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Effect of Reduced-Impact Logging on Seedling Recruitment in a Neotropical Forest

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Abstract

Seedling growth and survival are critical for tropical rainforest regeneration. Alterations to natural disturbance regimes, such as those brought about by logging, have the potential to shift relative species abundances and the community composition of forests, resulting in population declines for commercially valuable species. Timber operations therefore need to minimise such changes if long-term sustainability is to be achieved within the industry. Reduced-impact logging (RIL) has been promoted widely as an alternative management strategy to conventional selective logging, as it employs practices that decrease the negative impacts of logging within forests. However, the long-term sustainability of RIL, including the influence it has on the regeneration of species targeted for timber extraction, is still uncertain. Here we undertake a comparative study in Iwokrama forest, Guyana, examining seedling densities of four commercially valuable and two pioneer tree species in unlogged, 1.5 years and 4.5 years postharvest forest plots to ascertain how seedling regeneration is effected by RIL. We find that RIL had either a neutral or positive impact on the density of seedlings of timber species when compared to unlogged forest, with pioneer species densities remaining unaffected. We conclude that the forestry practices associated with RIL have little effect on the natural regeneration rates of key commercially valuable tree species in logged neotropical forests.

Key words: Guyana, Regeneration, Forest disturbance, RIL, Sustainable forestry, Timber

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1. Introduction

Logging rates throughout the world's tropical rainforests continue to increase (Arets 2005; FAO 2010; Gardner 2010) with approximately 30% of their areal extent designated for timber and non-timber product exploitation (FAO 2010). Indeed, over 40 million hectares are currently allocated to selective logging globally (Asner et al. 2009; Blaser et al. 2011). In tropical forests, seedling growth and survival are driven principally by small-scale disturbance dynamics of canopy gaps (Brokaw 1982; Hartshorn 1978; ter Steege et al. 1994; Zagt 1997). When a tree falls, either naturally or through logging, a canopy gap is created of varying size. The resultant gap alters the microclimate (light, moisture, and temperature) of the immediate area, stimulating the growth of any seedlings already present (climax species) or triggering seed germination (pioneer and climax species) (Yamamoto 2000). Changes to natural disturbance regimes, such as those brought about by logging, can thus affect the growth, survival and reproduction rates of plant species (Asner et al. 2004; Boot 1996; Brokaw 1982; de Avila et al. 2015; Fenner 1985; Karsten et al. 2014; Rose 2000; ter Steege & Hammond 2000). Consequently, forest assemblage composition can alter over time, due to species-specific variation in re-establishment following logging (Asner et al. 2004; Karsten et al. 2014; ter Steege et al. 2002) and applied silvicultural practices (de Avila et al. 2015). Low disturbance levels tend to favour slower growing hardwood climax species, resulting in relatively stable forest ecosystems that characterise lowland tropical rainforests. As disturbance levels rise, faster growing, less dense pioneer species tend to dominate (Karsten et al. 2014; ter Steege & Hammond 2000). Therefore, the extent to which rainforest structure and composition are impacted by logging is highly dependent on the intensity of logging, harvest interval, and management practices implemented (Gardner 2010; Waide & Lugo 1992; Zagt 1997).

Reduced-Impact Logging (RIL) was developed to provide a more sustainable alternative to conventional selective logging, whereby the detrimental effects inherent in many traditional forestry

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operations are minimised (Pinard & Putz 1996; Putz et al. 2008). Although the forestry techniques used under RIL vary from country to country, the aim is to retain forest canopy integrity and species diversity (Edwards et al. 2011; Gibson et al. 2011; Putz et al. 2012), reduce land degradation (Bryan et al. 2010; Dykstra 2002; Dykstra & Heinrich 1992; Dykstra & Heinrich 1996; Jonkers 2002; Putz et al. 2008), and decrease the carbon emissions associated with collateral damage to surrounding vegetation and soil disturbance (Pinard & Putz 1996; Putz et al. 2008), while maintaining a sustained timber supply for future cutting cycles (Putz et al. 2000). Tree inventories are undertaken in order to plan the most efficient and least destructive extraction of logged timber and, in some operations, selected harvest trees have attached vines cut several months prior to removal. The trees are then felled using directional techniques in order to facilitate extraction and minimise stand damage, with logs removed using a skidder and winch.

In this study, we examine natural regeneration levels of commercially valuable tree species in a RIL logging operation in Guyana. Guyana's commercial timber species occur in isolated stands dominated by one or two species (Johnston & Gillman 1995). Harvesting operations are therefore selective by necessity with extraction rates averaging 2-3 trees/ha^{-1} (Blaser et al. 2011; Jonkers 2002; van der Hout 1999), although they can be as high as 20 trees/ha^{-1} in some areas (Jonkers 2002). While the countries annual rate of 0.3% deforestation is relatively low compared with other tropical countries (FAO 2006), timber constitutes an important component of the national economy (Blaser et al. 2011; GFC 2002). As in many other tropical countries, Guyana's timber industry relies on natural regeneration (Hammond et al. 1996; van der Hout 1999), meaning that logging that has a detrimental impact on the natural regeneration of commercially important tree species will not be sustainable in the long-term. Historically, the timber industry in the country has centred on Chlorocardium rodiei (greenheart), but increased market demand has seen the number of species targeted by logging expand considerably in recent decades (Jonkers 2002).

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Presently, there is a paucity of research into the effects of RIL on natural seedling regeneration within the neotropics (Lobo et al. 2007; Rose 2000), with the majority of studies focusing on the application of silviculture (Dekker & de Graaf 2003; Forget et al. 2001; ter Steege et al. 1994), other forms of logging (Kuusipalo et al. 1996; Pinard et al. 1996), or seedling regeneration in the absence of logging disturbance (Baraloto & Goldberg 2004; Baraloto et al. 2005). Consequently, this paper fills an important gap in our understanding, thus contributing to the improvement of management practices within RIL forest stands and the long-term sustainable use of commercially important target species across their range (Arets 2005; Putz et al. 2000; van der Hout 2000).

2. Material and Methods

2.1 Study area

Iwokrama forest is located in central Guyana (Fig. 1.), covering an area of 371,000 ha^{-1}. It was established in 1996 as a demonstration site to exemplify how tropical forest exploitation can be sustainable, with commercially viable logging being balanced with biodiversity conservation and local community needs (Watkins 2005). The climate is tropical, with an annual rainfall ~ 3700 mm across two rainy seasons (May-August and December-January). Temperatures range from a mean minimum of 22 °C overnight in July, up to a daytime maximum of 36 °C in October.

The study area (Fig.1) is characterised by low-lying terra firme tropical rainforest on nutrient poor soils. Dominant forest types include: (i) mixed C. rodiei, Eschweilera spp. and Swartzia leiocalycina forest; (ii) Mora excelsa, Euterpe oleracea, Carapa guianensis and Pentaclethra macroloba forest; and, (iii) mixed C. rodiei, Catostemma fragrans, and Eperua falcata forest.

