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5 Regeneration changes in tree species abundance, diversity and structure 6 in logged and unlogged subtropical rainforest over a thirty six year 7 period

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14

15 **Abstract**

16 The long-term effects of logging treatments on rainforest regeneration are difficult to quantify due to
17 compounding interactions between natural dynamics, site characteristics and tree species. The aim of
18 this study was to compare regeneration differences over a 36-year period in stands subjected to various
19 levels of disturbance ranging from natural, through an increasing intensity of individual tree removal to
20 intensive logging. Data for trees ≥ 10 cm diameter at 1.3 m above the ground in subtropical rainforest of
21 north-east New South Wales, Australia were used. Multivariate and univariate analyses showed that
22 regeneration responses were generally correlated with disturbance gradient. In the undisturbed controls
23 there were gradual changes that had no significant effects on tree species richness and diversity, stem
24 density, or diameter distribution. Gradual changes were also observed during the early stages of
25 regeneration following logging. However, in logged sites changes in tree species richness and diversity,
26 stem density and diameter distribution became more rapid with time, and significant changes were
27 observed. This is because changes in logged sites were characterised by periods of distinct floristic
28 assemblages, marked initially by a few species and the most recent assessment revealed species
29 abundance and richness exceeding pre-logging levels. Similar regeneration events across site and
30 disturbance levels resulted in three identifiable stages. In the first stage, lasting about ten years, stem
31 density of abundant shade tolerant trees decreased, with no significant changes in tree species richness.
32 In the second stage, also lasting about ten years, tree species richness and diversity, as well as stem
33 density decreased to minima due to localised species turnover and net mortality. In the third stage,
34 recruitment surpassed mortality and reversed the net loss of both species and stems, as tree species
35 assemblages began to return to pre-disturbance levels. Sites subjected to individual tree selective logging
36 recovered their pre-logging tree species richness and diversity, and stem density within 30 years, but
37 diameter distribution of trees ≥ 40 cm dbh showed low density compared to that observed in the controls.
38 After 35 years, sites subjected to more intensive logging had low species diversity and high densities of
39 both the small sized stems and shade intolerant tree species. More intensively logged sites also had a low
40 density of shade tolerant tree species compared to the controls. This suggests that the restoration of
41 forest structure takes considerably more time than the restoration of tree species richness and abundance
42 following logging in these forests. A high rate of stand basal area growth was observed in moderate tree
43 selection. This indicates high timber production potential at moderate tree selection rates in this type of
44 forest. However, if the stem size distribution of larger trees is to be maintained, a logging cycle with a
45 longer return period than the period covered in this study is necessary.

46 **Key words:** Chronological clustering, functional-group compositions, disturbance levels, tree diameter
47 distribution.

48 1. Introduction

49 Post-disturbance regeneration and temporal variation in rainforest ecosystems are complex, and
50 involve a variety of responses including species successional replacement sequences (Hopkins, 1977;
51 Sheil, 2001). Models for species succession, and the underlying processes that involve changes in
52 biomass, species diversity and homeostasis are well documented (see Odum, 1971; Connell and
53 Slatyer, 1977; Brokaw and Busing, 2000). These species succession models have been used to
54 explain changes in rainforest regeneration in gap phases (Denslow, 1987; Webb, 1998; Schnitzer and
55 Carson, 2001), and the interaction of species life cycles and life history traits that promote survival
56 and persistence of species in time and space (Connell and Slatyer, 1977; Pickett et al., 1987;
57 Summerbell, 1991).

58 Disturbance that creates large canopy gaps in the rainforest disrupt the ecosystem, and initiate a
59 series of distinct species responses (Gomez-Pompa and Vazquez-Yanes, 1981; Olsen, 1989). These
60 responses are described in the intermediate disturbance hypothesis as a succession of rainforest
61 regeneration in which numbers of tree species and stem abundance show a unimodal rise-and-fall
62 over time (Connell, 1978). While the early stages of rainforest regeneration are relatively well
63 understood (Shugart et al., 1980; Denslow, 1995; Magnusson et al., 1999), studies have reached
64 contrasting conclusions on later stages of rainforest regeneration, with some supporting the
65 intermediate disturbance hypothesis (Eggeling, 1947; Sheil, 2001; Sheil and Burslem, 2003), and
66 others not supporting (Hubbell et al., 1999; Molino and Sabatier, 2001). According to Sheil and
67 Burslem (2003), the controversy surrounding the progression of rainforest regeneration lies not only
68 in the refinement of different interpretation and approaches, but also in the different characteristics of
69 study sites. Furthermore, the concept of rainforest stability in later successional stages, including that
70 of intact primary rainforest communities (Whitmore, 1975) is not consistent with the dynamics and
71 behaviour of natural systems (Brokaw and Busing, 2000). In addition, the apparent simplicity of the
72 intermediate disturbance hypothesis is unrepresentative of the involved range of distinct phenomena
73 that can be defined and examined (Brokaw and Busing, 2000; Sheil and Burslem, 2003).

74 For example, the number of species (species richness) and species commonness or rarity (species
75 relative abundance) in space and time are accepted measures and key indicators of both rainforest
76 community composition and dynamics (Bossel and Krieger, 1994; Philips et al., 1994; Burslem and
77 Whitmore, 1999). The overall measures of species richness and relative abundance coupled with total
78 stand basal area (BA) have been used in assessing long term changes and restoration of pre-logging
79 conditions (Shugart et al., 1980; Horne and Gwalter, 1982; Smith and Nichols, 2005). Accurate
80 descriptions of long term chronological changes in rainforest ecosystems following both natural and
81 anthropogenic disturbances can increase our understanding of how these systems respond to various
82 disturbances (Sheil, 2001).

83 This study describes both the short and medium term post-disturbance regeneration patterns in
84 rainforest stands subjected to various levels of disturbance ranging from unlogged controls through
85 increasing levels of individual tree selective logging to intensive logging. Changes in tree species
86 richness, stem density and diameter distribution were investigated using data for trees ≥ 10 cm
87 diameter at 1.3 m above the ground (dbh). In this study, we consider the following specific questions:
88 (1) can post disturbance regeneration in rainforest be identified by periods of distinct tree species
89 assemblages?; (2) are the regeneration patterns consistent across sites?; (3) how does post disturbance
90 regeneration differ between trees species functional-groups defined by level of shade tolerance?; and
91 (4) are these differences related to the disturbance intensity? We tested the null hypothesis that there
92 was no variation between one set of data and another set collected at a later time. If the probability
93 that the null hypothesis is true was larger than a chosen probability level, then the null hypothesis was
94 accepted and the datasets were fused to create a cluster of samples indicating a period of similar
95 floristic assemblage. The rates and direction of change in stem density, diameter distribution, and
96 stand BA were also investigated across logging intensities.

97

98 **2. Methods**99 **2.1. Study area**

100 The study area in the subtropical rainforests of north-east New South Wales, Australia lies between
 101 latitudes 28° 30' and 28° 45' south, and longitudes 152° 45' and 153° 30' east (Fig. 1). The altitude of
 102 the study area ranges from about 210 to 920 metres above sea level. The vegetation is Complex
 103 Notophyll Vine forest, the most floristically diverse and structurally complex form of subtropical
 104 rainforest in Australia (Hopkins, 1977; Webb et al., 1984). This vegetation type is widely distributed
 105 in the region on moist sites with deep, fertile and well-drained red krasnozems soils or ferrosols
 106 (Isbell, 1998). The geology of the area is related to the Mt. Warning and Focal Peak volcanic series,
 107 with basalt as the parent material.

108 Rainfall patterns show a pronounced maximum of about 160 mm per month in late summer (February
 109 and March) and a minimum of about 40 mm per month in late winter (August and September). At
 110 high altitude this seasonality may be masked by persistent low clouds and fog that can add about 50%
 111 of rainfall by way of fog drip (Floyd, 1990). Average annual rainfall ranges from 2500 to 3500 mm
 112 and mean monthly temperature ranges from 3-19° C in winter and 15-31° C in summer. The annual
 113 mean minimum and maximum are 10.3° C and 23.6° C respectively (NSW National Parks &
 114 Wildlife Services, 2004).

115 {Fig. 1}

116 **2.1.1. Study sites**

117 The study sites were determined by the distribution of twenty permanent sample plots (PSPs)
 118 covering a total area of approximately 5.4 hectares in four former State Forests. These PSPs were
 119 established at different times to address changing circumstances in forestry practices in the region. For
 120 example, in the Big Scrub Flora Reserve in the former Whian Whian State Forest (now part of
 121 Nightcap National Park), individual tree selective logging started around the turn of 20th Century
 122 to mid 1950s when the management of the area changed to that of informal flora reserve
 123 (formally declared a Flora Reserve in 1976). According to the Forestry Commission of NSW
 124 (1984), the individual tree selective logging moved in stages tapping fresh supplies. For example,
 125 as the supply of red cedar (*Toona ciliata* M.Roem.) dwindled, species such as rosewood (*Dysoxylum*
 126 *fraserianum* (A.Juss.) Benth.), native teak (*Flindersia australis* R.Br.) and white beech (*Gmelina*
 127 *leichhardtii* F.Muell.) were sought. As these species became harder to find on easier terrain, new
 128 technology permitted utilization of a wide range of rainforest species (Horne and Gwalter, 1982;
 129 Forestry Commission of NSW, 1984). In 1957 following the termination of repeated individual tree
 130 selective logging in the Big Scrub Flora Reserve, three plots each measuring approximately 30 x 25 m
 131 were established. These plots were established to monitor forest regeneration and establishment of
 132 high value timber species following repeated logging disturbances (Forrest, Unpublished report).

