref, Web of Science, Google Scholar**

¹⁷ Marsh C. W. & Greer A. G.. 1992 Forest-land use in Sabah, Malaysia: an introduction to Danum Valley. *Phil. Trans. R. Soc. Lond. B* **335**, 331–339. doi:10.1098/rstb.1992.0025 (doi:10.1098/rstb.1992.0025). **Link, Web of Science, Google Scholar**

Although the replicate trees within each forest type were far from each other (greater than 100 m), and may be considered independent samples, the conclusions of this study apply to the forests around the DVCA and YSFMA. Furthermore, we considered only one species. *Parashorea malaanonan* is very abundant and is a relatively fast-growing dipterocarp, making it an atypical species. Rarer species may be better able to escape from their natural enemies in space, and therefore show stronger distance and density dependence. Further studies at other paired areas of unlogged and logged forest, and with additional species, will be necessary to establish if the patterns discovered here apply to unlogged and logged forests in general.

(b) Causes of mortality

Vertebrates caused the vast majority of the observed seed and germinating seedling mortality in the field. It has been suggested that vertebrates are unlikely to cause such density dependence because they tend to be mobile generalists ([¹⁸, but see¹⁹). The mobility of these seed predators did not prevent them from generating strong negative density dependence in *P. malaanonan* survival. Because we did not consider heterospecifics here, we cannot determine if mortality increased with conspecific density or just density in general. For the Janzen–Connell mechanism to maintain species richness, increased density of a particular species must increase predation of heterospecifics less than conspecifics²⁰. It is quite possible that seeds of other species would not benefit from a rare species advantage if they had dispersed into plots with high densities of *P. malaanonan*. Other work at this site, however, suggests that small vertebrates prefer conspecific dipterocarp seeds to heterospecific dipterocarp seeds, but large vertebrates did not discriminate between them²¹.

Our field data probably underestimate insect predation of *P. malaanonan*. A proportion of insect-predated seeds would have been removed from the plots (assuming vertebrates did not discriminate against them). Such seeds would have been scored as vertebrate-predated, causing us to underestimate the role of invertebrates. While we

¹⁸ Hammond D. S.& Brown V. K.. 1998 Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. *Dynamics of tropical communities* (eds , Newbery D. M., Prins H. H. T.& Brown N. D.), pp. 51–78. Oxford, UK: Blackwell's. **Google Scholar**

¹⁹ Paine C. E. T.& Beck H.. 2007 Seed predation by neotropical rain forest mammals increases diversity in seedling recruitment. *Ecology* **88**, 3076–3087.doi:10.1890/06-1835.1 (**doi:10.1890/06-1835.1**). **Crossref, PubMed, Web of Science, Google Scholar**

²⁰ Hille R., Lambers J., Clark J. S.& Beckage B.. 2002 Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* **417**, 732–735.doi:10.1038/nature00809 (**doi:10.1038/nature00809**). **Crossref, PubMed, Web of Science, Google Scholar**

²¹ Hautier Y., Saner P., Philipson P., Bagchi R., Ong R. C.& Hector A.. 2010 Effects of seed predators of different body size on seed mortality in Bornean logged forest. *PLoS ONE* **5**, e11651.doi:10.1371/journal.pone.0011651 (**doi:10.1371/journal.pone.0011651**). **Crossref, PubMed, Web of Science, Google Scholar**

examined seeds for signs of insect emergence holes, these can be easily missed in the field, especially because insects often emerge from between the wings of dipterocarp seeds. These wings are formed from the calyx, and *P. malaanonan* has two long (9–16 cm) and three short (6–10 cm) wings²². The area between the wings is very rough, and emergence holes there might be overlooked. Emergence rates from seeds kept in the laboratory provide a more realistic estimate of invertebrate attack. In the absence of vertebrate predators, insects attacked about 9 per cent of seeds, low in comparison with other studies from the region^{23,24}. However, even our laboratory data will probably underestimate insect predation. About 54 per cent of the seeds we collected showed evidence of insect predation but did not produce any insects, and it is likely that seed predators left a proportion of these seeds before we collected them. Some weevils in the Nanophyidae have been recorded to emerge prior to seed dispersal²⁵. Furthermore, much of the insect-related mortality of dipterocarp seeds occurs early on in fruit development, leading to abortion. These early losses can be substantial²⁶, but we only started collecting seeds once they were mature, and therefore almost certainly underestimated the impact of insects.

²² Newman M. F., Burgess P. F. & Whitmore T. C.. 1999 *Malesian Dipterocarps. Foresters CD-ROM Manual*. Edinburgh, UK: Royal Botanic Garden, Edinburgh. **Google Scholar**

²³ Maycock C. R., Thewlis R. N., Ghazoul J., Nilus R. & Burslem D. F. R. P.. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646. doi:10.1111/j.1654-1103.2005.tb02406.x (doi:10.1111/j.1654-1103.2005.tb02406.x). **Crossref, Web of Science, Google Scholar**

²⁴ Toy R. J., Marshall A. G. & Pong T. Y.. 1992 Fruiting phenology and the survival of insect fruit predators—a case-study from the South-East Asian Dipterocarpaceae. *Phil. Trans. R. Soc. Lond. B* **335**, 417–423. doi:10.1098/rstb.1992.0033 (doi:10.1098/rstb.1992.0033). **Link, Web of Science, Google Scholar**

²⁵ Toy R. J., Marshall A. G. & Pong T. Y.. 1992 Fruiting phenology and the survival of insect fruit predators—a case-study from the South-East Asian Dipterocarpaceae. *Phil. Trans. R. Soc. Lond. B* **335**, 417–423. doi:10.1098/rstb.1992.0033 (doi:10.1098/rstb.1992.0033). **Link, Web of Science, Google Scholar**