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RIL became operational in Iwokrama forest during 2007, with operations certified by the Forestry Stewardship Council (FSC). Sustainable harvest levels are calculated based on species growth rates combined with a 60-year polycyclic felling rotation. Logging intensity (calculated within a 100 m radius from the sampling sites) ranged from 0.6-11.1 (mean = 3.7, median = 3.2, S.D. = 2.6) trees/ha^{-1}, with an average of 152 m/ha^{-1} of skid trails throughout the logging concession (Bicknell et al. 2015).

2.2 Study design

A comparative study was undertaken examining seedling density for six species, in both unlogged and postharvest forest stands, to ascertain how RIL influences forest regeneration. Following Rose (2000), we sampled seedlings (defined as up to 150 cm tall) of the four primary timber species logged in the Guianas (Hammond et al. 1996; van der Hout 2000): C. rodiei (greenheart), Dicorynia guianensis (basralocus), E. falcata (soft wallaba), and Goupia glabra (kabukalli). In addition, we also assessed the densities of the two most common pioneer species, Cecropia obtusifolia and Cecropia sciadophylla, which are indicators of disturbance as they grow along forest edges and within canopy gaps (Alvarez-Buylla & Martinez-Ramos 1992). Seedlings were then assigned to one of three height classes (0-50, 50-100 and 100-150 cm).

The study was conducted in May and June 2012, within the C. rodiei, Eschweilera spp. and S. leiocalycina forest type which is predominant in the Iwokrama logging concession. Two postharvest temporal logging treatments (1.5 and 4.5 years after timber extraction) and unlogged (control) forest were sampled. Sample plots of 20 x 20 m were used to determine seedling densities; this size was large enough for accurate estimates of seedling densities, but not too large to preclude maximum replication of plots per treatment (Bullock 2006). In total, sixty plots were sampled, comprising 20 within each of three harvesting blocks (Fig. 1). The sampling areas had been divided into a 20 x 20 m grid for tree inventory purposes prior to logging. The intersections of the grid were used to assign plot localities,

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using a random number generator to select coordinates. In logged treatments, the south-west corner of each plot was constrained to within a 50 m radius of a felled tree. This means that we inevitably sampled seedlings both within and on the edge of these gaps. In the unlogged forest, plots were similarly constrained to within a 50 m radius of inventoried trees allocated for felling, with many plots also falling within or adjacent to natural gaps. This was done to ensure a comparable adult community composition between the three treatments. Areas subject to much higher intensity impacts, such as skid trails, roads, mill sites and log landings (where vegetation is highly disturbed or removed), were excluded from sampling. This was so that the focus was on areas that will provide future timber yields, rather than sampling logging infrastructure which is likely to be cleared again during the next round of timber extraction and, thus, where commercially valuable species will not be able to grow to maturity between cutting cycles.

2.3 Reproductive ecology of six species

Whilst the specific reproductive and ecological traits of the species studied vary (summarised in Table 1), pioneers tend to have small seeds, which are readily dispersed and grow rapidly in large gaps (Martinez-Ramos et al. 1989; Pons et al. 2005) during the first 1-5 years post germination (Baraloto et al. 2005). Larger seeded climax species targeted for timber harvesting can persist as seedlings for a long time (Forget 1989) within shaded environments, attaining maturity as and when light levels increase (Martinez-Ramos et al. 1989).

2.4 Data analyses

Seedling densities for each species were compared between unlogged and the two temporal logging treatments to determine the effect of RIL on regeneration rates. Seedling densities within the three height classes were also compared across treatments to determine the effects of logging on the recruitment and regeneration of seedlings of different ages. All data were $\log_{10}$ transformed prior to

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analyses, and non-parametric Kruskal-Wallis tests were employed to examine differences in densities between treatments. Mann-Whitney U tests were used to make post-hoc comparisons. All analyses were conducted in SPSS (IBM v. 19).

Additionally, community analyses were used to determine if seedling densities differed between treatments for all six species. This was conducted via non-metric multi-dimensional scaling (NMDS), coupled with analysis of similarity (ANOSIM). The NMDS, based on Bray-Curtis dissimilarity coefficients, was implemented in PC-ORD v.6.07 (McClune & Mefford 2011). Five hundred iterations and 250 runs of both real and randomised data were used to produce a final ordination of minimum stress and consisting of two axes. ANOSIM was computed from 999 permutations in R (R Core Team 2013).

3. Results

In total, 13,771 seedlings of the six target species were sampled across the 60 plots. Of these, 69% were greenheart, 17% soft wallaba, 13% basralocus, and 0.5% kabukalli. The two pioneer Cecropia species combined comprised less than 0.5% of the total number of seedlings recorded. Greenheart had the highest seedling densities within both the treatment and control plots, followed by basralocus in unlogged forest, and soft wallaba in the 1.5 and 4.5 years postharvest plots. Both pioneer species were unrecorded in unlogged and 4.5 years postharvest plots (Fig. 2).

Plots occurring in the 4.5 years postharvest forest treatment contained the highest overall density of seedlings (42% of all seedlings), with unlogged forest (34%) and 1.5 years postharvest forest (24%) containing slightly lower densities (Table 3). Of the six species studied, overall densities of four species (greenheart, basralocus, and both Cecropia species) did not differ between the three types of plot (Table 2; Fig. 2). Significant increases in seedling densities of soft wallaba and kabukalli were

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apparent across the 1.5 years and 4.5 years postharvest forest compared to unlogged forest (Fig. 2; Table 2).

Within height classes, the seedling densities of soft wallaba were consistently greater in 4.5 years postharvest forest compared to both unlogged and 1.5 years postharvest forest ($p < 0.001$ in all comparisons). Greenheart and Cecropia obtusifolia seedling densities were significantly lower in the 100–150 cm height class ($p = 0.042$ and $p = 0.045$ respectively), and kabukalli seedling densities were significantly higher in 0–50 cm class ($p = 0.018$). All other species showed no significant differences within height classes across treatments ($p > 0.05$ in all cases) (Tables 2 and 3; Fig. 3).

The NMDS ordination of community structure represented 62% of the dissimilarity between treatments and control (Fig. 4), and analysis of similarity indicated that significant differences were evident between the 4.5 year plots and all others (ANOSIM - unlogged versus 1.5 year: $R = 0.02$, $p = 0.21$; unlogged versus 4.5 year: $R = 0.26$, $p < 0.01$; 1.5 year versus 4.5 year: $R = 0.17$, $p < 0.01$). This showed the community composition of the 4.5 year postharvest forest differed from both the 1.5 year postharvest and unlogged forest. However, there was no difference between the community composition of the 1.5 year postharvest plots and unlogged plots.

4. Discussion

Species specific biological responses, including regeneration rates and the original density of target species, retention of mature trees for seed dispersal, logging intensity and time between cutting cycles (Baraloto et al. 2005; Polak 1992; Sist et al. 2003, ter Steege & Hammond 2000), are key considerations in determining the long-term sustainability of logging. A failure to integrate such basic ecological information into forest management planning can lead to declines in exploited species populations, alter community composition and threaten future timber yields (Hammond et al. 1996;

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Shearman et al. 2012; Zimmerman & Kormos 2012). As RIL explicitly takes into account these factors, it is likely to have the least detrimental impact on commercially valuable timber species when compared with conventional selective logging (West et al. 2014).

