

1 Native forest individual-tree modelling in Papua New Guinea

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3 Julian C. Fox^{1*}, Ghislain Vieilledent^{2,3}, and Rodney J. Keenan^{1,4}

4 1. Department of Forest and Ecosystem Science, The University of Melbourne,
5 Burnley Campus, 500 Yarra Blvd, Richmond, Vic. 3121, Australia.

6 2. Cirad – UR105 Forest Ecosystem Goods and Services, TA C-105/D, Campus
7 International de Baillarguet, F-34398 Montpellier Cedex 5, France.

8 3. Cirad – Madagascar – DRP Forêt et Biodiversité, BP 904, Ambatobe, 101
9 Antananarivo, Madagascar.

10 4. Victorian Centre for Climate Change Adaptation Research, The University of
11 Melbourne

12 * Corresponding author: jcfox@unimelb.edu.au

13

14 **Abstract**

15 Quantitative study of the permanent sample plot (PSP) databases can provide insights
16 into growth, mortality and recruitment processes driving forest dynamics. Modelling
17 the dynamics of forest growth and yield provides opportunities for optimising
18 silvicultural systems, and generating accurate growth and yield estimates which are
19 fundamental to sustainable forest management. This paper will outline model
20 development based on analysis of a large native forest PSP database in Papua New
21 Guinea. We quantify the competitive influences affecting individual tree growth and
22 mortality, and build predictive models for growth and mortality based on a
23 hierarchical Bayesian modelling (HBM) methodology. The HBM method allows the
24 parameterisation of a global model with species-specific parameters; therefore species
25 level growth and mortality traits are preserved in model predictions, even for rare
26 species. We examine a range of spatial and non-spatial competition indices for the
27 PSP data and conclude that a simple non-spatial competition index (Basal area of
28 competing trees within 20 metres of the subject) adequately characterises competitive
29 influence on growth and mortality. In future work, species-specific HBM model
30 parameters can be used as the basis of a forest simulation system (see <http://twoe.org>
31 for developments) to improved the design and intensity of selective-harvesting
32 regimes at the community and concession level.

33

34

35 **Introduction**

36

37 Forest industries are a major contributor to the national economy of PNG; the log
38 export industry contributed 200 M Kina in 2003 and many people are dependent on
39 timber industries for employment and income. Aside from being economically
40 important, PNG's forests play a vital role in sustaining the traditional subsistence
41 livelihoods of most of the population and contribute significant environmental values.
42 Unfortunately, the current level of harvesting by the log export industry is
43 unsustainable and accessible primary forest is likely to be depleted in the next 15
44 years (Shearman et al. 2009, Filer et al. 2010). An economic challenge thus looms for
45 PNG as revenues from log export based on primary forest dwindle. A major
46 environmental challenge also looms from widespread forest degradation due to
47 unsustainable and inappropriate forest harvesting.

48

49 However, PNG's forest resources have the capacity to continue to make a major and
50 sustainable contribution to the PNG economy, while maintaining many of the other
51 values that PNG society values from their forests. To achieve this, forest management
52 needs significant reform. There are significant problems associated with many
53 commercial timber operations in PNG (Forest Trends 2006). However, sustainable
54 management of natural forests is considered an integral part of the future economic
55 development of PNG. The National Forest Policy states that the forest resource will
56 be managed for the broad range of commercial benefits and non-commercial values it
57 can provide for present and future generations. Sustainable forest management
58 requires a sound scientific understanding of the forest resource, enabling government
59 policy, operational guidelines and adequate supervision of operations. Integral to this,
60 information on forest growth and yield is required to identify more sustainable
61 management options for PNG forests. This would also improve the market reputation
62 of PNG timber and open new pathways and markets for forest products.

63

64 Tropical forests cover 10% of global land area but remain a scientific frontier due to
65 structural and biological complexity and high temporal variability associated with
66 complex successional processes (Chambers et al. 2001). A constraint is the limited
67 number of long-term studies quantifying tropical forest dynamics and the impacts of

68 anthropogenic and natural disturbances, such as harvesting and fire (Clark et al. 2001b;
69 Lewis et al. 2009). Long-term studies, whilst difficult to maintain, especially in
70 developing countries, are essential to the development and testing of hypotheses
71 regarding processes and rates of ecological recovery following disturbance, both
72 anthropogenic and natural (Taylor et al. 2008). The forests of PNG are structurally
73 diverse and complex, and have rarely been studied. The comprehensive PSP database
74 provides an opportunity to ameliorate this. Quantitative study of the PSP database can
75 provide insights into growth, mortality and recruitment processes driving forest
76 dynamics in PNG.

77

78 The development of growth and yield models for PNG's native forests has never been
79 a priority for PNG Forest Authority (PNGFA), and this limited development has
80 hindered the effective management of native forest resources. The only exception to
81 this is the work on growth and yield undertaken by Alder (1998). Alder (1998)
82 developed a stand level growth model called PINFORM based on the first
83 remeasurement of a permanent sample plot (PSP) dataset. Unfortunately, PINFORM
84 has not been routinely applied by PNGFA for forest planning or sustainable yield
85 purposes. However, growth and yield models can be used for optimising silvicultural
86 systems, and generating accurate growth and yield estimates which are fundamental to
87 sustainable forest management. As part of ACIAR project FST/2004/061 the limited
88 extent of growth and yield modelling in PNG is advanced with the development of
89 individual-tree models for competition, growth and mortality. In future work, models
90 will be developed for recruitment, and will be integrated into a forest simulation tool.
91 The forest simulation tool is under development at (<http://twoe.org>). The tool;

- 92 1) Manages and modifies PSP datasets for analysis of growth, mortality and
93 recruitment;
- 94 2) It estimates model parameters using Hierarchical Bayesian Modelling;
- 95 3) Can be used to simulate forest dynamics.

96

97 The individual-tree growth modelling approach is sufficiently flexible to
98 accommodate forests with virtually any species mixture or size structure. Individual-
99 tree models are also age-independent, making them applicable to uneven-aged stands
100 as commonly encountered in tropical forests. Many alternative growth and yield
101 modelling methodologies exist and have been reviewed elsewhere (e.g. Vanclay

102 1994). It is the flexibility of the individual-tree growth model that has lead to its
103 application to the native forest resource of PNG as much of the resource exists in
104 mixed-aged, mixed-species stands, often of indeterminate age.