133 In 1965 in the former Toonumbar and Edinburgh Castle State Forests (Toonumbar National Park)
 134 three PSPs each measuring 50 x 40 m were established in each forest. These plots were established to
 135 monitor forest regeneration and the establishment of timber species following a single event of
 136 individual tree selective logging.

137 Also in 1965 in the former Wiangaree State Forest (Border Ranges National Park), an experiment
 138 involving eleven PSPs; three controls and eight silvicultural treatments was established (see Horne and
 139 Gwalter, 1982). These treatments had been used to induce regeneration and improve the composition of
 140 structurally similar rainforest stands in various parts of the world (Baur, 1961). Plot size ranged from
 141 1.42 to 3.89 ha with an average of 2 ha. In each, a central experimental subplot measuring 60.4 x 60.4
 142 m was established. Detailed descriptions of the eight treatments including logging intensity has been

143 provided (Pattimore and Kikkawa, 1974; Horne and Gwalter, 1982; Smith and Nichols, 2005). In this
 144 study, treatments were first considered separately, then for further analysis the treatments were reduced
 145 into five levels of disturbance based on the percentage overstorey basal area removed (Table 1).

146 2.2. Data description

147 Trees ≥ 10 cm dbh including those that remained after treatment and those recruited later were
 148 measured on several occasions. For example, in the Big Scrub Flora Reserve measurements were
 149 carried out in 1957, 1958, 1960, 1962, 1964, 1966, 1968, 1972, 1976, 1979/80, 1988, and 2000/01. In
 150 the Toonumbar National Park measurements were carried out in 1966, 1968, 1972, 1976, 1980/81,
 151 1987/88, and 2001. In the Border Ranges National Park measurements were carried out in 1965/66,
 152 1970, 1971/73 (Pre-exploitation Shelterwood from Nigeria), 1975/76, 1980/81, 1987/88, 1995
 153 (controls only), 1999 and 2001. Quality control in 2001 using 5 randomly selected plots revealed
 154 previously wrongly identified trees. For example, there were cases where *Polyosma cunninghamii*
 155 (Benn) had been confused with *Doryphora sassafras* (Endl), *Guilfoylia monostylis* (Benth, F.Muell)
 156 with *Guioa semiglauca* (F.Muell, Radlk) and *Heritiera actinophylla* (Bailey, Kosterm) was not
 157 differentiated from *Heritiera trifoliolata* (F.Muell, Kosterm). This necessitated a complete review of
 158 field identification to reconcile the previously collected data records with those collected during the
 159 2000/01 census. Despite this review and data reconciliation, about 0.4% of stems remained as
 160 unidentified mortality (trees that had never been identified before they died). In addition, 0.6% was
 161 missing data in trees that had been recorded dead, but were found to be alive during the 2001/01
 162 census, and recruited stems that were missed on one or more occasions. Trees in the unidentified
 163 mortality were represented by a species category referred to as 'unknowns', so that the effects of
 164 change caused by stem recruitment or death could be accounted for during data analyses.

165 2.3. Tree species groups

166 To study rainforest dynamics, woody species are usually categorised into functional-groups, based on
 167 life history, light requirement for germination, establishment and growth, and trade-offs between the rate
 168 of growth and persistence in the canopy (Swaine and Whitmore, 1988; Kohler and Huth, 1998; Baker et
 169 al., 2003). Several classifications are bimodal (see Connell, 1978; Brokaw, 1985; Swaine and Whitmore,
 170 1988), while others are more complex with numerous categories (Summerbell, 1991; Condit et al.,
 171 1996). In this study, bimodal classification was adequate and tree species were categorised into two main
 172 groups; shade intolerant and shade tolerant. Shade intolerant species included pioneers with relatively
 173 fast growth rates and short life-spans such as *Acacia melanoxylon* R.Br and *Duboisia myoporoides* R.Br,
 174 and early successional species that arrive early, but are persistent and live considerably longer than the
 175 pioneers such as *Flindersia schottiana* F.Muell and *Toona ciliata* M.Roem. Members of the shade
 176 intolerant group regenerate in disturbed and relatively open sites, and form a minor plant component in
 177 mature subtropical rainforests of Australia (Kariuki and Kooyman, 2005). Shade tolerant species
 178 included later successional species such as *Dysoxylum mollissimum* Blume S.lat. syn. *D. muelleri* Benth
 179 and *Neolitsea dealbata* (R.Br) Merr, and mature phase species such as *Caldcluvia paniculosa* (F.Muell)
 180 Hoogland, *Heritiera trifoliolata* (F. Muell.) Kosterm and *Geissois benthamii* F.Muell. The shade tolerant
 181 group regenerates in shade, and forms the major plant component in mature subtropical rainforests of
 182 Australia.

183 2.4. Data analysis

184 Stochastic and small-scale effects that may lead to variations within similarly treated rainforest stands
 185 were not addressed in this study (see Queensland Department of Forestry, 1983; Franklin et al., 1997;
 186 Hickey and Wilkinson, 1999). This is because analysis of similarity using the number of species and
 187 stem abundance recorded during the 2001 census for tree ≥ 10 cm dbh did not show any significant
 188 difference between similarly treated plots (Kariuki, 2004). Furthermore, preliminary testing of the
 189 null hypothesis at the probability level of $\alpha = 0.01, 0.05$ and 0.1 produced similar clusters in similarly
 190 treated plots in each site. Thus, data series from similarly treated plots in a given site; the controls

191 (Border Ranges National Park; site 1), individual tree selective logging in former Toonumbar (site 2)
192 and Edinburgh Castle (site 3), and repeated individual tree selective logging in Big Scrub Flora
193 Reserve (site 4) were combined to effectively create one larger sampling station.

194 We sought to identify when ecological changes at a given plot or sampling station occurred. Thus,
195 matrices of species abundance and the sequence of assessments were analysed using the chronological
196 clustering method in the R-Package (Casgrain and Legendre, 2001b). The appropriate association
197 matrices ($n \times n$) required by this method were computed using Steinhaus coefficients (S17 in Casgrain
198 and Legendre, 2001a). The Steinhaus coefficients use species abundance data, and reflect similarities
199 in numbers of each species without standardisation (Tuomisto and Ruokolainen, 1993). The
200 chronological clustering method is a time constrained form of agglomerative clustering in which only
201 neighbouring samples can cluster (Legendre and Legendre, 1998). At each step of the intermediate-
202 link linkage agglomerative process, a Mantel test is performed to decide whether fusion of the
203 samples is warranted at a user defined level of significance (see Legendre et al., 1985). The rejection
204 of the null hypothesis was progressively relaxed at four levels of significance ($\alpha = 0.01, 0.05, 0.1,$
205 0.2). As the level of significance was relaxed finer details were revealed in identifying samples that
206 were significantly different in the data series.

207 Cluster-expansion tests were performed to determine whether a cluster could incorporate samples
208 from adjacent cluster(s) when the structures of the chronological neighbouring clusters were ignored.
209 This ascertained whether the observed pattern of regeneration represents a relatively similar subseries
210 of regeneration events within a continuum, or different and independent regeneration phenomena
211 succeeding one another. *A posteriori* tests were also carried out between non-neighbouring clusters
212 including singletons (aberrant samples significantly different from neighbouring cluster) to determine
213 their relationship.

214 Association matrices ($n \times n$) with Chord distance coefficients (D03 in Casgrain and Legendre, 2001a)
215 were also computed from the species abundance matrices and sequential assessments. The Chord
216 distance coefficients use species abundance data, and reflect differences in relative proportion of tree
217 species after standardisation by object-vector (Tuomisto and Ruokolainen, 1993). The chronological
218 clustering results from principal coordinate analysis in the R-Package were drawn in the space of the
219 first two principal coordinates to help interpret relationships among clusters, and to evaluate
220 identifiable ecological changes in the regeneration.

221 Changes in tree species diversity in the data series were investigated using the Brillouin diversity
222 index (H_b). The Brillouin statistics were calculated using matrices of species abundance and the
223 sequence of assessments in the PRIMER package (Clarke and Warwick, 1994). These statistics were
224 adequate in this study because they consider density per species as well as the overall density where
225 the randomness of the samples cannot be guaranteed (see Williams et al., 1969). The overall mean
226 diversity statistic for the controls was compared with those obtained in logged sites.

227 Changes in stem density, tree species richness and stand BA for the two main tree species groups
228 were also examined for trends across disturbance levels. Disturbance levels ranged from the controls
229 (0% overstorey stand BA removal) through individual tree selective logging (1-35%), moderate tree
230 selection (36-50%) and repeated individual tree selective logging (estimate 51-65%) to intensive
231 logging (66-80%).