Our findings suggest that disturbance arising from RIL operations may not have a lasting negative impact on seedling regeneration and, for some species, may even help to encourage establishment (ter Steege et al. 1994; Rose 2000; ter Steege et al. 2002; Putzel et al. 2011; Karsten et al. 2014). Of the species studied, soft wallaba showed the largest increase in seedling densities across the temporal logging treatments. It is likely that this species drove differences in overall assemblage composition between treatments. Previous research into the growth rate of soft wallaba after logging suggests that the relatively high abundance of seedlings found in our study could subsequently result in a greater abundance of soft wallaba over time, altering the forest assemblage and dynamics in the long-term (Herault et al. 2010). While this may be a desirable outcome for forest management if market demand for this species increases, soft wallaba is already one of the most widespread canopy species in the Guiana’s (ter Steege & Zondervan 2000; ter Steege et al. 2013). As such, limiting gap size and minimising disturbance through RIL will be important in maintaining the current tree assemblage composition of the forest (Herault et al. 2010). Without such precautions, this species may outcompete other commercially valuable but less responsive timber species.

While RIL had no effect on the overall seedling densities of either greenheart or basralocus, greenheart seedling density was greater within the taller height classes following logging, which is probably a response to moderate increases in light levels (ter Steege et al. 1994). Basralocus is also known to be negatively affected by some forms of selective logging (Degen et al. 2006), although no changes to seedling densities for this species across the height classes were observed in this study. Our results

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indicate, therefore, that disturbance levels following RIL operations remain sufficiently low enough to have little to no impact on the long-term persistence of these species.

Densities of kabukalli seedlings increased across the logged treatments compared with unlogged forest, indicating regeneration of this species was stimulated by logging disturbance. However, seedling numbers for this species were the lowest of the four timber species surveyed, paralleling more closely with regeneration responses of the two pioneer species, and consistent with the reported regeneration responses of other light preferring species in logged forests (Karsten et al. 2014; Putzel et al. 2011; Rose 2000). The outcome of our study implies that the regeneration potential of kabukalli may be constrained within RIL concessions to outside the extraction forest in areas where disturbance is highest, such as along skid trails, within log landings and mill sites, or where larger gaps open within the forest canopy.

Neither of the two pioneer species showed a difference in seedling densities between the temporal logging treatments. Recorded numbers of both Cecropia species were very low in 1.5 years forest, with none documented in unlogged or 4.5 years postharvest forest plots. This reflects the biology of Cecropia species where successful recruitment is restricted to gaps less than three years old and larger than 100 m^2 (Alvarez-Buylla & Martinez-Ramos 1992; Vazquez-Yanes & Smith 1982) on disturbed mineral soils (Lawton & Putz 1988), dropping off markedly as the canopy closes (Rose 2000). This suggests that structural and soil disturbance within the standing forest area may have been kept to a minimum. However, as skid trails and other logging infrastructure constitute the greatest damage caused by RIL (Asner et al. 2004), additional research within the Guiana's is warranted to determine the full impact of logging on commercially valuable species (Karsten et al. 2014).

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Overall our work demonstrates that disturbance levels following RIL in Iwokrama forest, within the vicinity of logged gaps, is minimal, with regeneration rates of four commercially harvested timber species either unchanged or increasing after logging. As none of the timber species included in this study showed a reduction in density postharvest, it is likely that RIL will allow effective natural regeneration to occur without the need for further silvicultural intervention (Putz et al. 2008). Furthermore, recent research has shown that the community composition of important seed dispersing animals remain relatively unaltered by RIL (e.g. Bicknell & Peres 2010; Bicknell et al. 2014; Bicknell et al. 2015), and thus the important role they play in forest regeneration is likely to be maintained.

5. Conclusion

Though arguments remain against the sustainability of logging across the tropics (Shearman et al. 2012; Zimmerman & Kormos 2012) the timber industry will undoubtedly persist into the future. As lowland rainforests in the Neotropics, including Guyana, contain a large number of tree species with highly restricted distributions (Gentry 1992), it is crucial that logging has the least detrimental impact possible on the overall integrity of forest ecosystems and exploited species populations. Adjusting harvesting practices to ensure the effective natural regeneration of commercially valuable species is an important step in safeguarding the long-term viability of the industry. The results from this study indicate that RIL may provide a sustainable alternative to other forms of logging, and efforts should be made to implement it more widely to maintain the ecological and economic value of rainforests indefinitely.

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References

Alvarez-Buylla, E. R., and M. Martinez-Ramos. 1992. Demography and allometry of Cecropia obtusifolia, a neotropical pioneer tree – an evaluation of the climax-pioneer paradigm for tropical rain forests. Journal of Ecology **80:**275-290.

Arets, E. J. M. M. 2005. Long-term responses of populations and communities of trees to selective logging in tropical rain forests in Guyana. Tropenbos Guyana Series 13, Georgetown, Guyana.

Asner, G. P., M. Keller, and J. N. M. Silva. 2004. Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. Global Change Biology **10:**765-783.

Asner, G. P., T. K. Rudel, T. M. Aide, R. Defries, and R. Emerson. 2009. A contemporary assessment of change in humid tropical forests. Conservation Biology **23:**1386-1395.

Baraloto, C., P. Forget, and D. E. Goldberg. 2005. Seed mass, seedling size and neotropical tree seedling establishment. Journal of Ecology **93:**1156-1166.

Baraloto, C., and D. E. Goldberg. 2004. Microhabitat associations and seedling bank dynamics in a neotropical forest. Oecologia **141:**701-712.

Bicknell, J. and C.A. Peres, 2010. Vertebrate population responses to reduced-impact logging in a neotropical forest. Forest Ecology and Management **259:**2267-2275.

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http://creativecommons.org/licenses/by-nc-nd/4.0/

Bicknell, J.E., S.P. Phelps, R.G. Davies, D.J. Mann, M.J. Struebig, and Z.G. Davies. 2014. Dung beetles as indicators for rapid impact assessments: Evaluating best practice forestry in the neotropics. Ecological Indicators **43:**154-161.

Bicknell, J.E., M.J. Struebig, and Z.G. Davies, 2015. Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging. Journal of Applied Ecology **52:**379-388.

Blaser, J., A. Sarre, D. Poore, and S. Johnson. 2011. Status of tropical forest management 2011. ITTO, Yokohama. Available at: www.itto.int/sfm/.

Boot, R. G. A. 1996. Chapter 11: The significance of seedling size and growth rate of tropical rain forest tree seedlings for regeneration in canopy openings. Pages 267-283 in M. D. Swaine, editor. The Ecology of Tropical Forest Tree Seedlings. Man and the Biosphere Series 17. UNESCO, Paris, France.

Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica **14:**158-160.

Bryan, J., P. Shearman, J. Ash, and J. B. Kirkpatrick. 2010. Impact of logging on aboveground biomass stocks in lowland rain forest, Papua New Guinea. Ecological Applications **20:**2096-2103.