105

106 Forest utilisation in PNG is increasingly occurring at the community level using
107 small-scale sawmills to extract individual trees. This small-scale utilization is the
108 basis of Forest Stewardship Council (FSC; an international body that outlines the
109 social, environmental and economic requirements for certification) certification
110 efforts that aim to empower landowners, improve livelihoods, preserve the natural
111 environment, whilst facilitating sustainable development (Bun & Scheyvens 2007).
112 To examine whether these operations are sustainable, growth models are required for
113 predicting tree growth at the scale of the individual tree. They can then be used in
114 community forestry to inform small-scale (individual-tree) scenario analysis; species-
115 specific carbon sequestration; and the impact of small-scale utilisation on carbon
116 stocks.

117

118 Individual-tree models characterise the competitive, growth, mortality and recruitment
119 dynamics of individual trees; this is challenging in the complex and diverse tropical
120 forests of PNG. This paper will outline model development based on analysis of a
121 large permanent sample plot (PSP) network in PNG. We quantify the competitive
122 influences affecting individual tree growth, and build predictive models for growth
123 and mortality based on a hierarchical Bayesian modelling (HBM) methodology (Fox
124 et al. 2011). One of the challenges with statistical analysis of PSP data is
125 autocorrelation between measurements. Autocorrelation eventuates when spatial,
126 temporal, or hierarchical variation cannot be captured by deterministic model
127 structures (such as a simple mean) reducing estimation efficiency and biasing
128 hypothesis tests on estimated parameters (Fox et al. 2001). PSP data has implicit
129 hierarchical structure; trees are nested within plots which are repeatedly measured
130 through time and/or space. HBMs are applied here because they can facilitate the
131 explicit modeling of autocorrelation (Clark 2005; Clark and Gelfand 2006; Cressie et
132 al. 2009). The hierarchical Bayesian approach also quantifies the response of growth
133 and mortality to competition and tree size across the entire tree community; using
134 hierarchical models with species random effects, we can estimate the variability of the

135 growth/mortality response between all species, including rare species with few
136 observations (Dietze et al. 2008).

137

138 Competition indices have been the subject of much attention in the forestry literature.

139 Distance-dependent indices use the spatial positions of individual trees in their

140 formulations whereas distance-independent indices do not. Because distance-

141 dependent indices incorporate the spatial pattern of competitors, it should follow that

142 they provide an improved quantitative expression of competition. The various

143 competition indices can be organised into several groups. Distance-dependent indices

144 consist of distance weighted size ratio indices (e.g. Hegyi 1974), area overlap indices

145 (e.g. Bella 1971), and area potentially available indices (e.g. Nance et al. 1987).

146 Distance-independent indices consist of functions of subject tree attributes compared

147 to the attributes of other trees on the plot (e.g. Stage 1973), and stand-level indices

148 such as basal area per hectare and stems per hectare. The various competition indices

149 described above have been quantified for trees from the PSP database in PNG, and

150 will be compared in terms of their ability to predict individual tree dynamics.

151

152 **Methods**

153

154 *PSP data*

155 Over the last 20 years Papua New Guinea Forest Research Institute has established

156 and remeasured over 125 PSPs across PNG covering all major forest types. Each plot

157 is one hectare in size and is divided into 25 sub-plots of 20 m x 20 m. The spatial

158 location, diameter, height, and crown characteristics are recorded for all trees over

159 10cm. The PSP database represents a strong basis for the development of individual-

160 tree models. Because individual trees in PSPs are spatially mapped, we can extricate

161 the spatial competitive processes governing tree growth. The PSP data is described in

162 detail elsewhere (see Fox et al. 2010 and Yosi et al. 2011). The PSP data is a

163 compilation of plot remeasurements undertaken by PNG Forest Research Institute

164 (FRI) since 1994. It has been affected by persistent errors that have hindered its

165 usefulness for modelling. A considered error correction methodology was required to

166 correct persistent errors affecting the PSPs as described in Fox et al 2010. Following

167 this, the PSP dataset was clean and ready for analysis.

168

169 Initially, competition indices are evaluated against individual tree growth for the PSP
170 data. The outcomes of this evaluation then inform individual-tree model development
171 for growth and mortality. Prior to evaluation of competition indices, allometric
172 modelling was required to determine species specific relationships between diameter
173 and crown diameter.

174

175 *Allometric modelling*

176

177 Diameter-Crown Diameter (DCD) allometry is required to quantify individual tree
178 competitive dynamics. To achieve species-specific DCD models we fitted several
179 non-linear models that were found to perform well for tropical forests in the study of
180 Fang and Bailey (1998): the log-linear model (Alexandros & Burkhardt 1992; 1); the
181 hyperbolic model (Huang & Titus 1992; 2); and the exponential model (Fang &
182 Bailey 1998; 3);

183

184 $H = a + b \text{Log}D$ (1)

185 $H = aD / (b + D)$ (2)

186 $H = a + b(1 - e^{-c(D - D_{min})})$ (3)

187

188 Where: a , b and c are parameters estimated for each of the tree species; and D_{min} is the
189 minimum observed diameter for the species.

190

191 Analysis revealed that the hyperbolic model (4) had a consistently lower mean
192 squared error across species represented on PSPs. It was thus selected for crown
193 diameter prediction on PSPs. This is the same model that was used to describe
194 Diameter-Height (DH) allometry in Fox et al. (2010). To predict individual-tree
195 merchantable volume, the same model was fitted to Diameter-Merchantable Height

196 (DMH) allometry. Table 1 provides species specific allometric parameters for DCD,
 197 DH, and DMH models for the 30 most numerous species on the PSPs.