232 To investigate the effect of logging intensity on diameter distribution we examined the number of
233 stems in various dbh classes across treatments. Trees in each assessment were grouped into four
234 diameter classes; (10-19.9), (20-39.9), (40-59.9), and (≥ 60 cm). This ensured a small number of
235 classes with an adequate representation of stems in each. To enhance this approach the rate of change
236 in the number of stems in various diameter classes was investigated by fitting a two-level
237 hierarchical multilevel model in the MLwiN package (Rasbash et al., 1999; Snijders and
238 Bosker, 1999). The rate of change in stem distribution in the hierarchical multilevel model

239 was analysed assuming that one mean function is valid for the subtropical rainforest population, and
 240 that, mean functions for single plots vary randomly around the population mean. Accordingly, the
 241 functions for rate of change in the number of stems within a given dbh class and plot and stand are
 242 assumed to vary randomly around the mean function for the corresponding dbh-class and stand. The
 243 natural logarithm of sampled stems rather than the actual counts were used as the dependent
 244 variable. Explanatory variables including tree size (dbh classes), logging intensity (disturbance
 245 levels), time since disturbance, and the interaction of these variables were tested for
 246 significance using both the log likelihood and Wald's tests statistics (Rasbash et al., 1999).

247 3. Results

248 A total of 117 species in 45 families were represented in the data series. Families that had the highest
 249 number of species included Sapindaceae (19 species), Lauraceae (17), Rutaceae (17), and Myrtaceae
 250 (15). Ten species with the highest overall occurrence included shade tolerant species such as
 251 *Caldcluvia paniculosa* (2345 occurrences), *Heritiera actinophylla* and *H. trifoliolata* (2815),
 252 *Doryphora sassafras* Endl. (1403), *Geissois benthamii* (1161), *Cinnamomum oliverii* F. M. Bailey
 253 (923), *Baloghia inophylla* (G. Forst) P. S. Green (909), *Diospyros pentamera* (Woolls & F. Muell) F.
 254 Muell (906), *Sloanea woollsii* F. Muell (904), and *Pouteria australis* (syn. *Planchonella australis*) (R.
 255 Br) (637). Two pioneer species in the shade intolerant group; *Duboisia myoporoides* (365) and
 256 *Polyscias elegans* (337) were the 15th and 16th most frequently encountered species.

257 3.1. Chronological clustering and clusters arising from the analysis

258 We present the testing of the null hypothesis at the probability level of $\alpha = 0.2$ (the alpha level that
 259 illustrates most breakpoints), which identifies significantly different samples in the data series (Fig.
 260 2). In each series, the cluster-expansion tests revealed that the last cluster was not distinct from the
 261 others. This indicates that sample(s) in the last cluster were less similar to one another due to species
 262 turnover and recruitment of both, locally new and previously lost species.

263 {Fig. 2}

264 The *a posteriori* test results indicate that the chronological clusters depicted in Fig. 2 remain distinct
 265 at the probability level of $\alpha = 0.2$, except in the case of the post-exploitation shelterwood (Fig. 2j).
 266 However, if a smaller probability level (< 0.2) was used for rejection of sample fusion, then
 267 non-neighbouring clusters were not distinct. In post-exploitation shelterwood, the initial assessment
 268 carried out before logging, appeared as a singleton (aberrant sample that is significantly different from
 269 its neighbouring cluster). However, the singleton is not significantly different compared to the last
 270 cluster ($P = 0.25$), but could not fuse because the samples were not adjacent. This indicates that the
 271 last chronological cluster in this data series comprised of tree assemblages with species abundance
 272 and richness comparable to pre-logging levels.

273 In the unlogged controls, three clusters were produced (*i*, *ii* and *iii*; Fig. 2a). The cluster expansion
 274 results show that the first cluster (*i*) is not distinct and can be expanded to include samples in the
 275 second cluster (*ii*) when tested one at a time. Cluster (*ii*) is also not distinct and can be expanded to
 276 include samples in cluster (*i*) as well as samples 6 and 7 in cluster (*iii*) when tested one at a time. This
 277 indicates that the changes between neighbouring clusters in this series were gradual and that clusters
 278 consisted of tree assemblages with relatively similar species abundance and richness.

279 Individual tree selective logging produced two clusters across sites (*i* and *ii*). In all cases, the cluster
 280 expansion tests show sharp separation of the first cluster (*i*) from its neighbour. This indicates a
 281 distinct tree assemblage in cluster (*i*), due to decrease in both the species abundance, and in richness
 282 following logging. Thus, cluster (*i*) cannot be expanded to include samples in cluster (*ii*) when tested
 283 one at a time, except in the case of site 3 (Fig. 1d) where cluster (*i*) can only be expanded to include
 284 the first sample in cluster (*ii*). These results indicate similar and significant regeneration events across

285 sites associated with individual tree selective logging treatment. However, the regeneration events
 286 became evident between 5 and 20 years since logging, indicating that these events could be site
 287 specific.

288 The clustering structure for the more intensively logged sites showed distinct differences between
 289 clusters. This indicates significant regeneration events in these sites. The cluster-expansion test results
 290 indicate distinct floristic assemblages between neighbouring clusters (*i* and *ii*, *ii* and *iii*, and so on).
 291 Excluding the last cluster, no other cluster can be expanded to include samples from neighbouring
 292 cluster(s), except in the case of the first cluster in the clear cutting treatment from Sabah Malaysia
 293 (Fig. 2h), and repeated individual tree selective logging (Fig. 2e) that can only be expanded to include
 294 the first sample in the neighbouring cluster.

295 Like the post-exploitation shelterwood (Fig. 2 j), the initial assessment in heavy individual tree
 296 selective logging is a singleton (Fig. 2 g). The singletons reflect a similar ecological event resulting
 297 from decrease in both the tree density and species richness caused by a high mortality following heavy
 298 individual tree selective logging, and the removal of merchantable trees in the post-exploitation
 299 shelterwood.

300 Silvicultural improvement from the Democratic Republic of Congo (Fig. 2 k) showed the most recent
 301 assessment (2001) as a singleton and an important ecological change between the 1975 and 1976
 302 assessments. The singleton indicates missing data, whereby some trees apparently missed in earlier
 303 censuses were included as new recruits in the 2001 census. The ecological change (confirmed by
 304 cluster-expansion tests) indicates a sharp difference in stem density, and both species abundance and
 305 richness before, and after the removal of merchantable stems from the stand.

306 Fig. 2 also shows changes (many gaps) in the majority of the data series corresponding to the period
 307 between 1980 and 1988. These changes show when the species abundance and diversity as well as the
 308 number of stems decrease to minima, indicating the end of net mortality, and the beginning of net
 309 recruitment in trees \geq cm dbh.

310 3.2. *Regeneration stages*

311 The relationships between species abundance and floristic composition are illustrated in the biplot
 312 drawn on equal scale in the reduced space of the first two axes of principal coordinate analysis (Fig.
 313 3). The variance accounted for by the two axes (88.3 to 96.7%) is indicative of the similarity of
 314 objects in Fig. 3 compared to objects in the multi-dimensional space. The chronological regeneration
 315 responses traces a U-shaped redevelopment trend (Fig. 3). Clusters of similar floristic assemblages at
 316 the $\alpha = 0.2$ level of significance are delineated for ease of interpretation in this and subsequent
 317 sections. {Fig. 3}

318 The general pattern of regeneration illustrated in Fig. 3 shows three identifiable stages. The initial
 319 stage of regeneration represents gradual changes between successive assessments (closely grouped
 320 samples) with a few exceptions. The exceptions were where induced mortality (poisoning) of stems
 321 with no timber values (Fig. 3 i), and removal of merchantable stems (Fig. 3 i, j, k) occurred after the
 322 initial assessment. The gradual changes between successive assessments are associated with a
 323 decreased stem density, mainly in the abundant shade tolerant species. This caused changes in stem
 324 size distribution (Fig. 4), but no discernable change in species richness. {Fig. 4}

325 The second regeneration stage indicates a net loss of species, and a decrease in stem density,
 326 culminating in the sites attainment of the lowest values in both characteristics (Fig.3, 4). These results
 327 indicate that the vertical axis is significantly associated with changes in species abundance.

328 The reversal in the direction of the biplots marks the beginning of a third stage, which is associated
 329 with increased species turnover and a net recruitment of both locally new and previously lost species.

330 This indicates that the first (horizontal) axis in Fig. 3 is significantly related to tree species
 331 composition. Thus, the 2001 positions indicate different tree composition between the initial and the
 332 2001 assessments (different positions in relation to the first axis), as well as a lack of significant
 333 differences in their species abundances (relatively similar positions in relation to the second axis).

334 3.3. *Changes in species diversity*

335 The controls did not show any significant change in the Brillouin diversity statistic, which ranged
 336 between 3.03 and 3.13 with an overall mean of 3.07. In contrast, the overall average Brillouin
 337 statistics for the logged sites decreased relative to logging intensity from individual tree selective
 338 logging (2.76), moderate tree selection (2.56) and repeated individual tree selective logging (2.52) to
 339 intensive logging (2.48). The percentage range between the minimum and maximum number of
 340 species (2001) shows a similar trend. In general, the trends of the Brillouin diversity statistics parallel
 341 the three regeneration stages defined above.