Bullock, J. M. 2006. Chapter 4: Plants. Pages 186-213. In: W. J. Sutherland, editor. Ecological Census Techniques: A Handbook. Second Edition. Cambridge University Press, Cambridge.

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http://creativecommons.org/licenses/by-nc-nd/4.0/

De Avila, A. L., A. R. Ruschel, J. O. P. de Carvalho, L. Mazzei, J. N. M. Silva, J. D. C. Lopes, M. M. Araujo, C. F. Dormann, and J. Bauhus. 2015. Medium-term dynamics of tree species composition in response to silvicultural intervention intensities in a tropical rain forest. Biological Conservation **191:**577-586

De Grandcourt, A., D. Epron, P. Montpied, E. Louisanna, M. Bereau, J. Garbaye, and J. M. Guehl. 2004. Contrasting responses to mycorrhizal inoculation and phosphorus availability in seedlings of two tropical rainforest tree species. New Phytologist **161**:865-875.

Degen, B., L. Blanc, H. Caron, L. Maggia, A. Kremer, and S. Gourelt-Fleury. 2006. Impact of selective logging on genetic composition and demographic structure of four tropical tree species. Biological Conservation **131:**386-401.

Dekker, M., and N. R. de Graaf. 2003. Pioneer and climax tree regeneration following selective logging with silviculture in Suriname. Forest Ecology and Management **172:**183-190.

Dykstra, D. P., and R. Heinrich. 1992. Sustaining tropical forests through environmentally sound harvesting practices. Unasylva **43:**9-15.

Dykstra, D. P., and R. Heinrich. 1996. FAO model code of forest harvesting practice. Food and Agriculture Organization of the United Nations, Rome, Italy.

Dykstra, D.P. 2002. Chapter 2: Reduced impact logging: concepts and issues. In T. Enters, P. B. Durst, G. B. Applegate, P. C. S. Kho, and G. Man, editors. Applying Reduced Impact Logging to Advance Sustainable Forest Management. Food and Agriculture Organization of the United Nations, Bangkok,

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http://creativecommons.org/licenses/by-nc-nd/4.0/

Thailand. Available from http://www.fao.org/docrep/005/AC805E/ac805e04.htm#bm04 (accessed March 2014).

Edwards, D. P., T. H. Larsen, T. D. S. Docherty, F. A. Ansell, W. W. Hsu, M. A. Derhe, K. C. Hamer, and D. S. Wilcove. 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. Proceedings of the Royal Society B: Biological Sciences **278:**82-90.

FAO (Food and Agriculture Organization of the United Nations). 2006. Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management. FAO Forestry Paper 147. Food and Agriculture Organization of the United Nations, Rome, Italy. Available from http://www.fao.org/forestry/fra/fra2005/en/ (accessed July 2014).

FAO (Food and Agriculture Organization of the United Nations). 2010. Global Forest Resources Assessment 2010: Main Report. FAO Forestry Paper 163. Food and Agriculture Organization of the United Nations, Rome, Italy. Available from http://www.fao.org/docrep/013/i1757e/i1757e.pdf (accessed July 2014).

Fenner, M. 1985. Seed Ecology. Chapman and Hall, London.

Forget, P. M. 1989. Natural regeneration of an autochorus species of the Guianese forest: Eperua falcata Aublet – Caesalpinaceae. Biotropica **21**:115-125.

Forget, P., J. M. Rankin-De Merona, and C. Julliot. 2001. The effects of forest type, harvesting and stand refinement on early seedling recruitment in a tropical rain forest. Journal of Tropical Ecology **17:**593-609.

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Fournier-Origgi, L. A. 2002. Cecropia obtusifolia Bertol. Pages 382-383. In: J. A. Vozzo, editor. Tropical Tree Seed Manual. Agriculture Handbook 721, USDA Forest Service, Washington DC.

Gardner, T. 2010. Monitoring Forest Biodiversity: Improving Conservation Through Ecologically Responsible Management. Earthscan, London and New York.

Gentry, A. H. 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. Oikos **63:**19-28.

Gerard, J., R. B. Miller, and B. J. H. ter Welle. 1996. Major Timber Trees of Guyana: Timber Characteristics and Utilization. Tropenbos Series 15. The Tropenbos Foundation, Wageningen, The Netherlands.

GFC (Guyana Forestry Commission). 2002. Code of Practice for Timber Harvesting. Second Edition. Guyana Forestry Commission website. Available from http://www.forestry.gov.gy/Downloads/CoP%20Timber%20Harvesting.pdf (accessed March 2012).

Gibson, L., T. M. Lee, L. P. Koh, B. W. Brook, T. A. Gardner, J. Barlow, C. A. Peres, C. J. A. Bradshaw, W. F. Laurance, T. E. Lovejoy, and N. S. Sodhi. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature **478:**378-381.

Hammond, D. S., S. Gourlet-Fleury, P. van der Hout, H. ter Steege, and V. K. Brown 1996. A compilation of known Guianan timber trees and the significance of their dispersal mode, seed size and taxonomic affinity to tropical rain forest management. Forest Ecology and Management **83:**99-116.

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Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. Pages 617-638. In P. B. Tomlinson, and M. H. Zimmerman, editors. Tropical Trees as Living Systems. Cambridge University Press, Cambridge.

Herault, B., J. Ouallet, L. Blanc, F. Wagner, and C. Baraloto. 2010. Growth responses of neotropical trees to logging gaps. Journal of Applied Ecology **47**: 821-831.

Horsley, T.W., Bicknell, J.E., Lim, B.K. and Ammerman, L.K. 2015. Seed dispersal by frugivorous bats in central Guyana and a description of previously unknown plant-animal interactions. Acta Chiropterologica. **17**: 331-336.

ITTO (International Timber Organization). 2015. ITTO Lesser Used Species: Tropical Timber Information (website). Available from http://www.tropicaltimber.info/specie/basralocus-dicorynia-guianensis (accessed 27 December 2015)

Johnston, M., and M. Gillman. 1995. Tree population studies in low-diversity forests, Guyana. I. Floristic composition and stand structure. Biodiversity and Conservation **4:**339-362.

Jonkers, W. B. J. 2002. Reduced impact logging in Sarawak, Guyana and Cameroon - the reasons behind differences in approach. In T. Enters, P. B. Durst, G. B. Applegate, P. C. S. Kho, and G. Man, editors. Applying Reduced Impact Logging to Advance Sustainable Forest Management. Food and Agriculture Organization of the United Nations, Bangkok, Thailand. Available from http://www.fao.org/DOCREP/005/AC805E/ac805e0n.htm#bm23 (accessed July 2014).

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Karsten, R. J., H. Meilby, and J. B. Larsen. 2014. Regeneration and management of lesser known timber species in the Peruvian Amazon following disturbance by logging. Forest Ecology and Management **327**:76-85.

Kuusipalo, J., Y. Jafarsidik, G. Adjers, and K. Tuomela. 1996. Population dynamics of tree seedlings in a mixed dipterocarp rainforest before and after logging and crown liberation. Forest Ecology and Management **81:**85-94.

Lawton, R. O. and F. E. Putz. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology **69**:764-777.