198

199 Table 1. Individual-tree allometric parameters for the hyperbolic model (2) fitted to
 200 DH, DMH, and DCD for the 16 most numerous species on PSPs

Species	Sp Code	Character	DH- <i>a</i>	DH- <i>b</i>	DMH- <i>a</i>	DMH- <i>b</i>	DCD- <i>a</i>	DCD- <i>b</i>
<i>Calophyllum</i> sp.	CAL SP	climax	66.1	43.7	30.5	32.7	49.6	217.9
<i>Canarium</i> sp.	CAN SP	climax	56.1	34.4	30.0	31.6	24.4	77.2
<i>Celtis</i> sp.	CEL	climax	71.5	49.0	31.7	38.9	22.3	65.9
<i>Cryptocarya</i> sp.	CRY SP	climax	50.2	30.3	24.6	25.4	18.2	54.0
<i>Dysoxylum</i> sp.	DYS SP	climax	55.1	38.8	24.2	29.3	19.3	54.2
<i>Ficus</i> sp. (Fig)	FIC SP	climax	61.5	49.6	32.3	53.6	27.5	86.8
<i>Garcinia</i> sp.	GAR SP	climax	57.6	39.3	32.4	40.6	15.5	38.7
<i>Horsfieldia</i> sp.	HOR SP	climax	65.9	47.1	33.6	37.1	15.9	43.8
<i>Litsea</i> sp.	LIT SP	climax	55.7	36.4	28.5	32.4	16.5	47.6
<i>Macaranga</i> sp.	MAC SP	pioneer	52.7	36.5	28.6	40.7	10.9	21.8
<i>Myristica</i> sp.	MYR SP	climax	51.0	33.0	23.5	24.5	9.1	16.8
<i>Pimeleodendron amboinicum</i>	PIM AMB	climax	53.3	35.6	26.5	34.4	14.4	38.9
<i>Planchonella</i> sp.	PLA SP	climax	56.8	33.7	30.0	30.3	21.9	74.9
<i>Pometia pinnata</i>	POM SP	climax	53.1	32.4	25.5	30.5	21.0	58.7
<i>Syzygium</i> sp.	SYZ SP	climax	55.7	37.1	27.9	32.3	18.3	56.3
<i>Terminalia</i> sp.	TER SP	climax	62.4	41.1	38.9	48.0	20.6	56.9

201

202 Allometric parameters described in Table 1 are the basis of look up tables in the forest
 203 assessment tool described in Fox et al. (2011)

204

205

206 *Competition indices*

207

208 Distance weighted size ratio competition indices

209 The distance weighted size ratio (DWSR) competition indices include those that use
 210 the distance between trees weighted by their respective sizes in their formulations.
 211 Two for the most successful DWSR variants were quantified in this study and include
 212 that of Hegyi (1974) and Newnham (1966). The index of Newnham quantifies local
 213 density as the sum of angles subtended from the subject to either side of the stems of
 214 competitors. The two DWSR indices are described in Table 2.

215

216 Table 2. Distance Weighted Size Ratio competition indices.

Index	Formulation	Author
<i>HEG</i>	$HEG_i = \sum_{j=1}^{n_i} \left[\frac{D_j}{D_i} \times \frac{1}{Dis_{ij}} \right] \quad (4)$	Hegyí (1974)
<i>NEW</i>	$NEW_i = \sum_{j=1}^{n_i} 2 \left[a \tan \frac{0.5D_j}{Dis_{ij}} \right] \quad (5)$	Newnham (1966)

217 Where; n_i = total number of competitors for the subject i , D_i = diameter at breast height for the subject
 218 tree i , D_j = diameter at breast height of the j^{th} competitor, Dis_{ij} = the distance in meters between the
 219 subject i and competitor j ,

220

221 The choice of which competitors to include when calculating DWSR indices is an
 222 unresolved problem (Burton 1993). To reduce subjectivity in estimates of competitor
 223 search radius, a methodology was used whereby an optimal search radius (OSR) was
 224 identified mathematically for each species. This could also provide insight into the
 225 range of the competitive dynamic affecting particular rainforest species. By
 226 examining the relationship between index performance and competitor search radius,
 227 it was confirmed that generally index performance approached a maximum value
 228 asymptotically. The point at which performance first began to level off was then
 229 estimated mathematically using a segmented, non-linear equation similar to the
 230 spherical semivariogram employed in geostatistics (e.g. Journel and Huijbregts 1978).
 231 This segmented, non-linear model was fitted to characterise the relationship between
 232 correlation of the index with growth and competitor search radius and can be
 233 described as (6):

234
$$Corr_i = \alpha \left[1.5(sr_i / \beta) - 0.5(sr_i^3 / \beta^3) \right], \quad sr_i \leq \beta \quad (6)$$

235
$$Corr_i = \alpha, \quad sr_i > \beta$$

236 Where; sr_i is the search radius ($i = 2$ to 20 meters at 2 meter increments), $Corr_i$ is the correlation
 237 between the competition index and annual diameter increment for search radius i , and α and β are
 238 parameters estimated using the NLIN procedure in SAS (SAS Institute Inc. 1996). α can be
 239 interpreted as an estimate of the maximum correlation and β interpreted as an estimate of the OSR.

240

241 *Area overlap competition indices*

242 The area overlap (AO) indices were formally introduced by Opie (1968), but the most
 243 successful formulation was presented by Bella (1971) as (7):

244
$$AO_i = \sum_{j=1}^{n_i} \left[\left(\frac{ZO_{ij}}{Z_i} \right) \left(\frac{D_j}{D_i} \right)^{EX} \right] \quad (7)$$

245 Where; AO_i is the AO index of Bella (1971) for tree i , Z_i is the area of the ‘zone of influence’ of the
 246 subject tree i , ZO_{ij} is the area of ‘zone of influence’ overlap between the subject i and competitor j . EX
 247 is the exponent applied to ratios, and previous studies have identified the optimal exponent as being
 248 between 1 and 3 (e.g. Bella 1971).