342 3.4. *Stem density and stand basal area*

343 Changes in stem density for trees ≥ 10 cm dbh and stand BA contribution for both shade tolerant and
 344 intolerant groups are presented in Figure 5. Chi-squared tests on the count of recruited stems indicated
 345 that logged sites recruited a higher proportion of both shade tolerant and intolerant species in
 346 comparison with the unlogged controls ($P < 0.003$). The densities of both shade tolerant and intolerant
 347 species in individual tree selective logging recovered to levels comparable to those of the unlogged
 348 controls within 30 years after logging (Fig. 5). Although the density of shade tolerant species in
 349 repeated individual tree selective logging had recovered to similar levels, the density of shade
 350 intolerant species was high, and comparable to that observed in the intensively logged sites. Both
 351 moderate tree selection and intensive logging showed high densities of shade intolerant species, while
 352 the densities of the shade tolerant species were lower in comparison with the unlogged controls.

353 {Fig. 5}.

354 There was a net increase in the overall stand BA in both logged and unlogged sites. The average
 355 contribution of shade intolerant species to the pool of the stand BA for both the unlogged controls and
 356 individual tree selective logging was negligible ($<2.0\%$), but increased through moderate tree
 357 selection and repeated individual tree selective logging (6.0%) to intensive logging (9.5%). However,
 358 the annual rate of stand BA growth for both the shade tolerant and intolerant species showed a switch
 359 between moderate tree selection and intensive logging. Thus, average annual rate of stand BA growth
 360 increased from the unlogged controls (0.31% and nil) through individual tree selective logging (0.39
 361 and negligible), intensive logging (0.64 and 0.30%) and repeated individual tree selective logging
 362 (0.68 and 0.35%) to moderate tree selection (0.88 and 0.39%). These indicate poor recruitment and
 363 growth of shade intolerant species in less disturbed sites (controls and sites subject to individual tree
 364 selective logging), while significant recruitment and growth occurred in both species groups in sites
 365 subjected to more intensive logging.

366 3.5. *Diameter distribution*

367 The trends associated with diameter distribution in the various dbh-classes are shown in Fig. 6. A
 368 small intra-plot correlation value of 0.26 (the proportion of the total variance explained by the within
 369 plot variance) indicates that the diameter distribution remained relatively similar within a sampling
 370 station (plot or amalgamated similarly treated plots in site), but varied considerably between stations.

371 {Fig. 6}

372 The parameter estimates shows that the rate of change in diameter distribution is influenced by tree
 373 size, level of disturbance, time since the last major disturbance and the interaction between these
 374 factors (Table 2). There were no significant changes in diameter distributions in the unlogged controls
 375 (Fig. 6). However, the overall linear rate of change in tree diameter distribution across levels of

376 disturbance was significantly different from zero. For example, the number of stems in both the
 377 smallest (10-19.9 cm) and largest (over 60 cm) dbh-classes decreased initially, reaching minima
 378 between 10 and 20 years, and then increased. A positive quadratic effect with time indicates the
 379 overall tendency for the number of stems to increase with time across dbh-classes (Fig. 6). In general,
 380 the trends depicted by tree diameter distribution correspond to the defined regeneration stages.

381 *{Tables 1}*

382 **4. Discussion**

383 This study has demonstrated that post disturbance regeneration responses in subtropical rainforest of
 384 north-east New South Wales, Australia, are correlated with disturbance intensity. The exception was
 385 in the case of average annual rate of stand BA growth for both the shade tolerant and intolerant
 386 species, which varies depending on the post-logging stage and successional events. Although
 387 intensive logging shows high annual growth rates at the tree level (Kariuki et al., 2006), low density
 388 of retained large trees, small sized recruited shade tolerant stems and high turnover of recruited shade
 389 intolerant trees lowered the overall stand BA contribution in the intensively logged sites. High post
 390 logging mortality in the moderately logged sites, especially in heavy tree selection was a transient
 391 event, and mortality rapidly returned to lower levels. This is consistent with studies by Nebel et al.
 392 (2001) and Smith and Nichols (2005). Thus, despite the initial mortality, moderately logged sites
 393 retained a high density of large sized shade tolerant stems. Moderate growth rate in the retained large
 394 shade tolerant stems and low turnover in recruited trees resulted in high overall stand BA contribution
 395 in both shade tolerant and intolerant species.

396 *4.1. Regeneration patterns in logged and unlogged sites*

397 The unlogged controls showed limited and gradual changes where the overall rate of change in
 398 species abundance and diversity as well as in stem size distribution was not significantly different
 399 from zero. However, in the intervening 36 years, there was an overall 8.7% (approximately 0.24% per
 400 year) increase in stem density. In addition, the overall stand BA contribution to the BA pool for the
 401 shade tolerant species group increased by 10% (0.28% per year). This can be attributed to enhanced
 402 recruitment and growth following natural mortality (Fig. 4, 5). It has also been suggested that such
 403 changes could result from climatic change over the last 3 decades of the 20th Century, especially
 404 changes in solar radiation and increases in both air temperature and atmospheric concentration of
 405 carbon dioxide (Lewis et al., 2004). Furthermore, natural unlogged rainforest rather than being a static
 406 community is in a process of continuous (albeit sometimes gradual) change (Gomez-Pompa and
 407 Vazquez-Yanes 1981). This change includes the slow replacement of the dominant tree species, while
 408 maintaining a relatively similar floristic assemblage (Richards, 1952; Schulz, 1960).

409 As would be expected, increased logging intensity was negatively associated with stem densities, and
 410 species abundance and richness. This was due to targeted removal of large commercial and non
 411 commercial (silvicultural treatments) tree species, and an increased mortality soon after logging.
 412 These results are consistent with studies in tropical rainforests (Walters et al., 1982; de Graff, 1986)
 413 as well as in other vegetation (Korning and Baslev, 1994). Initial changes in the logged sites for the
 414 first five to ten years after logging were gradual, as small changes between successive samples were
 415 observed. This was attributed to post-logging mortality leading to decreased stem density of the most
 416 abundant species, but without any significant change in species richness. The gradual phase was
 417 followed by rapid changes marked with periods of distinct floristic assemblages, and a rate of stem
 418 size distribution significantly different from zero. This can be attributed to both local species loss, and
 419 gains of previously lost and locally new species. Oliver and Larson (1996) argue that following
 420 disturbance in rainforests, the regeneration pattern further affects the arrangement of stand structure,
 421 reflecting the impact of the initial disturbance.

422 Species abundance and richness returned to levels similar to those observed in the unlogged controls
 423 (pre-logging state) within 30 years of logging, supporting the findings of King and Chapman (1983),

424 and Smith and Nichols (2005). However, apart from the sites subjected to individual tree selective
 425 logging, which had recovered their pre-logging species diversity, moderate to intensively logged sites
 426 had not recovered to similar levels 36 years after logging (Fig. 5). This is contrary to the findings by
 427 Smith and Nichols (2005). Although stem density in the individual tree selective logging have
 428 returned to their pre-logging levels, when trees were grouped into dbh-classes, the majority of these
 429 stems were in the smaller sized category, and density of the larger stems ≥ 40 cm dbh were yet to
 430 recover to pre-logging levels (Fig. 4).

431 This study shows that while the overall species abundance and richness, and stem density measures
 432 redeveloped rapidly, species diversity and stand structure developed more slowly during regeneration,
 433 especially in the more intensively logged stands. Similar findings were reported in a successional
 434 study of a rain forest in Mexico (Gomez-Pompa and Vazquez-Yanes, 1981). Thus, the restoration of
 435 species abundance and richness to levels similar to that of intact primary forest takes considerably less
 436 time than structural and diversity restoration (King and Chapman, 1983; Olsen, 1989; Hubbell and
 437 Foster, 1990). This can be further complicated by continuous or repeated disturbances (see Hitimana
 438 et al., 2004), as observed in repeated individual tree selective logging.

439 4.2 *Regeneration stages*

440 The regeneration patterns detected in this study indicate three stages across both sites and levels of
 441 disturbance. The first stage depicted small changes between successive assessments that lasted for
 442 about 10 years (Fig. 3). This was attributed to mortality in species with high frequency, especially the
 443 shade tolerant species due to natural causes, in the controls and logging injuries in logged sites (Fig.
 444 5a). This mortality decreased stem density with no significant change in species richness, but an
 445 observable impact on diameter distributions (Fig. 4). Thus, although logging injuries and hence post
 446 logging mortality are common in the frequently encountered tree species (de Graff, 1986; Oavika,
 447 2002; Silva et al., 2002), a decrease in the number of stems in these species without substantial
 448 change in species abundance reflected very little or gradual change in the floristic assemblage.

449 The second stage also lasted about 10 years. This stage was associated with rapid changes and decline
 450 in both stem density and species richness due to continued net mortality and species turnover. Thus,
 451 during this stage, the sites registered the lowest values in both the stems ≥ 10 cm dbh and species
 452 richness (Fig. 3, 4). Compared to the 2001 floristic compositions, the lowest values in species richness
 453 were positively correlated with levels of disturbance. For example, the floristic assemblage in the
 454 unlogged controls registered 12% less species, individual tree selective logging 16 - 28%, moderate
 455 and repeated single-tree selection 28% and the intensively logged sites 39 - 46%.