Lobo, J., G. Barrantes, M. Castillo, R. Quesada, T. Maldonado, E. J. Fuchs, S. Solis, and M. Quesada. 2007. Effects of selective logging on the abundance, regeneration and short-term survival of Caryocar costaricense (Caryocaceae) and Peltogyne purpurea (Caesalpinaceae), two endemic timber species of southern Central America. Forest Ecology and Management **245:**88-95.

Martinez-Ramos, M., E. Alvarez-Buylla, and J. Sarukhan. 1989. Tree demography and gap dynamics in a tropical rain forest. Ecology **70:**555-558.

McClune, B., and M.J. Mefford. 2011. PC-ORD. Multivariate analysis of ecological data.

Pinard, M., B. Howlett, and D. Davidson. 1996. Site conditions limit pioneer tree recruitment after logging of dipterocarp forest in Sabah, Malaysia. Biotropica **28:**2-12.

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http://creativecommons.org/licenses/by-nc-nd/4.0/

Pinard, M. A., and F. E. Putz. 1996. Retaining forest biomass by reducing logging damage. Biotropica **28**:278-295.

Polak, A. M. 1992. Major Timber Trees of Guyana: A Field Guide. Tropenbos Series 2. The Tropenbos Foundation, Wageningen, The Netherlands.

Pons, T. L., E. E. Alexander, N. C. Houter, S. A. Rose, and T. Rijkers. 2005. Ecophysiological patterns in Guianan forest plants. Chapter 3. In: D. S. Hammond (Ed). Tropical Forests of the Guiana Shield: Ancient Forests in a Modern World. CABI Publishing, CAB International, Wallingford UK.

Putz, F. E., K. H. Redford, J. G. Robinson, R. Fimbel, and G. M Blate. 2000. Biodiversity Conservation in the Context of Tropical Forest Management. World Bank Biodiversity Series - Impact Studies 1. Paper No. 75. World Bank Environment Department, Washington, D.C., USA.

Putz, F. E., P. Sist, T. Fredricksen, and D. Dykstra. 2008. Reduced-impact logging: challenges and opportunities. Forest Ecology and Management **256**:1427-1433.

Putz, F. E., P. A. Zuidema, T. Synnott. 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. Conservation Letters **5:**296-303.

Putzel, L., Peters, C. M., and Romo, M. 2011. Post-logging regeneration and recruitment of shihuahuaco (Dipteryx spp.) in Peruvian Amazonia: Impications for management. Forest Ecology and Management **261**:1099-1105.

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http://creativecommons.org/licenses/by-nc-nd/4.0/

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rose, S. A. 2000. Seeds, seedlings and gaps - size matters: a study in the tropical rain forest of Guyana. Tropenbos-Guyana Series 9. Tropenbos-Guyana Programme, Georgetown, Guyana.

Shearman, P., J. Bryan, and W. F. Laurance. 2012. Are we approaching 'peak timber' in the tropics? Biological Conservation **151:**17-21.

Sist, P., R. Fimbel, D. Sheil, R. Nasi, and M. H. Chevallier. 2003. Towards sustainable management of mixed dipterocarp forests of Southeast Asia: Moving beyond minimum diameter cutting limits. Environmental Conservation **30:**364-374.

ter Steege, H. 1990. A monograph of Wallaba, Mora and Greenheart. Tropenbos Technical Series 5. The Tropenbos Foundation, Ede, The Netherlands.

ter Steege, H., C. Bokdam., M. Boland., J. Dobbelsteen., and I. Verburg. 1994. The effects of man made gaps on germination, early survival, and morphology of Chlorocardium rodiei seedlings in Guyana. Journal of Tropical Ecology **10:**245-260.

ter Steege, H., and D. S. Hammond. 2000. An analysis at the ecosystem level: community characteristics, diversity, and disturbance. In H. ter Steege, editor. Plant Diversity in Guyana: With Recommendations for a National Protected Area Strategy. Tropenbos Series 18. The Tropenbos Foundation, Wageningen, The Netherlands.

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http://creativecommons.org/licenses/by-nc-nd/4.0/

ter Steege, H., and Zondervan, G. 2000. A preliminary analysis of large-scale forest inventory data of the Guiana Shield. In. H. ter Steege, editor. Plant diversity in Guyana: With recommendations for a National Protected Area Strategy. Tropenbos Series 18. The Tropenbos Foundation, Wageningen, The Netherlands. 35-54.

ter Steege, H., I. Welch., and R. Zagt. 2002. Long-term effect of timber harvesting in the Bartica Triangle, Central Guyana. Forest Ecology and Management **170:**127-144.

ter Steege, H., N. C. A. Pitman, D. Sabatier, C. Baraloto, R. P. Salomão, J. E. Guevara, O. L. Phillips, C. V. Castilho, W. E. Magnusson, J. Molino, A. Monteagudo, P. N. Vargas, J. C. Montero, T. R. Feldpausch, E. N. H. Coronado, T. J. Killeen, B. Mostacedo, R. Vasquez, R. L. Assis, J. Terborgh, F. Wittmann, A. Andrade, W. F. Laurance, S. G. W. Laurance, B. S. Marimon, B. Marimon Jr., I. C. G. Vieira, I. L. Amaral, R. Brienen, H. Castellanos, D. C. López, J. F. Duivenvoorden, H. F. Mogollón, F. D. de Almeida Matos, N. Dávila, R. García-Villacorta, P. R. S. Diaz, F. Costa, T. Emilio, C. Levis, J. Schietti, P. Souza, A. Alonso, F. Dallmeier, A. J. D. Montoya, M. T. F. Piedade, A. Araujo-Murakami, L. Arroyo, R. Gribel, P. V. A. Fine, C. A. Peres, M. Toledo, G. A. Aymard C., T. R. Baker, C. Cerón, J. Engel, T. W. Henkel, P. Maas, P. Petronelli, J. Stropp, C. E. Zartman, D. Daly, D. Neill, M. Silveira, M. R. Paredes, J. Chave, D. de Andrade Lima Filho, P. M. Jørgensen, A. Fuentes, J. Schöngart, F. C. Valverde, A.D. Fiore, E. M. Jimenez, M. C. P. Mora, J. F. Phillips, G. Rivas, T. R. van Andel, P. von Hildebrand, B. Hoffman, E. L. Zent, Y. Malhi, A. Prieto, A. Rudas, A.R. Ruschell, N. Silva, V. Vos, S. Zent, A. A. Oliveira, A. C. Schutz, T. Gonzales, M. T. Nascimento, H. Ramirez-Angulo, R. Sierra, M. Tirado, M. N. U. Medina, G. van der Heijden, C. I. A. Vela, E. V. Torre, C. Vriesendorp, O. Wang, K. R. Young, C. Baider, H. Balslev, C. Ferreira, I. Mesones, A. Torres-Lezama, L. E. U. Giraldo, R. Zagt, M. N. Alexiades, L. Hernandez, I. Huamantupa-Chuquimaco, W. Milliken,

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W. P. Cuenca, D. Pauletto, E. V. Sandoval, L. V. Gamarra, K. G. Dexter, K. Feeley, G. Lopez-Gonzalez, and M. R. Silman. 2013. Hyperdominance in the Amazonian Tree Flora. Science **342:**6156.

van der Hout, P. 1999. Reduced Impact Logging in the Tropical Rain Forest of Guyana: Ecological, Economic and Silvicultural Consequences. Tropenbos – Guyana Series 6. Tropenbos-Guyana Programme, Georgetown, Guyana.

van der Hout, P. 2000. Testing the applicability of reduced impact logging in greenheart forest in Guyana. International Forestry Review **2:**24-32.