249

250 The AO indices use a function of the area of overlap between a subject’s and a
 251 competitor’s ‘zone of influence’ to quantify competition. Their success depends on a
 252 suitable estimate of ‘zone of influence’ which is defined as the total area over which a
 253 tree obtains or competes for resources (Opie 1968). We use a prediction of crown area
 254 to quantify the zone of influence of each tree. Studies on the zone of influence have
 255 found that the area over which a tree obtains or competes for resources is
 256 approximately equivalent to the area enclosed by 2 crown radii (e.g. Bi and Jurskis
 257 1996). A crown radii prediction for each tree in the PSP dataset was generated using
 258 the allometric model for diameter to crown-diameter described in Fox et al. (2011b)

259

260 *Area potentially available competition indices*

261

262 The area potentially available (APA) indices, first introduced in the forestry literature
 263 by Brown (1965), are derived from the classical Voronoi diagram. The Voronoi
 264 diagram is a continuous tessellation of an area into non-overlapping polygons. Brown
 265 (1965) introduced APA indices to forestry as a means of quantifying the area
 266 potentially available for growth, and they have since been widely adopted as
 267 competition indices. Several variants exist, including the weighted APA (Moore *et al.*
 268 1973) and the weighted and constrained APA (Nance *et al.* 1987). The weighted APA
 269 (Moore *et al.* 1973) weights the position of the perpendicular bisector on the line
 270 joining a tree to its competitor by a ratio of tree sizes. Nance *et al.* (1987) proposed a
 271 weighted and constrained APA to curtail the development of large irregular polygons
 272 when spatial arrangements become irregular. When constructing the tessellation they
 273 selected the smaller of the distance to the polygon boundary or the output of a
 274 constraining function. Nance *et al.* (1987) proposed a function of crown radius as a
 275 constraining function, and this was realized using a constraining function based on the
 276 predicted crown radius for the subject tree.

277

278 Three variants of the APA index are described in Table 3.

279

280 Table 3. Area potentially available competition indices.

Index	Weighting function	Constraining function	Author
APA	-	-	Brown (1965)
APAW	$DB_{ij} = \left[\frac{D_i^2}{(D_i^2 + D_j^2)} \right] Dis_{ij}$	-	Moore <i>et al.</i> (1973)
APAWC	$DB_{ij} = \left[\frac{D_i^2}{(D_i^2 + D_j^2)} \right] Dis_{ij}$	$CF_i = \sqrt{\frac{(PA \times (D_i / \sum_{j=1}^I D_j))}{\pi}}$	Nance <i>et al.</i> (1987)

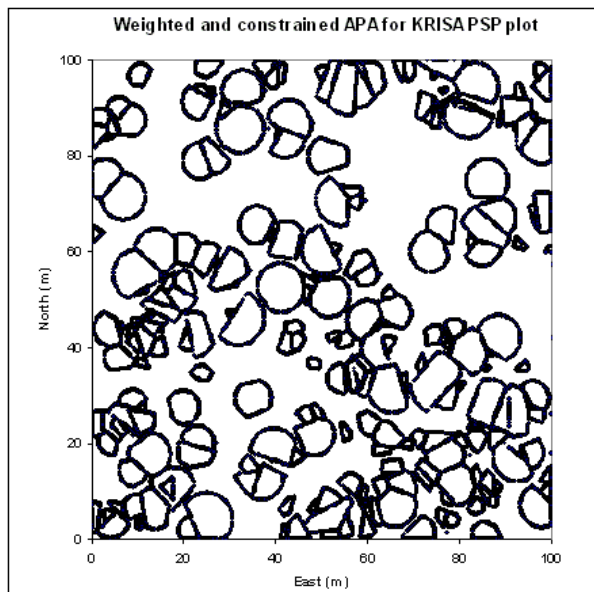
281 Where; DB_{ij} = the distance to the perpendicular bisector located on the straight line between the subject
 282 i and competitor j

283

284 The APA class of competition indices is the most complex to compute. A SAS Macro
 285 (SAS Institute Inc. 1990) was written for efficient computation of all APA variants
 286 along with DWSR, AO, and distance-independent. SAS Macros for quantifying the
 287 various competition indices detailed in this study are available upon request from the
 288 primary author. An example of the weighted and constrained APA (APAWC) for the
 289 Krisa PSP plot is shown in Figure 1. The spatial irregularity of the PSP plot can be
 290 observed.

291

292 Figure 1. Graphic of the weighted and constrained APA for the Krisa PSP plot



293

294

295 *Alleviating boundary effects*

296

297 A boundary effect is generated when boundary trees are subject to competition from
 298 outside the plot that is not incorporated in competition indices. To minimize
 299 information loss from exclusion of trees subject to edge effects, we used a toroidal
 300 edge correction scheme commonly used in spatial statistical applications (Ripley
 301 1981). Toroidal edge correction is implemented by considering a rectangular spatial
 302 array as a torus. This can be realized simply by translating the spatial arrangement to
 303 create eight new adjoining arrays. The validity of toroidal edge correction depends
 304 upon the assumption that boundary trees are subject to equivalent competition from
 305 both outside and inside the plot which is tenuous for trees close to the boundary in an
 306 irregularly structured tropical forest, i.e., less than 5 meters. But it should be
 307 permissible for trees more than 5 meters from the boundary. Following this trees
 308 within 5 meters of the boundary were excluded from analysis and toroidal edge
 309 correction was applied to all other trees.

310

311 Distance-independent Competition indices

312

313 Distance-independent indices consist of functions of subject tree attributes compared
 314 to the attributes of other trees on the plot (Stage 1973). They do not use spatial

315 information. The summed basal area of trees within 20 metres of the subject tree was
316 quantified (*BAS*). The index developed by Stage (1973) was also quantified (8);

317
$$DAL_i = \sum_{i=1}^{n_i} D_i \quad (8)$$

318

319 *Evaluating competition indices*

320

321 Competition indices were evaluated for their ability to predict annual diameter
322 increment in the next growing period using two criteria. The first criterion was the
323 correlation between the index and annual diameter increment in the next growing
324 period. If the relationship between each variable and annual diameter increment was
325 found to be non-linear, a transformation was sought which rendered the relationship
326 linear. In these instances the fit of the transformed variable was evaluated.

327

328 The second criterion was the significance of the competition index as fixed effect in a
329 mixed model with basal area against annual diameter increment. Basal area was
330 included as a fixed effect to extricate the influence of differing stand density on tree
331 growth. A mixed model was used to account for the nested dependence (Fox et al.
332 2001) affecting PSPs; the growth of trees within each PSP will be more similar than
333 that between each PSP, as trees on the same plot will be subject to the same local
334 environmental conditions, and will be of a similar forest type. To account for this a
335 random effect was used for each PSP measurement. This will ensure correct statistical
336 inference on the growth and competition dynamics within and between PSP plots
337 (Fox et al. 2001).