456 Rapid changes were also evident in the third stage of regeneration, which was characterised by
 457 increased species turnover and a net increase in recruitment of trees ≥ 10 cm dbh. Recruitment
 458 surpassed mortality, and reversed the decreasing trends. An increase in species abundance and
 459 richness, as well as stem density in both shade tolerant and intolerant species occurred, particularly in
 460 the smallest dbh class (10-19 cm). Successive assessments at this stage included sample(s) that were
 461 less similar to one another due to species turnover, recruitment of both locally new and previously lost
 462 species, and recovery from past disturbances. The cluster-expansion results showed that the
 463 regeneration patterns represent a sub-series of regeneration events within a continuum (Fig. 2).

464 Although natural dynamics in the unlogged controls did not show any significant changes in species
 465 diversity, and stem size distribution remained unchanged, the death of a few large stems created
 466 canopy gaps. These canopy gaps albeit few, initiated regeneration activities similar to those observed
 467 in the logged sites. This could explain the similar regeneration patterns observed in some unlogged
 468 rainforest stands (Molino and Sabatier, 2001; Sheil, 2001).

469 4.3. *Regeneration patterns of tree species functional-groups*

470 The regeneration patterns and trends showed the combined effects of functional group compositions
471 along the disturbance gradient. For example, low disturbance in both unlogged controls and sites
472 subjected to individual tree selective logging created small canopy gaps. The small gaps were quickly
473 reoccupied by the retained stems and advance regeneration with no significant recruitment of shade
474 intolerant species. Similar results and conclusions were reported for a study in a semideciduous
475 tropical forest in Mexico (Dickinson et al., 2000). In our study, stem densities of the shade intolerant
476 species returned to levels comparable to that of the unlogged controls within fifteen years of
477 individual tree selective logging. However, stem densities of the shade tolerant species required about
478 twice as much time to return to similar levels (Fig. 5).

479 Although the density of shade tolerant species in repeated individual tree selective logging has also
480 returned to pre-logging levels, the density of shade intolerant species was high and comparable to that
481 observed in the intensively logged sites. This is not surprising given that repeated individual tree
482 selective logging only targeted large commercial trees for removal without culling the non
483 commercial species including shade intolerant species. Therefore, although individual tree selective
484 logging may mimic natural disturbance, if it is repeated without silvicultural stand improvement or
485 ecological restoration, the proportion of shade intolerant species is likely to increase in comparison
486 with unlogged stands (see also Kariuki and Kooyman, 2005).

487 Moderate tree selection and intensive logging removed more trees than individual tree selective
488 logging. This created large canopy gaps and significantly decreased both stem density and species
489 richness. The large canopy gaps also facilitated significant germination, establishment, and
490 recruitment of both shade tolerant and intolerant species. However, high densities of shade intolerant
491 species and low densities of shade tolerant species in comparison with the unlogged controls
492 accompanied moderate tree selection and intensive logging (Fig.5). This indicates that the large
493 canopy gaps created by moderate and intensive logging facilitated the recruitment of more shade
494 intolerant species at the expense of shade tolerant species. These results support the findings of
495 Hawthorne (1993) on forest regeneration in the Bia South Game Production Reserve Ghana and
496 Dickinson et al. (2000) in semi-deciduous tropical forest in Mexico.

497 The overall average contribution of shade intolerant species to the stand BA pool increased with
498 disturbance intensity, with the converse occurring for shade tolerant species (Fig. 5). The results of
499 this study indicate slow growth, and fewer stems of the shade intolerant species group in less
500 disturbed sites, while both species groups registered increased recruitment of stems and high growth
501 rates in sites subjected to moderate and intensive logging.

502 It appears that logging disturbance produced characteristic changes in the biotic and abiotic
503 environments that not only influence the floristic composition at the onset of regeneration, but also
504 affected later stages (Gomez-Pompa and Vazquez-Yanes, 1981; Webb, 1998; Magnusson et al.,
505 1999). For example, a return to the pre-logging state in logged sites with a high proportion of shade
506 intolerant species is expected to take a relatively long time due to continuing species turnover and
507 secondary treefall disturbances that characterize the dynamics of stands dominated by this species
508 group (see Smith and Nichols, 2005). This process will increase the overall level of mortality for a
509 longer period (Silva et al., 2002). As this trend continues, the proportion of short-lived shade
510 intolerant species ≥ 10 cm dbh in logged sites may decrease, as the individuals in this species group
511 are replaced by long-lived shade tolerant tree species (Kariuki and Kooyman, 2005). As a result, the
512 rate of change in species diversity and stand structure will slow as the logged sites gradually approach
513 their pre-logging states.

514 **5. Conclusions**

515 This study demonstrates that in subtropical rainforests post disturbance regeneration responses are
516 correlated with disturbance gradient. Rainforest tree species-specific levels of shade tolerance during
517 establishment, recruitment and development as well as life history, and trade-offs between rate of growth

518 and persistence in the canopy can be used to explain the observed patterns of regeneration. This is
 519 because tree species group (shade tolerant and intolerant) responses relate to the interaction between the
 520 regeneration niche and the successional status of the trees. Individual tree selective logging removed
 521 only a few large trees and the retained trees together with advance regeneration reoccupied the created
 522 gaps that healed quickly without a significant regeneration of shade intolerant species. Thus, sites
 523 subjected to this type of treatment appear to have returned to their pre-logging states in all aspects,
 524 except stem size distribution. Because of their slow growth, the density of trees ≥ 40 cm dbh was low in
 525 comparison with the controls. More intensive logging created large canopy gaps that facilitated
 526 regeneration and recruitment of both shade intolerant and tolerant species. Thus, the overall species
 527 abundance and richness, as well as stem density in the smaller sized trees were generally higher
 528 compared to pre-logging levels. However, the sites had low species diversity and low stem density of
 529 shade tolerant species. Conversely, the number of shade intolerant species was high compared to that
 530 observed in the controls. This suggests that the restoration of forest structure takes considerably more
 531 time than the restoration of tree species abundance and richness following logging in these forests.

532 Post disturbance regeneration events across both sites and levels of disturbance were similar resulting
 533 in three identifiable stages; (1) initial period of slight change where the density of the abundant shade
 534 tolerant species decline without significant change in species richness, (2) a period where both species
 535 and stem density decrease to minima, and (3) a period where the species richness and stem density
 536 increased surpassing previous levels.

537 This study also showed that moderate tree selection may facilitate high stand level BA growth rate
 538 compared to single-tree selection or intensive logging. This indicates high timber production potential at
 539 moderate tree selection in this type of forest. The long time taken for stem size distribution to return to
 540 pre-logging levels suggests a need to consider logging cycles with a long return period in these forests.

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 548

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720 **Figure captions**

721 Fig. 1. Rainforests of north-east New South Wales and the study sites

722 Fig. 2. Chronological clustering showing time series response of changes over 3 decades in permanent
 723 sample plots subjected to disturbance levels ranging from natural to intensive logging in
 724 subtropical rainforests of north-east New South Wales, Australia. Steinhaus coefficients using
 725 association matrices derived from species abundance of repeated sampling are shown.
 726 Clusters of consecutive assessments are shown by a thick line segment, cluster expansion
 727 tests for $\alpha = .2$ a thin line segment, singleton (aberrant sample) by a (*), and logging at the
 728 plot by a downwards pointing arrow.