Vazquez-Yanes, C., and H. Smith. 1982. Phytochrome control of seed germination in the tropical rain forest pioneer trees Cecropia obtusifolia and Piper auritum and its ecological significance. New Phytologist **92:**477-485.

Waide, R. B., and A. E. Lugo. 1992. A research perspective on disturbance and recovery of a tropical montane forest. Pages 173-190 in J. G. Goldammer, editor. Tropical Forests in Transition: Ecology of Natural and Anthropogenic Disturbance Processes. Birkhauser Verlag, Basel, Switzerland.

Watkins, G. G. 2005. The Iwokrama Centre and Forest: Introduction to special papers. Proceedings of the Academy of Natural Sciences of Philadelphia **154:**1-5.

West, T.A.P., E. Vidal, & F.E. Putz. 2014. Forest biomass recovery after conventional and reduced-impact logging in Amazonian Brazil. Forest Ecology and Management **314:** 59-63.

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http://creativecommons.org/licenses/by-nc-nd/4.0/

Yamamoto, S.I. 2000. Forest gap dynamics and tree regeneration. Journal of Forest Research **5:**223-229.

Zagt, R. J. 1997. Tree Demography in the Tropical Rain Forest of Guyana. Tropenbos–Guyana Series 3. Tropenbos-Guyana Programme, Georgetown, Guyana.

Zimmerman, B. L., and C. F. Kormos. 2012. Prospects for sustainable logging in tropical forests. BioScience **62:**479-487.

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Table 1: Summary information related to the reproductive ecology of four commercially valuable (CV) and two pioneer (PI) tree species, including seed mass, shade tolerance, primary seed dispersal vectors (u, unassisted; m, mammal; b, bat and/or bird; w, wind and/or water), seed dispersal distance, tree height at maturity and diameter at breast height (DBH) at maturity (Fournier-Origgi 2002; Gerard et al. 1996; Hammond et al. 1996; Horsley et al. 2015; ITTO 2015). Market information for the Iwokrama operations is provided for the four timber tree species, and comprises minimum cutting size (DBH) for logs, and mean annual increments (MAI).

			Reproductive ecology						Market information	
Species	Common name	Species type	Seed Mass[1] (g)	Shade tolerant Y/N	Seed dispersal vectors	Seed dispersal distance (m)	Height at maturity (m)	DBH at maturity (m)	Minimum cutting DBH (m)*	MAI $m^3/ha/yr^{-1*}$
Chlorocardium rodiei	Greenheart	CV	65.5±22.3	Y	u/m	30	20-45	0.3-0.6	0.45	0.129
Eperua falcata	Soft wallaba	CV	9.22	Y	u/m	50	15-30	0.6-1	0.5	0.166
Dicorynia guianensis	Basralocus	CV	1.36	Y	u/m	>50	20-45	0.5-1.5	0.5	unknown
Goupia glabra	Kabukalli	CV	0.001	Y	w/b	>100	20-40	0.6-1.5	0.4	0.037
Cecropia obtusifolia	Cecropia	PI	<0.001	N	w/b	>100	10-40	0.2-0.5	-	-
Cecropia sciadophylla	Cecropia	PI	<0.001	N	w/b	>100	10-40	0.2-0.5	-	-

[1] Fresh seed weight for Chlorocardium rodiei, Eperua falcata, and Dicorynia guianensis. Dry seed weight Goupia glabra, Cecropia obtusifolia, and Cecropia sciadophylla.(de Grandcourt et al. 2004; Rose 2000; ter Steege 1990).

* In Iwokrama Forest, Guyana

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Table 2: Comparison of seedling densities between 1.5 year and 4.5 year postharvest logging treatment and control (unlogged) plots, using Kruskal-Wallis and Mann-Whitney U post-hoc tests, for four commercially valuable (CV) and two pioneer (PI) tree species.

						Post-hoc comparison					
			Seedling density			1.5 years vs. Unlogged		4.5 years vs. Unlogged		1.5 years vs. 4.5 years	
Species name	Common name	Species type	X^2	df	p	U	p	U	p	U	p
Chlorocardium rodiei	Greenheart	CV	2.7	2	0.25	149.0	0.17	181.5	0.62	147.5	0.16
Eperua falcata	Soft wallaba	CV	20.5	2	<0.001	184.5	0.65	45.0	<0.001	73.5	<0.001
Dicorynia guianensis	Basralocus	CV	1.7	2	0.42	166.5	0.36	155.0	0.22	181.5	0.61
Goupia glabra	Kabukalli	CV	10.5	2	<0.01	121.0	<0.05	98.0	<0.01	180.0	0.57
Cecropia obtusifolia	Cecropia	PI	6.2	2	<0.05	170.0	0.08	N/A	N/A	170.0	0.08
Cecropia sciadophylla	Cecropia	PI	4.1	2	0.13	180.0	0.15	N/A	N/A	180.0	0.15

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Table 3: Mean seedling densities per hectare for each species within three height classes (0-50, 50-100 and 100-150 cm) across unlogged and 1.5 year and 4.5 year postharvest logging plots. One decimal place is provided where densities are <1 seedling per hectare.

			Mean density (seedlings/ha^{-1})		
			Plot type		
Height class	Species		Unlogged	1.5 years	4.5 years
0-50	Chlorocardium rodiei	Greenheart	476	198	422
	Eperua falcata	Soft wallaba	17	127	303
	Dicorynia guianensis	Basralocus	228	60	133
	Goupia glabra	Kabukalli	0.5	8	5
	Cecropia obtusifolia	Cecropia	0	0.5	0
	Cecropia sciadophylla	Cecropia	0	0.3	0
50-100	Chlorocardium rodiei	Greenheart	405	372	460
	Eperua falcata	Soft wallaba	14	15	88
	Dicorynia guianensis	Basralocus	7	7	7
	Goupia glabra	Kabukalli	0	1	1
	Cecropia obtusifolia	Cecropia	0	1	0
	Cecropia sciadophylla	Cecropia	0	0	0
100-150	Chlorocardium rodiei	Greenheart	10	22	24
	Eperua falcata	Soft wallaba	3	4	18
	Dicorynia guianensis	Basralocus	1	2	0.3
	Goupia glabra	Kabukalli	0	0.8	1
	Cecropia obtusifolia	Cecropia	0	0.8	0
	Cecropia sciadophylla	Cecropia	0	0.3	0
All height classes combined	Chlorocardium rodiei	Greenheart	891	592	906
	Eperua falcata	Soft wallaba	34	146	409
	Dicorynia guianensis	Basralocus	236	68	140
	Goupia glabra	Kabukalli	0.8	10	7
	Cecropia obtusifolia	Cecropia	0	3	0
	Cecropia sciadophylla	Cecropia	0	0.5	0

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Figure legends

Figure 1. The location of the study area in Iwokrama forest, Guyana, South America. The Reduced-Impact Logging 1.5 and 4.5 year postharvest treatment plots are indicated by dark grey and black squares respectively. Unlogged forest plots are shown as light grey squares. Logging roads and skid trails (dashed lines) are shown within logged forest to indicate the level of logging disturbance. Inset: The location of Iwokrama forest (shaded grey) within Guyana.