338

339 *Individual tree models*

340

341 *HBM model fitting*

342

343 Conditional posterior for each parameter was obtained using a Gibbs sampler (Gelfand 1990)
344 written in C++. We used non-informative flat prior (with large variance) for each parameter.
345 We ran one MCMC of 20 000 iterations for each parameter. The ‘burn-in’ period was set to

346 10 000 iterations and the ‘thinning’ to 1/10. We then obtained 1000 estimations for each
 347 parameter.

348

349 *Growth-model*

$$\log(G_{ik} + 2) = (\beta_0 + b_{0,k}) + (\beta_1 + b_{1,k}) \log(D_i) + (\beta_2 + b_{2,k}) \log(C_i + 1) + \varepsilon_i$$

$$\varepsilon_i \sim \text{Normal}(0, V)$$

350 $[\beta_0, \beta_1, \beta_2] \sim \text{Normal}_3(0, V_\beta)$ (9)

$$[b_{0,k}, b_{1,k}, b_{2,k}] \sim \text{Normal}_3(0, V_b)$$

$$V_b \sim \text{Inverse-Wishart}(r, rR)$$

$$V \sim \text{Inverse-Gamma}(s_1, s_2)$$

351 Where; G_{ik} is the growth (mm.yr⁻¹) of tree i of species k between dates t and $t + 1$

352 D_i is the diameter (cm) of tree i at date t

353 C_i is the competition index (m².ha⁻¹) in the neighborhood of tree i at date t

354 $\beta_0, \beta_1, \beta_2$ are global averages on the intercept, the slope of D and the slope of C ,
 355 respectively

356 $b_{0,k}, b_{1,k}, b_{2,k}$ are the species random effects on the intercept, the slope of D and the
 357 slope of C , respectively.

358

359 *Mortality-model*

360

$$S_{ik} \sim \text{Bernoulli}(\theta'_{ik})$$

$$\theta'_{ik} = 1 - (1 - \theta_k)^{Y_i}$$

$$\text{logit}(\theta_{ik}) = (\beta_0 + b_{0,k}) + (\beta_1 + b_{1,k})(D_i - 20) + (\beta_2 + b_{2,k})(C_i - 20) + \varepsilon_i$$

361 $\varepsilon_i \sim \text{Normal}(0, V = 1)$ (10)

$$[\beta_0, \beta_1, \beta_2] \sim \text{Normal}_3(0, V_\beta)$$

$$[b_{0,k}, b_{1,k}, b_{2,k}] \sim \text{Normal}_3(0, V_b)$$

$$V_b \sim \text{Inverse-Wishart}(r, rR)$$

362

363 Where; S_{ik} is the status (0=alive, 1=dead) of tree i of species k between dates t and $t +$

364 1

365 Y_i is the time interval (yr) between dates t and $t + 1$

366 θ'_{ik} is the mortality rate for time interval Y_i

367 θ_k is the annual mortality rate

368

369 For the mortality model, we included in the expression of $\text{logit}(\theta_{ik})$ a residual error

370 term $\varepsilon_i \sim \text{Normal}(0, V)$ to account for overdispersion in the data (Hadfield, 2010). We
371 fixed V to 1. Using this parametrisation was convenient as it placed the estimation in
372 the linear Gaussian regression framework and allowed us to use conjugated priors for
373 parameters.
374

375 Results

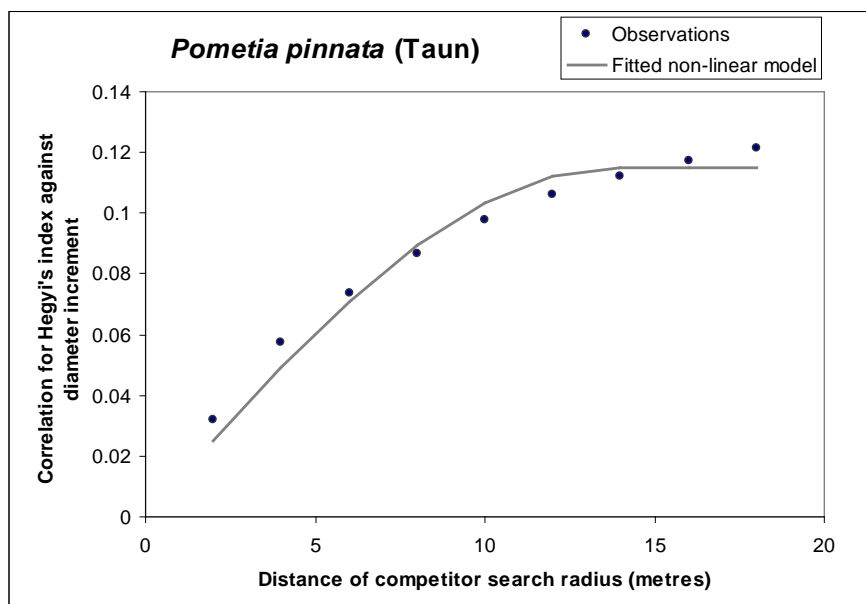
376 Competition indices

377 Optimal competitor search radii

378

379 Different trends in correlation across different search radii emerged for different
380 species. An example of the fitted non-linear model for Hegyi's (1974) index is shown
381 in Figure 2. For *Pometia Pinnata* α was estimated as 0.12, and β was estimated as
382 13.7. These can be interpreted as an asymptotic correlation of 0.12, and an optimal
383 search radius of 13.7 meters.
384

385 Figure 2. Fitted non-linear model for estimating optimal competitor search radius for
386 *Pometia pinnata*.



387

388

389 Estimated optimal search radii (OSR) for different species are detailed in Table 4. It
390 can be observed that some species such as *Calophyllum* have small OSR values (3 m),
391 while other species such as *Horsfieldia* have large OSR values (20m). These results
392 suggest that the range of the competitive effect is different among tropical species.
393 For example, it could be hypothesized that *Calophyllum* is most affected by
394 competition for light among immediate neighbors (competitors within 3 meters)

395 whilst for *Horsfieldia* competition for light and nutrients is more diffuse and
396 occurring over a larger area (up to 20 meters).