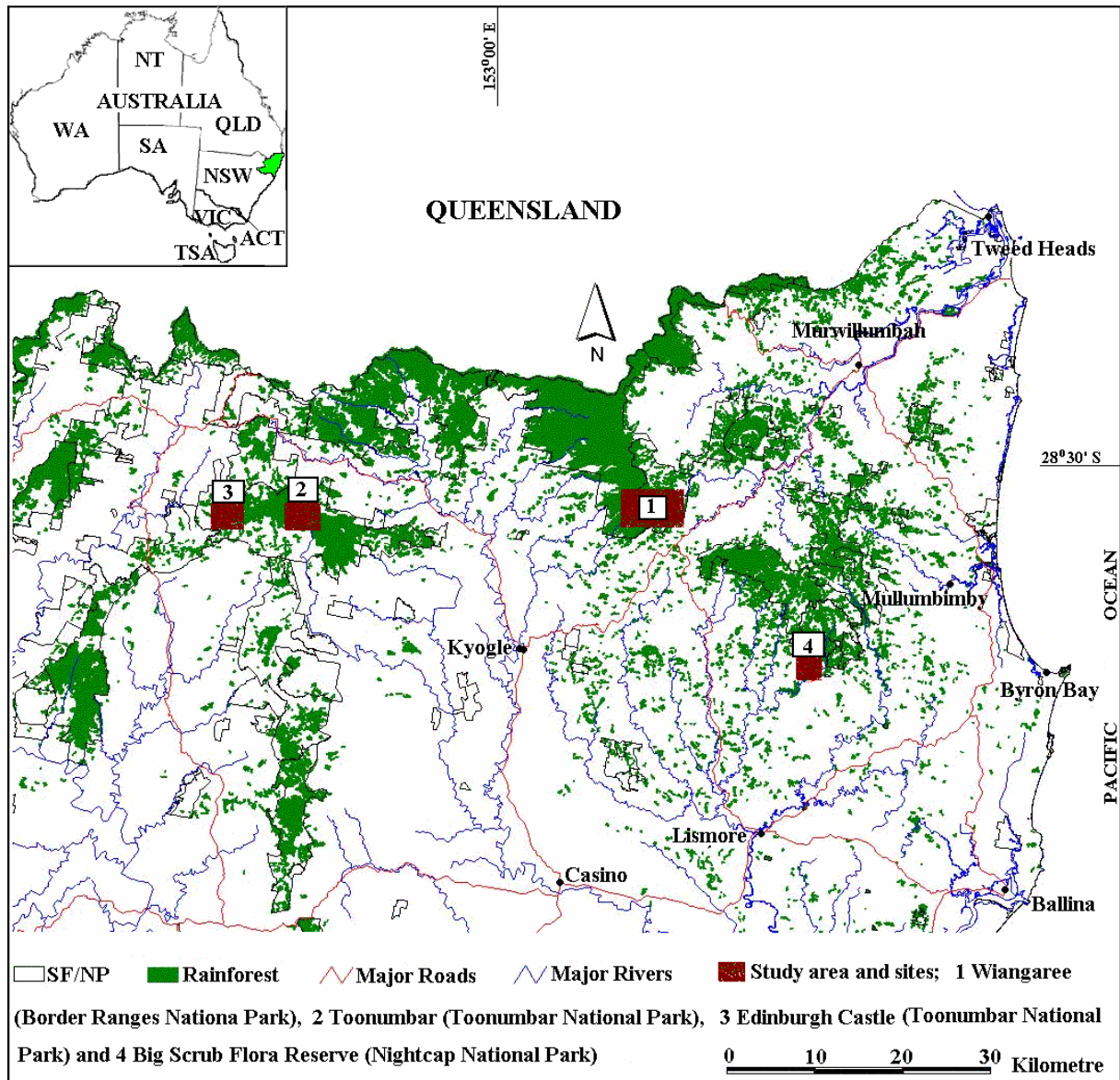
729 Fig. 3. Regeneration changes in subtropical rainforests of north-east New South Wales, Australia.
 730 Biplots show the first two axes of principal coordinate analysis using Chord coefficient
 731 association matrices derived from species abundances standardised by object vector on
 732 repeated sampling in permanent sample plots. Samples with similar species abundance at $\alpha =$
 733 0.2 are enclosed. Treatments: controls 0% basal area removed (a), individual tree selective
 734 logging 1-33% in 3 sites; (b c & d), repeated individual tree selective logging estimated
 735 51-65% (e), moderate logging 36-50%; tree group selection from Queensland (Australia) 47%
 736 (f) and heavy tree selection from New South Wales (Australia) 50% (g), intensive logging 66-
 737 80%; clear cut from Sabah Malaysia 70% (h), Pre-exploitation shelterwood from Nigeria 70%
 738 (i) Post-exploitation Shelterwood from Trinidad and Guyana 74% (j), Improvement treatment
 739 from the Democratic Republic of Congo 71% (k) and logging with enrichment 78% (l).
 740 Numbers beside plotted points indicate sampling dates (e.g. 57 represents 1957, 01 represent
 741 2001).

742 Fig. 4. Changes in the number of tree stems in various dbh-classes in relation to time in both unlogged
 743 and logged stands in subtropical rainforests in north-east New South Wales, Australia.
 744 Average percentage of individuals occurring in relation to the maximum observed is shown in
 745 parenthesis (logged stands show average since logging). Samples with similar species
 746 abundance at $\alpha = 0.2$ are enclosed. Treatments: controls 0% basal area removed (a),
 747 individual tree selective logging 1-33% in 3 sites; (b c & d), repeated individual tree
 748 selective logging estimated 50-65% (e), moderate logging 36-50%; tree group selection from
 749 Queensland (Australia) 47% (f) and heavy tree selection from New South Wales 50% (g),
 750 intensive logging 66-80%; clear cut from Sabah Malaysia 70% (h), Pre-exploitation
 751 shelterwood from Nigeria 70% (i) Post-exploitation Shelterwood from Trinidad and Guyana
 752 74% (j), Improvement treatment from the Democratic Republic of Congo 71% (k) and
 753 logging with enrichment planting 78% (l).

754 Fig. 5. Population dynamics showing the number of stems ≥ 10 cm dbh and their basal area
 755 contribution on a per hectare basis in shade tolerant (a and c) and shade in tolerant species (b
 756 and d) across disturbance intensities in subtropical rainforests of north-east New South Wales,

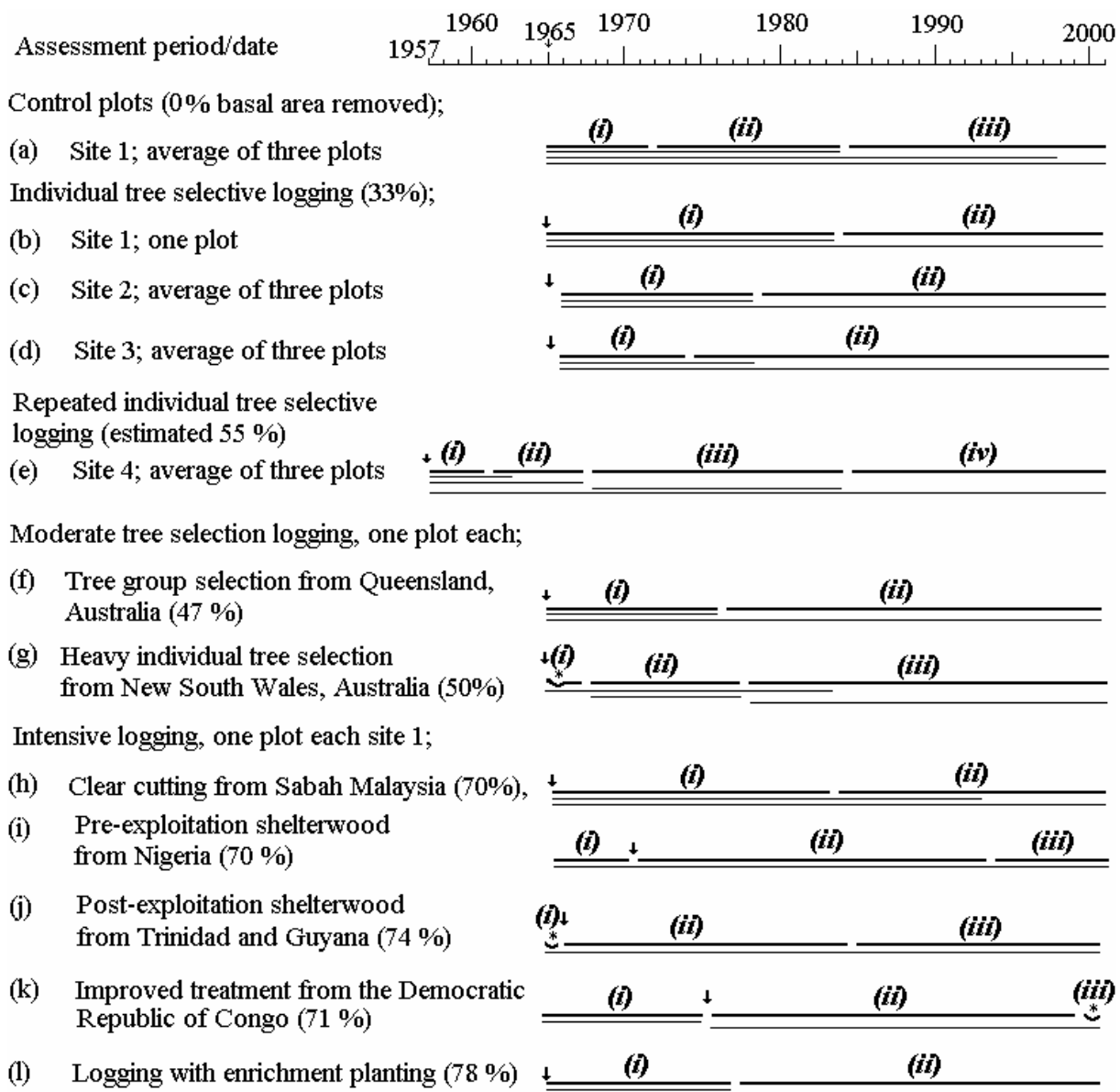
757 Australia. Treatment Treatments: controls 0% basal area removed (disturbance score of 1),
758 individual tree selective logging 1-33% (2), moderate logging 36-50% (3), repeated
759 individual tree selective logging estimated 50-65% (4), intensive logging 66-80% (5).

760 Fig. 6. Estimated log frequencies showing the patterns and trends of changes in number of stems in
761 various diameter classes in relation to time across disturbance intensities in subtropical
762 rainforests of north-east New South Wales, Australia. Disturbance intensity; controls 0%
763 basal area removed (*a*), individual tree selective logging 1-35% (*b*), moderate logging 36-
764 50% (*c*) repeated individual tree selective logging estimated 51 65% (*d*) and intensive
765 logging 66-78% (*e*).



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767 Fig. 1.



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769 Fig. 2.