Figure 2. Box plots showing median $\log_{10}$ densities of seedlings for four commercially valuable timber and two pioneer tree species, across 20 unlogged, Reduced-Impact Logging (RIL) 1.5 years postharvest and RIL 4.5 years postharvest treatment plots: (a) Chlorocardium rodiei (greenheart); (b) Dicorynia guianensis (basralocus); (c) Eperua falcata (soft wallaba); (d) Goupia glabra (kabukalli); (e) Cecropia obtusifolia; and, (f) Cecropia sciadophylla. Thick horizontal lines indicate median values, the boxes show the interquartile range, and the vertical lines specify either the maximum value or 1.5 times the interquartile range (whichever is smaller), ^{o} indicates a moderate outlier and * an extreme outlier. Associated statistics are given in Table 2.

Figure 3. Box plots showing median $\log_{10}$ densities of seedlings for four commercially valuable timber and two pioneer tree species, across 20 unlogged, Reduced-Impact Logging (RIL) 1.5 years postharvest and RIL 4.5 years postharvest treatment plots, within three height classes (0-50, 50-100 and 100-150 cm): (a) Chlorocardium rodiei (greenheart); (b) Dicorynia guianensis (basralocus); (c) Eperua falcata (soft wallaba); (d) Goupia glabra (kabukalli); (e) Cecropia obtusifolia; and, (f) Cecropia sciadophylla. Dark grey boxes are for 0-50 cm, light grey boxes for 50-100 cm and white boxes for 100-150 cm height classes. Thick horizontal lines indicate median values, the boxes show the interquartile range, and the vertical lines specify either the maximum value or 1.5 times the

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interquartile range of the data (whichever is smaller), ^{o} indicates a moderate outlier and * an extreme outlier. Associated statistics are given in the results text.

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of seedling community structure across the two Reduced-Impact Logging (RIL) treatment and unlogged forest plots: white, unlogged; grey, RIL 1.5 year postharvest; black, RIL 4.5 years postharvest. The first NMDS axis explains 27% of the variation, and the second axis 35%. Stress = 0.15.