397

398 *Evaluating competition indices*

399

400 10 competition indices were quantified for approximately 85,000 individual tree
401 measurements across the 125 permanent sample plots. The 300 most numerous
402 species on PSPs were selected for specific study of competition indices. Preliminary
403 analysis was used to identify a subset of competition indices for further study. The
404 best performing indices were selected on the basis of strength of correlation with tree
405 growth across the 300 species. The following subset was identified for further study;

- 406 • DBHOB (Diameter at Breast Height Over Bark)
- 407 • BAS (Sum of tree BA within 20m of subject)
- 408 • SQAPAWC (Square Root of APASWC)
- 409 • LNNEW (Natural Logarithm of NEW)
- 410 • LNAO1 (Natural Logarithm of AO with exponent 1)

411

412 The best performing competition index was then identified for each of the 300 species.
413 Table 3 shows the competition indices ranked for the percentage of the 300 species
414 for which they were optimal (in terms of correlation with annual diameter increment).
415 Table 3 also shows the competition indices ranked for the number of times they were
416 optimal in terms of fixed effect significance in a mixed model with basal area across
417 the 300 species

418

419 Table 3. Percentage of species for which each competition index was optimal

Competition Index	Correlation - Percentage of species optimal	Mixed model - Percentage of species optimal
DBHOB	14	18
BAS	28	21
SQAPAWC	15	13
LNNEW	29	29
LNAO1	14	19

420

421 Table 3 demonstrates that no single competition index is optimal across the 300
 422 species. It also demonstrates that distance-independent indices such as DBHOB and
 423 BAS are equally as effective as distance-dependent indices. BAS (28%, 21%) and
 424 LNNEW (29%, 29%) appear to be optimal most often across the 300 species. when
 425 basal area was included as a fixed effect in a mixed model, distance-dependent indices
 426 performed better (optimal for 61% of indices). This may be due to total basal area
 427 characterizing stocking differences across PSPs, and negating the influence of the
 428 distance-independent index BAS (28% down to 21%).

429 To provide more detail of competition index performance, Table 4 provides further
 430 statistics for a subset of the 16 most observed species.

431
 432 Table 4. Competition index performance and other statistics for the 16 most observed
 433 species on PSP plots

Species	Sp Code	Character	Obs	OS R	Optimal Corr	Optimal Corr Mixed	Effect Sig	Wood Density	Diameter 90 th Quan	Mean Incr	
<i>Calophyllum</i> sp.	CAL SP	climax	1072	3	BAS	-0.16	BAS	4.00E-03	0.5	47	0.53
<i>Canarium</i> sp.	CAN SP	climax	2323	6.9	BAS	-0.2	BAS	6.30E-08	0.48	36.5	0.42
<i>Celtis</i> sp.	CEL	climax	990	5.5	LNNEW	-0.21	BAS	2.00E-04	0.55	50	0.52
<i>Cryptocarya</i> sp.	CRY SP	climax	1993	7.4	BAS	-0.09	LNAO1	6.00E-02	0.46	34.7	0.44
<i>Dysoxylum</i> sp.	DYS SP	climax	1846	14.2	BAS	-0.2	BAS	3.00E-17	0.62	39.9	0.38
<i>Ficus</i> sp. (Fig)	FIC SP	climax	1536	5.9	BAS	-0.2	DBHOB	2.90E-10	0.34	45.5	0.51
<i>Garcinia</i> sp.	GAR SP	climax	1018	11.8	LNNEW	-0.16	LNNEW	1.10E-04	0.64	31.5	0.37
<i>Horsfieldia</i> sp.	HOR SP	climax	1682	20	LNNEW	-0.14	LNNEW	1.30E-04	0.36	31.2	0.35
<i>Litsea</i> sp.	LIT SP	climax	1022	5.7	BAS	-0.25	LNAO1	7.30E-11	0.4	38.4	0.51
<i>Macaranga</i> sp.	MAC SP	pioneer	1426	14.3	BAS	-0.27	LNNEW	9.50E-12	0.3	22.8	0.96
<i>Myristica</i> sp.	MYR SP	climax	3113	9.6	BAS	-0.16	LNNEW	1.40E-03	0.38	25.7	0.31
<i>Pimeleodendron amboinicum</i>	PIM AMB	climax	1745	15.7	LNNEW	-0.17	DBHOB	3.20E-07	0.48	39.8	0.42
<i>Planchonella</i> sp.	PLA SP	climax	1683	9	LNNEW	-0.21	LNAO1	4.90E-09	0.45	37.6	0.44
<i>Pometia pinnata</i>	POM SP	climax	2777	13.7	LNAO1	-0.16	LNAO2	2.60E-10	0.58	54.4	0.67
<i>Syzygium</i> sp.	SYZ SP	climax	2854	10.8	BAS	-0.17	BAS	4.10E-12	0.61	41.1	0.37
<i>Terminalia</i> sp.	TER SP	climax	638	8.3	BAS	-0.21	LNAO1	3.40E-07	0.45	46.3	0.67

434 Where; Obs is the number of observations, OSR is Optimal Search Radius, Optimal Corr is the
 435 competition index with optimal correlation against annual diameter increment whilst Corr is the
 436 Spearman's correlation coefficient, Optimal Mixed is the competition index with optimal effect
 437 significance in a mixed model and Effect Sig is the t test that the parameter is significantly different to
 438 zero, Wood Density is Basic Density; the weight of wood at 0% moisture content occupying one cubic
 439 meter (units: 10³ kg/m³) from Eddowes (1977), Diameter 90th Quan is the 90th quantile of the diameter
 440 distribution, and Mean Incr is the average annual diameter increment in the next growing period.