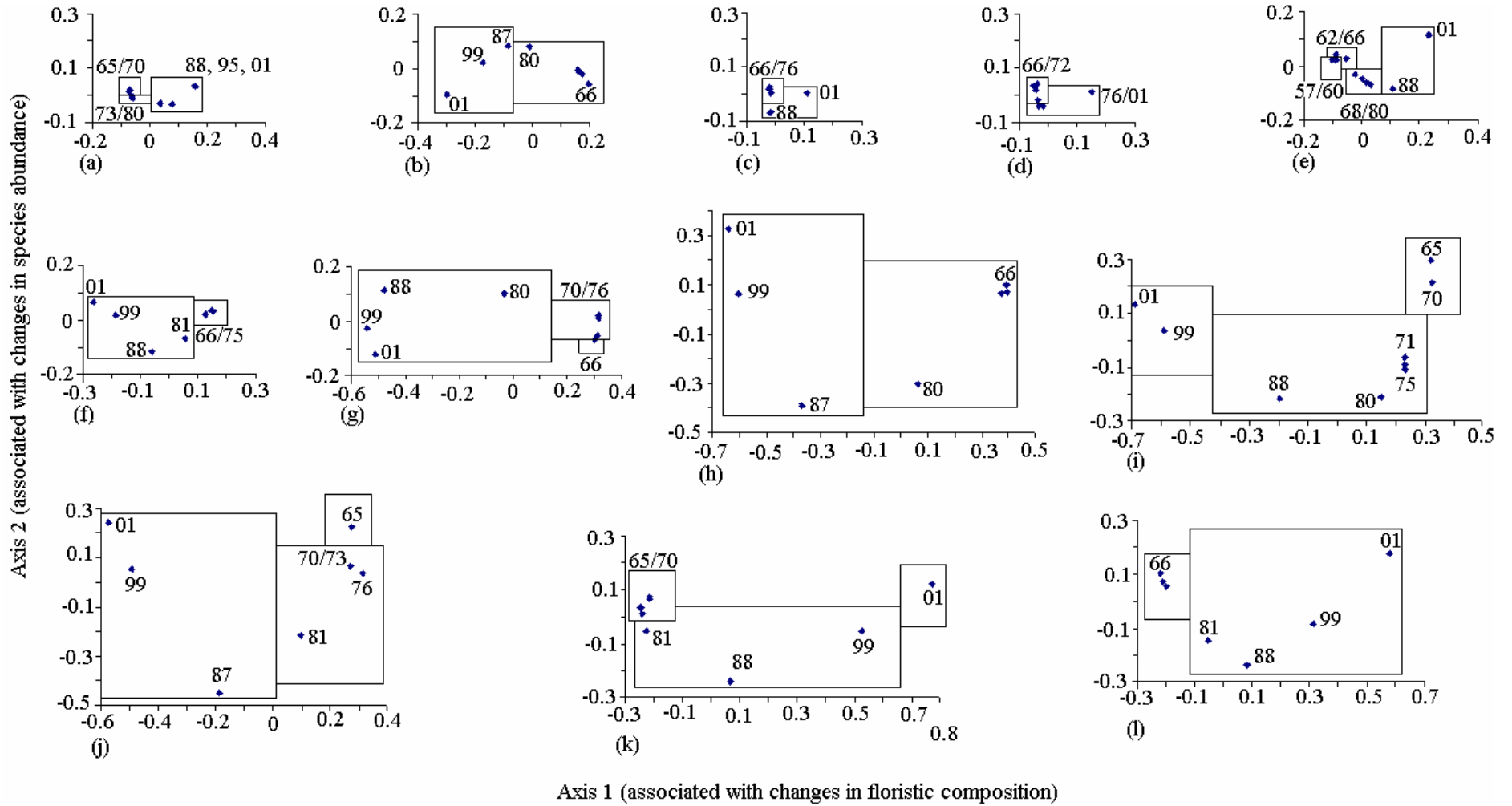
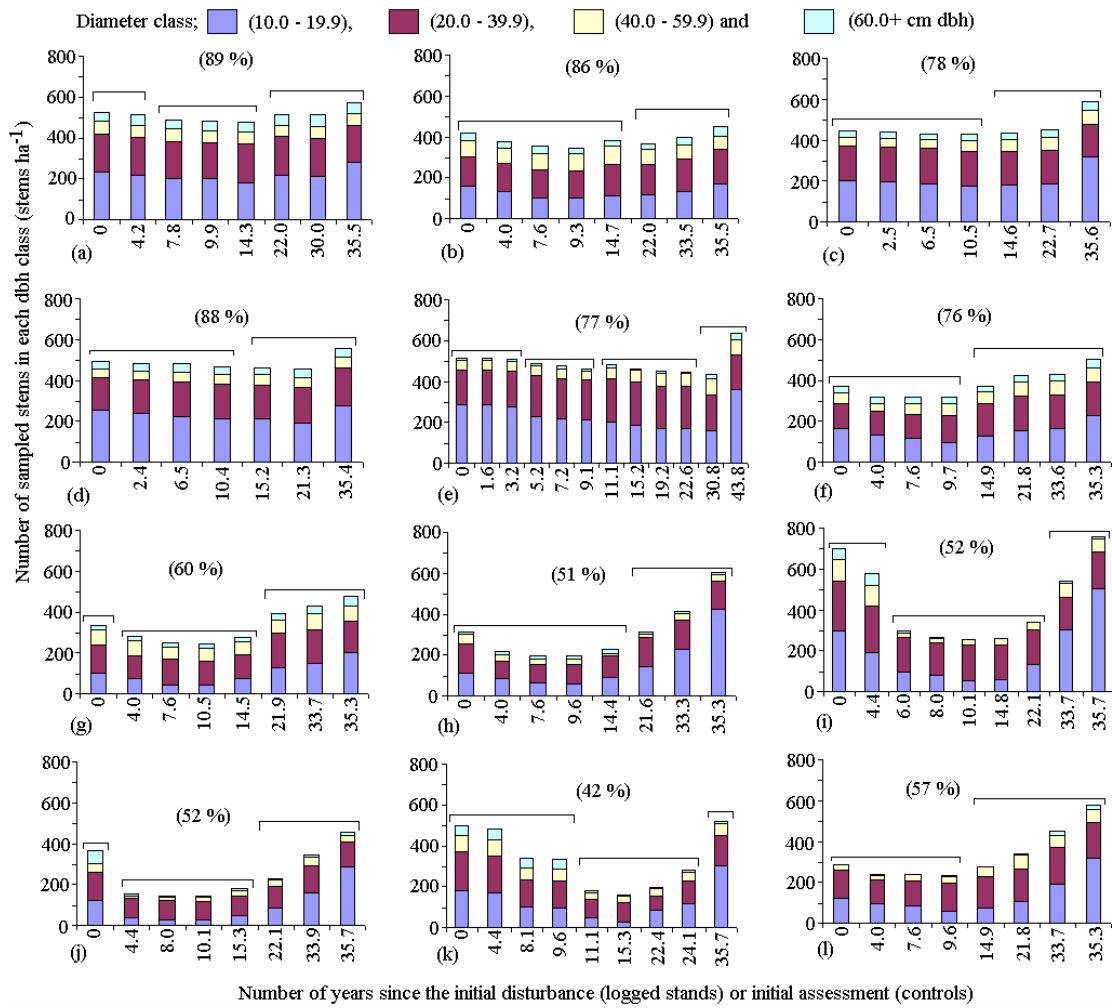


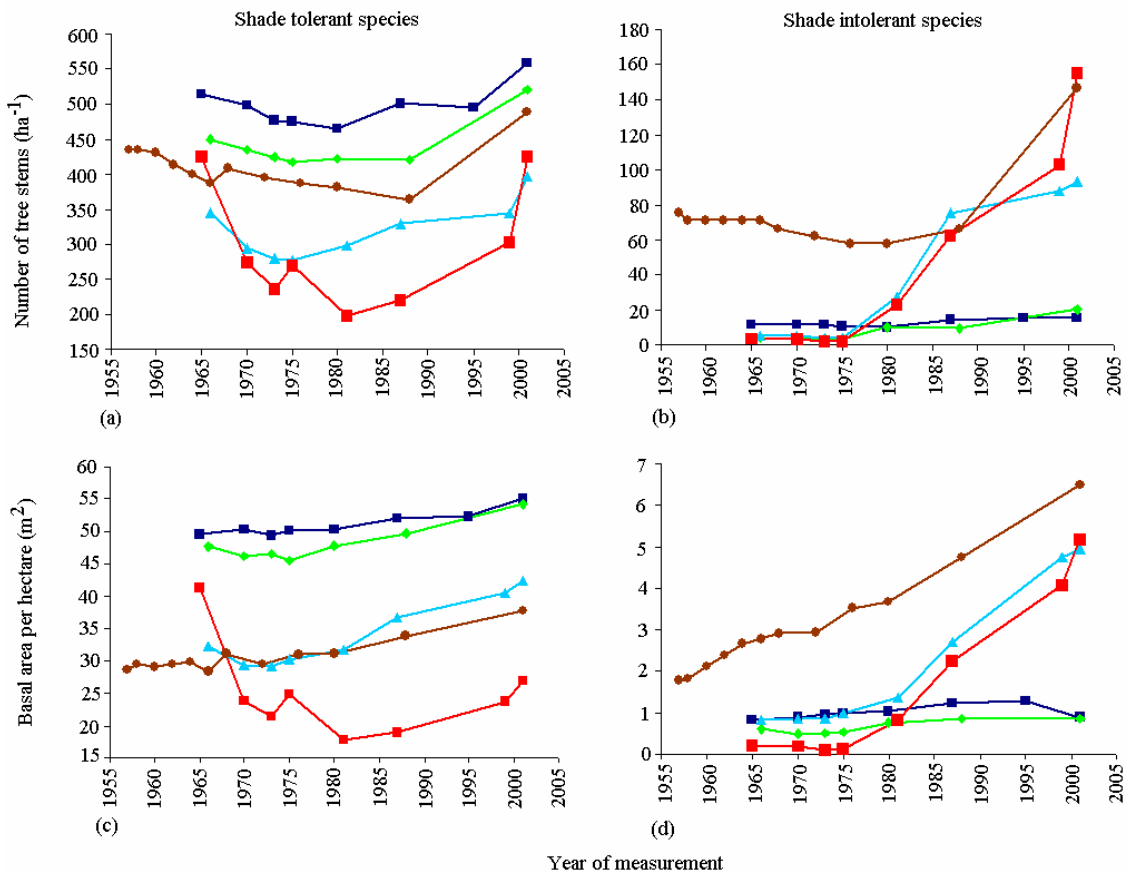
Fig. 3.