²⁶ Toy R. J., Marshall A. G. & Pong T. Y.. 1992 Fruiting phenology and the survival of insect fruit predators—a case-study from the South-East Asian Dipterocarpaceae. *Phil. Trans. R. Soc. Lond. B* **335**, 417–423. doi:10.1098/rstb.1992.0033 (doi:10.1098/rstb.1992.0033). **Link, Web of Science, Google Scholar**

(c) Mast fruiting and the Janzen–Connell mechanism

It is generally thought that practically no dipterocarp recruitment occurs in South East Asian forests outside community-wide mast-fruiting events^{27,28}. However in this study, 35 per cent of seeds in the unlogged forest and 17 per cent in logged forest survived until the end of two months. About 8 per cent of the original seedlings in the non-manipulated plots (18 individuals) were still alive in the unlogged forest sites 10 months later, equivalent to 0.45 seedlings m⁻² (R. Bagchi 2005, unpublished data). Therefore, contrary to the general consensus, at least some dipterocarps recruited in a non-mast year, albeit in small numbers. It is of course very possible that these individuals will die before they reach maturity, or that their recruitment makes a negligible contribution to the population dynamics of *P. malaanonan*. While mortality rates are very high during the seed and early seedling stage described here, the seedlings that survived the duration of this study will probably have to survive for several decades in order to reach the canopy²⁹. Without comparable data from a mast year, it is difficult to determine how the density of survivors in this study compares, but it is likely to be much lower than expected after a mast fruiting.

Maycock *et al.*³⁰ similarly reported recruitment outside major fruiting events of the congeneric *Parashorea tomentella* at Sepilok Forest Reserve, another lowland forest in Sabah. However, Maycock *et al.*³¹ also reported negligible survival of other dipterocarp species in the same fruiting event. One possible explanation could be that *P. malaanonan* seeds are unpalatable. However, various seed predators (vertebrates and

²⁷ Curran L. M. & Leighton M.. 2000 Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* **70**, 101–128. doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2 (doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2). **Crossref, Web of Science, Google Scholar**

²⁸ Janzen D. H.. 1974 Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica* **6**, 69–103. doi:10.2307/2989823 (doi:10.2307/2989823). **Crossref, Google Scholar**

²⁹ Whitmore T. C.. 1984 *Tropical rainforests of the Far East*, 2nd edn. Oxford, UK: Oxford University Press. **Google Scholar**

³⁰ Maycock C. R., Thewlis R. N., Ghazoul J., Nilus R. & Burslem D. F. R. P.. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646. doi:10.1111/j.1654-1103.2005.tb02406.x (doi:10.1111/j.1654-1103.2005.tb02406.x). **Crossref, Web of Science, Google Scholar**

³¹ Maycock C. R., Thewlis R. N., Ghazoul J., Nilus R. & Burslem D. F. R. P.. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646. doi:10.1111/j.1654-1103.2005.tb02406.x (doi:10.1111/j.1654-1103.2005.tb02406.x). **Crossref, Web of Science, Google Scholar**

invertebrates) have been recorded attacking *P. malaanonan* seeds and seedlings³²³³, so this seems unlikely. Maycock *et al.*³⁴ suggested that *P. tormentella* satiated seed predators because a high proportion of trees fruited over a large area. *Parashorea* species are extremely common in both Danum and Sepilok, and this may partly explain its success outside community-wide mast events. However, data from very abundant species at other sites suggest no such patterns. Two very abundant dipterocarp species, *Shorea lamellata* and *Shorea quadrinervis*, both failed to recruit after producing seeds in non-mast years³⁵³⁶.

³² Wells K.& Bagchi R.. 2005 Eat in or take away—seed predation and removal by rats (Muridae) during a fruiting event in a dipterocarp rainforest. *Raffles B Zool.* **53**, 125–130. **Web of Science, Google Scholar**

³³ Slade E. M.. 2007 The effects of tropical forest management on biodiversity and ecosystem functioning. PhD thesis, University of Oxford, Oxford, UK. **Google Scholar**

³⁴ Maycock C. R., Thewlis R. N., Ghazoul J., Nilus R.& Burslem D. F. R. P.. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646.doi:10.1111/j.1654-1103.2005.tb02406.x (doi:10.1111/j.1654-1103.2005.tb02406.x). **Crossref, Web of Science, Google Scholar**

³⁵ Curran L. M.& Leighton M.. 2000 Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* **70**, 101–128.doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2 (doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2). **Crossref, Web of Science, Google Scholar**

³⁶ Blundell A. G.& Peart D. R.. 2004 Seedling recruitment failure following dipterocarp mast fruiting. *J. Trop. Ecol.* **20**, 229–231.doi:10.1017/S0266467403001123 (doi:10.1017/S0266467403001123). **Crossref, Web of Science, Google Scholar**

5. Conclusion

In this study, seeds and seedlings produced during a non-mast year were predated by vertebrate predators and, to a lesser extent, insects. This predation was negatively density dependent at small spatial scales in both forest types, suggesting species diversity of logged forests will return to pre-logging levels more rapidly than might have been expected otherwise. However, survival increased with density at a larger spatial scale, probably because predators were satiated. Seed production was much lower in logged forest, and combined with the positive effects of large-scale density on survival, this resulted in recruitment being almost completely concentrated in unlogged forest. The failure of *P. malaanonan* to recruit in logged forest raises concerns about the ability of some tree species to recover from logging. If similar patterns were observed during mast years, this would have serious implications for the viability of logged forests in the region. Determining whether this is the case should be considered a research priority.

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