441
 442

443 *Individual-tree models*

444 Growth (9) and mortality (10) individual tree models were fitted to the PSP data with
 445 random species effects. Fitted models resulted in global average parameters ($\beta_0, \beta_1, \beta_2$
 446 in Equation 9 for growth, and Equation 10 for mortality) as well as species-specific
 447 parameters describing growth and mortality processes for each species ($\beta_{0,k}, \beta_{1,k}, \beta_{2,k}$
 448 in Equation 9 for growth, and Equation 10 for mortality for species k). The growth
 449 and mortality of individual trees was a function of tree size (diameter), and the local
 450 competitive environment (sum of BA within 20m of subject). The Global model with
 451 global average parameters is detailed in Equation 11 for growth and Equation 12 for
 452 mortality;

$$453 \log(G_{ik} + 2) = (1.781 + b_{0,k}) + (0.055 + b_{1,k}) \log(D_i) + (-0.100 + b_{2,k}) \log(C_i + 1) \quad (11)$$

454

$$455 \log it(\theta_{ik}) = (-3.741 + b_{0,k}) + (-0.00262 + b_{1,k}) \log(D_i - 20) + (0.02069 + b_{2,k}) \log(C_i - 20)$$

456 (12)

457

458 Global trends in growth and mortality against tree size (D_i) and competition (C_i) can
 459 be observed in Equation 11 and 12. Growth increases with increasing tree size
 460 (positive parameter on D_i) but decreases with increasing competition (negative
 461 parameter on C_i). Both these observations are consistent with biological reality in
 462 tropical forests. Probability of mortality decreases with increasing tree size, but
 463 increases with increasing competition (parameters in Equation 12). Again, these
 464 observations are consistent with biological reality.

465

466 Species-specific parameters such as $b_{I,k}$ in Equations (11) and (12) allow each species
 467 to express its individual traits with respect to growth and mortality. Species-specific
 468 model parameters for the 16 most numerous species on PSPs as well as predictions of
 469 growth and mortality for trees under conditions of low (10 m²/ha) and high
 470 competition (50 m²/ha) are detailed in Table 5. All predictions are for medium sized
 471 trees (40cm dbh).

472

473 Table 5. Growth and mortality parameters and example predictions for 16 most
 474 numerous species on PSPs

Species	Sp Code	Character	G- b_0	G- b_1	G- b_2	M- b_0	M- b_1	M- b_2	GLC	GHC	MLC	MHC
<i>Calophyllum</i> sp.	CAL SP	climax	1.514	0.171	-0.093	-3.203	-0.003	-0.024	3.425	3.100	0.018	0.047
<i>Canarium</i> sp.	CAN SP	climax	1.501	0.106	-0.074	-3.539	-0.005	-0.016	2.919	2.683	0.016	0.030

<i>Celtis</i> sp.	CEL SP	climax	2.484	-0.025	-0.221	-3.895	-0.007	-0.014	7.158	5.905	0.012	0.020
<i>Cryptocarya</i> sp.	CRY SP	climax	1.610	0.071	-0.068	-3.300	0.014	-0.010	3.218	2.986	0.034	0.051
<i>Dysoxylum</i> sp.	DYS SP	climax	1.261	0.190	-0.098	-3.904	0.003	-0.010	2.321	2.049	0.016	0.023
<i>Ficus</i> sp. (Fig)	FIC SP	climax	1.786	0.094	-0.134	-3.362	-0.006	-0.017	4.029	3.513	0.018	0.035
<i>Garcinia</i> sp.	GAR SP	climax	1.771	0.074	-0.149	-3.392	0.003	-0.019	3.664	3.129	0.020	0.041
<i>Horsfieldia</i> sp.	HOR SP	climax	1.543	0.025	-0.042	-3.990	0.018	-0.004	2.664	2.537	0.023	0.027
<i>Litsea</i> sp.	LIT SP	climax	1.728	0.138	-0.142	-3.428	0.013	-0.006	4.058	3.512	0.034	0.042
<i>Macaranga</i> sp.	MAC SP	pioneer	2.482	0.002	-0.163	-2.712	0.000	0.018	8.133	7.089	0.052	0.102
<i>Myristica</i> sp.	MYR SP	climax	1.591	0.045	-0.086	-3.873	0.017	-0.005	2.827	2.559	0.024	0.030
<i>Pimeleodendron amboinicum</i>	PIM AMB	climax	2.631	-0.230	-0.091	-4.139	0.027	-0.027	6.736	6.223	0.012	0.035
<i>Planchonella</i> sp.	PLA SP	climax	1.565	0.132	-0.107	-3.544	0.013	-0.008	3.289	2.925	0.029	0.039
<i>Pometia pinnata</i>	POM SP	climax	1.493	0.109	-0.111	-3.663	0.007	-0.051	2.720	2.382	0.006	0.047
<i>Syzygium</i> sp.	SYZ SP	climax	1.636	0.057	-0.102	-3.564	0.006	-0.021	3.060	2.728	0.017	0.038
<i>Terminalia</i> sp.	TER SP	climax	1.889	0.073	-0.083	-3.814	0.019	-0.002	4.824	4.459	0.030	0.032

475 Where $G-b_0$, $G-b_1$, $G-b_2$ are parameters for the growth model (9), while $M-b_0$, $M-b_1$,
476 $M-b_2$ are parameters for the mortality model (10). GLC, GHC, MLC, MHC are
477 growth (cm/yr) under low competition (10m²/ha), growth under high competition
478 (50m²/ha), probability of mortality (between zero and one) under low competition,
479 probability of mortality under high competition.
480

481 It can be observed that growth under low competition is always higher than under
482 high competition, and this makes biological sense. Similarly, probability of mortality
483 under low competition is always lower than under high competition. For *Macaranga*,
484 a pioneer species, probability of mortality is twice as high under conditions of high
485 competition relative to low competition.
486

487 Discussion

488

489 Tropical forests are characterised by a high diversity of woody species, and no
490 universally applicable species groupings exist that capture the continuum of growth,
491 mortality and recruitment dynamics (Clark and Clark 1999). However, there is a need
492 to group species for the development of forest growth models as grouping similar
493 species increases the sample size, thus reducing parameter variance, and may result in
494 fewer and more parsimonious models that can be more easily applied in forest
495 management contexts. It is also important in the ecological insights it can offer on
496 species growth habits. Ever since Whitmore (1975) first described tropical tree
497 functional groups (fast growing shade intolerant pioneers, and slower growing shade
498 tolerant climax species) researchers have been attempting to group species using a
499 variety of strategies as reviewed by Gourlet-Fleury et al. (2005). Future work will

500 explore if competition indices can be used for species classification. For example, we
501 can relate OSR values to the shade-tolerance of different species. We would expect
502 that species with small OSR values that are most effected by competition for light are
503 shade-intolerant, while species with large OSR with a more diffuse competitive affect
504 are shade-tolerant.