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Figure 1

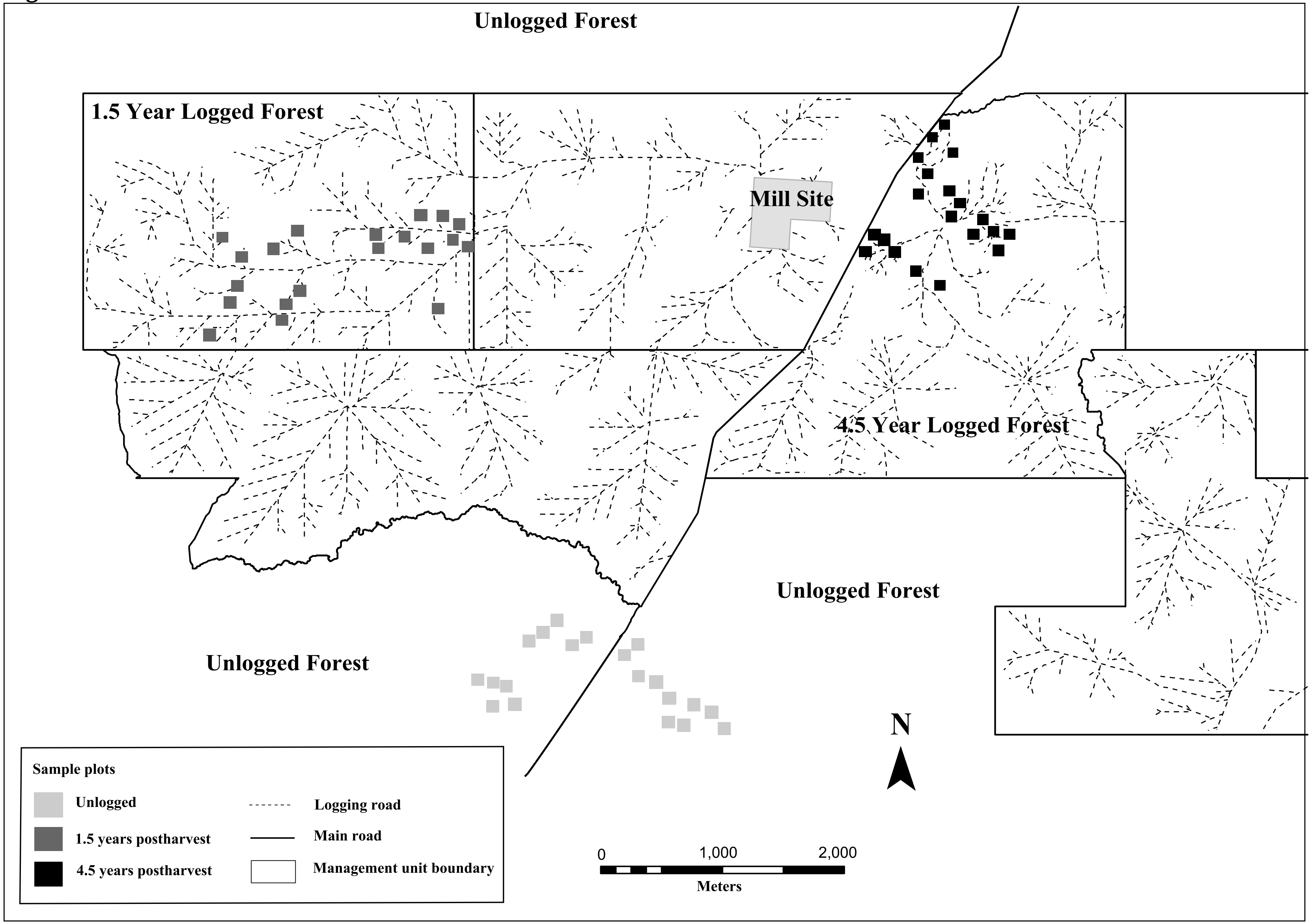

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Figure 2

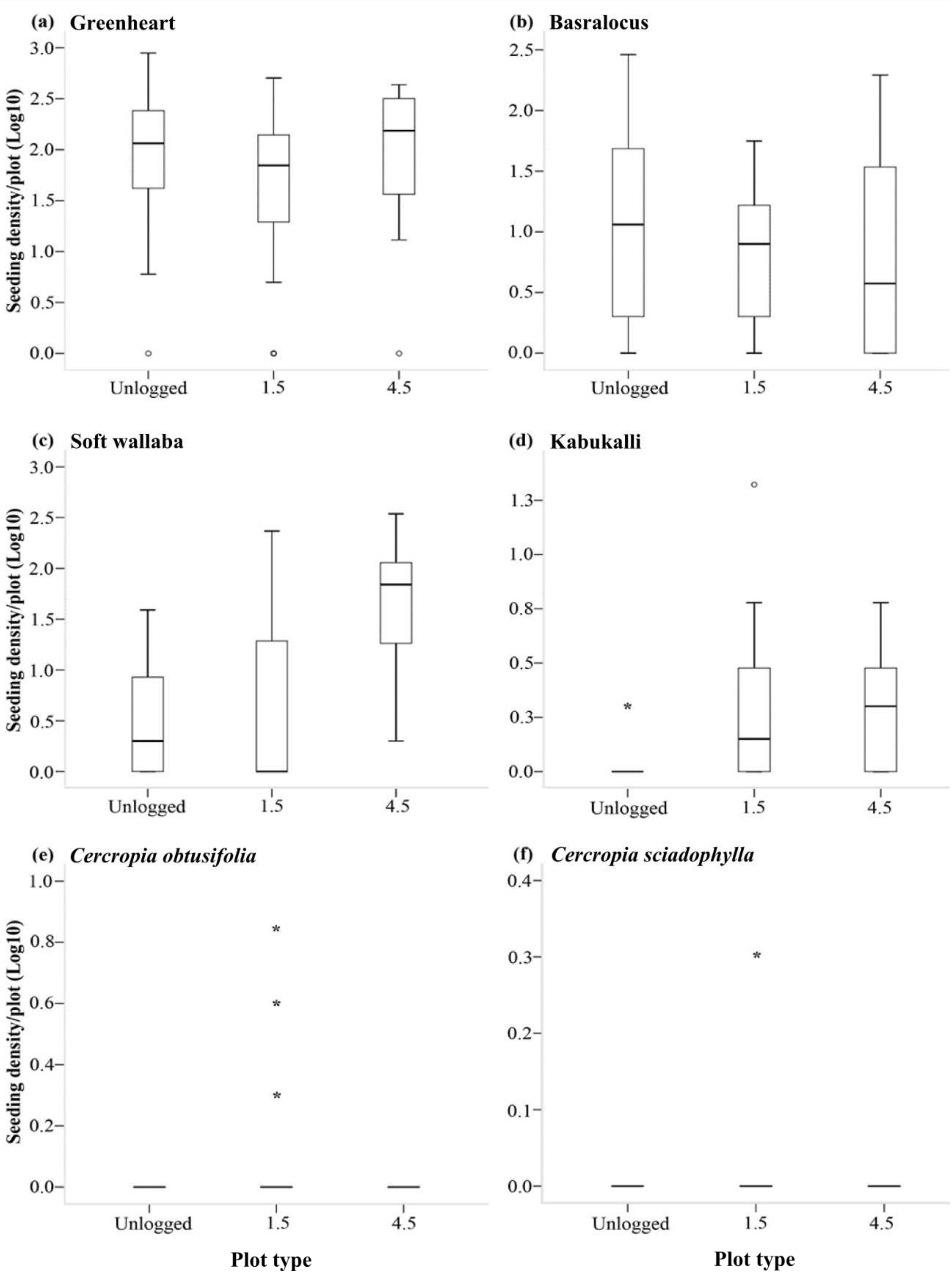

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Figure 3

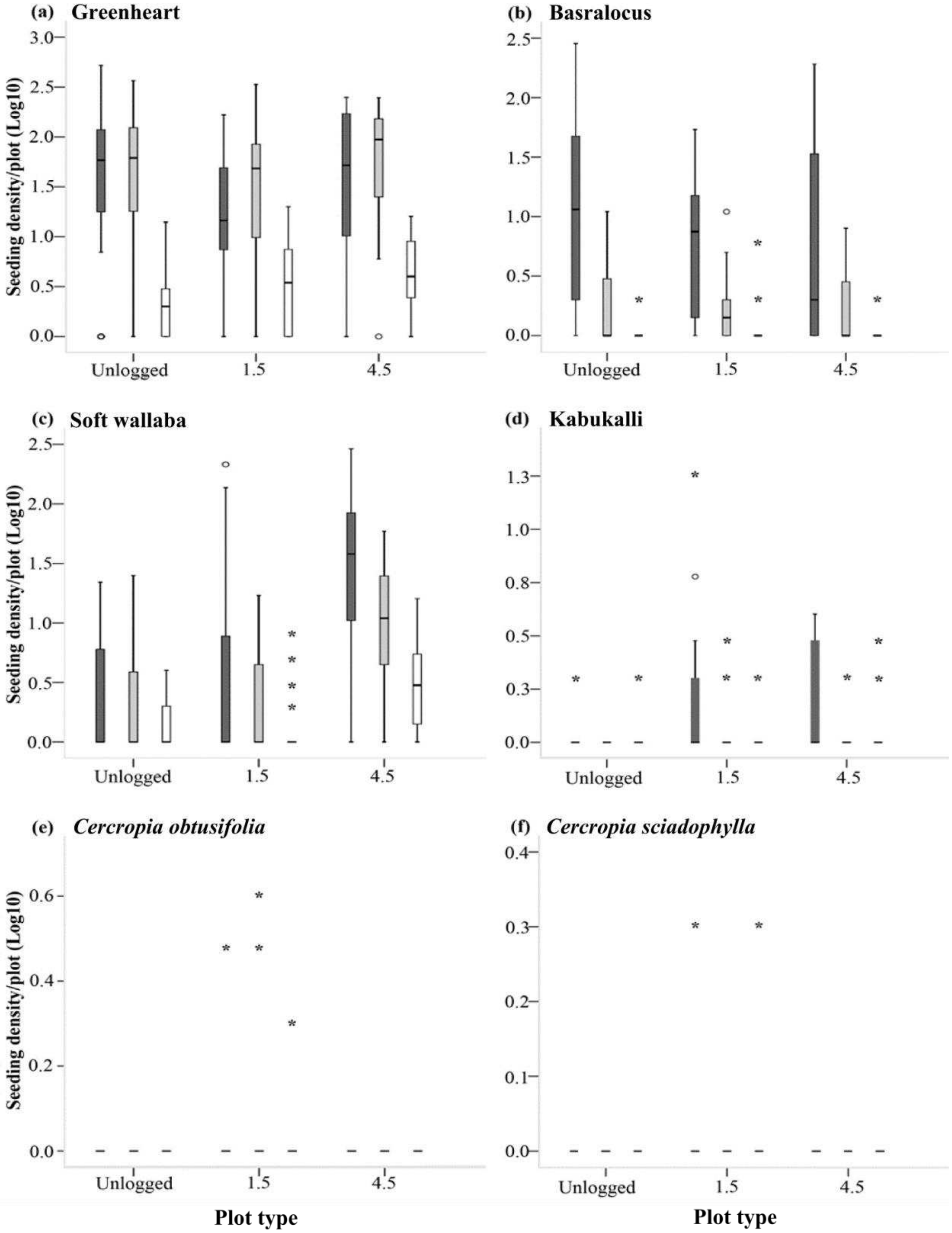

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Figure 4