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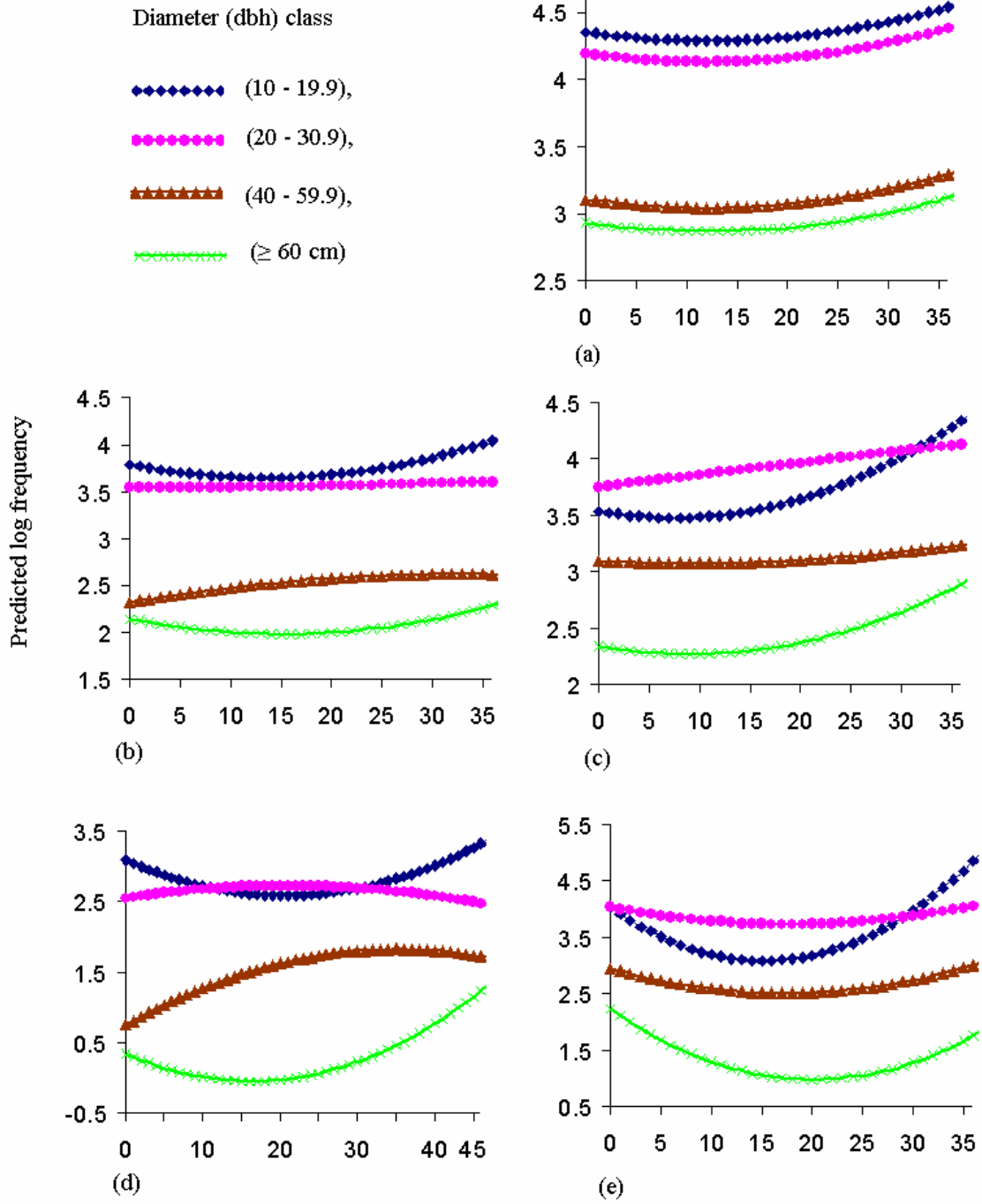
Fig. 4.

■ Unlogged control ◆ Individual tree selective logging ▲ Moderate logging ● Repeated individual tree selective logging
 ■ Intensive logging



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6
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Fig. 5.



8 Time showing the number of years since disturbance (logged) and initial assessment in control sites

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10 Fig. 6.

11 *Table 1.* Sites and silvicultural treatments (9 categories) showing logging intensity (based upon the
 12 percentage basal area (BA) removed). The BA removed in treatment that occurred in phases such
 13 as the Congo treatment refers to the total BA removed.

Site location, treatments description and the percentage BA removed.

Control (0% BA removed) disturbance level score of 1:

Three plots in the Border Ranges National Park (site 1)

Individual tree selective logging (1-35%) with a disturbance level score of 2:

One plot in site 1; Individual merchantable stems were logged in 1965 and a nominal 50% canopy cover was retained (33%).

Former Toonumbar State Forest (site 2), three plots: Individual merchantable stems logged in 1965 during a routine timber harvest, and plot established in 1966 (33%).

Former Edinburgh Castle State Forest (site 3), three plots: Individual merchantable stems logged in 1965 during a routine timber harvesting, and plot established in 1966 (33%).

Moderate tree selection in site 1 (36-50%) with a disturbance level score of 3, one plot per treatment:

Group selection from Queensland, Australia; climbers and undergrowth with no timber value were cut and merchantable stems greater than 61 cm dbh except seed trees were logged in 1965 followed by enrichment planting. A regeneration release operation was carried out in 1970 (47% BA removed).

Heavy individual tree selective logging from NSW, Australia; similar to individual tree selective logging above, but with more merchantable stems were removed in 1965 (50%).

Repeated individual tree selection logging at the Big Scrub Flora Reserve in Nightcap National Park (site 4) with a disturbance level score of 4:

Repeated individual tree selective logging (between 1900s and mid 1950s - approximately 51 to 65% BA removal), three plots established in 1957.

Intensive logging in site 1 (66-80%) with a disturbance level score of 5, one plots per treatment:

Clear cut method from Sabah Malaysia; Assessment of regeneration carried out in 1965 followed by removal of merchantable stems (70% BA removed). Regeneration release operation performed in 1970.

Pre-exploitation Shelterwood from Nigeria; Vines were cut and stems with no timber value poisoned in 1965. Merchantable stems were logged 5/6 years later (1970/71 - 70% BA removed).

Post-exploitation Shelterwood from Trinidad & Guyana; Vines were cut in 1965 and logging of all merchantable stems in 1966. Selective poisoning of remaining stems in 1966 formed Shelterwood. Regeneration release operation performed 5 years later (1970 - 74% BA removed).

Improvement treatment from Democratic Republic of the Congo; Vines were cut in 1965 and stems with no timber value poisoned in 1970. All merchantable stems logged 10 years later (1975 - 71% BA removed).

Logging with enrichment planting; All merchantable stems logged in 1965, shelterwood created by selective removal of remaining trees or trees with no timber value, and enrichment planting with valuable faster growing species carried out. Regeneration progressively liberated over a 10-year period (78.4% BA removed).

14 *Table 2.* Summary for the hierarchical multilevel model building describing the association of
 15 diameter distribution in various dbh classes across logging intensities (control, light selection,
 16 moderate, light selection over time and heavy logging) in subtropical rainforests at the north-east
 17 NSW Australia. *; $P \leq 0.0001$.

Association term or model	-2*loglikelihood (IGLS)= χ^2	Difference in -2*loglikelihood statistic (χ^2)	Degrees of freedom
A baseline variance components model	1919.99		
The dhh classes main effects	1032.19	887.8*	3
Logging intensity main effects	984.74	47.45*	4
Duration (time since logging) main effects	951.64	33.1*	1
Duration squared (quadratic) effects	920.74	30.9*	1
Logging intensity by dbh interaction effects	903.86	16.88*	12
Duration by dbh interaction effects	731.80	172.86*	3
Duration squared by dbh interaction effects	726.77	5.03	3
Logging intensity by duration plus logging intensity by duration squared by interaction effects	684.89	41.88*	8
Logging intensity by duration by dbh plus logging intensity by duration squared by dbh interaction effects	579.27	105.62*	24

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