505

506 Table 4 also provides insights into tree attributes that could be used as a basis for
507 species grouping. Wood density, growth rate, and potential size have been used in
508 other studies to group species. *Macaranga* is a pioneer species with the largest growth
509 rate (0.96 cm/yr), smallest potential size (22.8 cm), lowest wood density (300 kg/m³),
510 and the strongest correlation for competition indices (0.27). This is congruent with
511 previous findings that pioneer species tend to be fast growing, tend have small
512 potential size, low wood density, and tend to be shade-intolerant with a life cycle
513 characterized by rapid growth to capitalize on canopy gaps. Intolerance to shade from
514 nearby trees explains the importance of competition indices in explaining future
515 growth. In contrast to this *Pometia Pinnata* (Taun) is a climax species with a slower
516 growth rate (0.67 cm/yr), large potential size (54.5 cm), denser wood (580 kg/m³), and
517 weaker correlation for competition indices (0.16). Again, this is congruent with
518 climax species being slower growing, having larger potential size, denser wood, and
519 being more tolerant of shade from nearby trees. More tolerance to competition
520 explains the weaker correlation of competition indices with future growth. The local
521 spatial arrangement of soil fertility, topographic, geologic and climatic factors will be
522 more important in explaining growth for shade-tolerant species. Other species in
523 Table 4 fall on the continuum between pioneers such as *Macaranga* and climax
524 species such as *Pometia Pinnata*. This brief analysis suggests that competition
525 response as characterized by competition indices could be used as an additional
526 attribute for species groupings in tropical forests.

527

528 This analysis suggested that no single competition index is dominant, with indices
529 BAS and LNNEW performing well. The optimal index for each species explained
530 only a modest amount (14-27%) of the variability in diameter increment. However,
531 indices were highly significant when evaluated in a mixed model with basal area per
532 hectare. Failure to identify a single index as optimal in the mixed tropical forests of
533 PNG could be associated with variability in competition response across the 300

534 species. Shade-intolerant species will compete strongly with first order neighbors for
535 light and nutrients. The SQAPAWC most accurately characterizes these first order
536 interactions. The LNAO1, and LNNEW competition indices may perform better for
537 more shade-tolerant species as competition for light and nutrients would be more
538 diffuse, less intense, and be occurring over a larger area. Following this hypothesis,
539 distance-independent indices such as BAS and DBHOB would perform well for very
540 shade-tolerant species for which the location and size of nearby competitors is
541 relatively unimportant. Future work will attempt to align the shade tolerance of
542 different species with the performance of different competition indices.

543

544 Diameter performed well as a predictor of growth performing better than competition
545 indices for 14% & 18% of species. This is in agreement with previous studies that
546 have found that diameter is an excellent predictor of growth (Lorimer 1983). Diameter
547 can be considered a historical log of past competitive interactions, genotypic
548 differences, and localized environmental heterogeneity, and therefore tends to be
549 strongly correlated with future growth.

550

551 Tree growth is a complex process. It is influenced by an intricate network of above-
552 and below-ground competitive interactions as well as the local spatial arrangement of
553 soil fertility, topographic, geologic and climatic factors. The vast majority of current
554 competition indices and growth models remain overly simplified (Fox et al. 2001).
555 This over-simplification results in large amounts of unexplained variability, and
556 growth modelers have come to accept this as an ‘occupational hazard’ (Burkhart and
557 Gregoire 1994). Competition indices explained at best 25% of the variability in
558 individual tree growth in mixed tropical forest in PNG. Future work requires insights
559 into this unexplained variability that can improve growth model performance. Despite
560 these shortcomings, the competition indices examined here, and the insights into
561 competitive dynamics they provided, can guide further growth model development for
562 mixed tropical forest in PNG. Work described in this paper represents an initial
563 investigation of;

- 564 1) competition index selection in tropical forests
- 565 2) application of individual based models with demographic hierarchical
566 Bayesian models including species random effects.

567 Results suggest that the approach shows promise. Future work will fit a recruitment

568 model and use species-specific competition indices in growth/mortality
569 models.

570

571 The forest assessment tool is described elsewhere and is based on a stratified random
572 variable radius plot inventory (Fox et al. 2011a). The assessment tool incorporates
573 lookup tables that facilitate the calculation of plot- and estate-level above ground live
574 biomass (AGLB; Mg/ha) and merchantable volume (MV; m³/ha). In future work, this
575 forest assessment tool can then used as a basis for the individual-tree growth and yield
576 module which can be used to simulate forest development into the future. Data from
577 the forest assessment tool can be read into the forest simulation tool which is under
578 development at (<http://twoe.org>). Using individual-tree HBM model parameters
579 estimated from the PSPs, assessment data can be used as the basis of a simulation.
580 Lookup tables for species-specific HBM parameters for a growth, mortality and
581 recruitment models are available from the primary author. Each tree measured in the
582 assessment therefore becomes a tree in the simulation that is subject to perturbations
583 from growth and possible mortality into the future. New trees eventuate in the
584 simulation from the recruitment model that uses tree density and species present on
585 each plot to create a probability of recruitment.

586

587 A simple tree level simulator housed in accessible software (<http://twoe.org>) can
588 assist community-level decision making with regards to the design and intensity of
589 selective harvesting regimes. For example, after the forest assessment is complete, a
590 simulation of a harvesting event can be implemented with different size limits, cutting
591 intensities, and different species. For community forest management, this will allow
592 communities to maximise returns from harvesting while preserving other forest values.
593 Small-scale, high-value utilisation scenarios can be effectively explored using such
594 models. Utilisation below unsustainable levels, which has been set in the simulator
595 according to species specific growth rates, will ensure that high-end products can be
596 harvested in community areas in perpetuity.

597

598 PNGFA are moving to a new pre-harvest inventory method based on a stratified
599 random variable radius plot inventory. This will replace the 1% strip-line inventory
600 that is both inefficient and biased. Therefore, PNGFA can populate the assessment
601 tool with inventory information and run scenarios for large scale logging using

602 software available at (<http://twoe.org>). The scenarios can help identify mode
603 appropriate and sustainable harvesting in terms of size limits, species mixes and
604 cutting cycles. Currently, a default size limit of 50cm is used on a 35 year cutting
605 cycle. It is intended that the assessment and modelling tools developed as part of
606 ACIAR project FST/2004/061 can help refine this approach for more sustainable
607 forest harvesting.

608

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