

1 **Title:**

2 Reforestation methods influence seedling diversity in tropical forest understoreys

3 Jarrah Wills^{1*}, John Herbohn^{1,2}, Jessie Wells³, Maria Opelia Maranguit Moreno⁴, Angela
4 Ferraren⁴, Jennifer Firm^{2,5}

5 ¹ School of Agriculture and Food Science, University of Queensland (UQ), Brisbane, Qld
6 4072, Australia jarrahwills@hotmail.com (*Corresponding author).

7 ²Tropical Forests and People Research Centre, University of the Sunshine Coast (USC),
8 Maroochydore, Qld 4558, Australia. jherbohn@usc.edu.au

9 ³ Australian Research Council Centre of Excellence for Environmental Decisions, School of
10 Biological Sciences, The University of Queensland (UQ), Brisbane, Qld 4072, Australia.
11 jessie.wells@uqconnect.edu.au

12 ⁴ Department of Soil Science, Visayas State University, Visca, Baybay City, Leyte
13 Philippines 6521

14 ⁵School of Earth, Environmental and Biological Sciences, Queensland University of
15 Technology (QUT), Gardens Point, Brisbane Australia, 4000. jennifer.firm@qut.edu.au

16

17

18

19

20

21

22

23 **Abstract**

24 **1.** Alternative methods for restoring tropical forests influence the ecological processes
25 that shape recruitment of understorey species. In turn, the traits of species recruited
26 will influence the ecological processes the forests provide now and over the long-
27 term.

28 **2.** We assess the phylogenetic and functional structure of seedlings beneath monoculture
29 plantations, mixed-species plantations and regenerating selectively logged native
30 forests, considering traits of specific leaf area (SLA, including within-species
31 variation), leaf nitrogen and phosphorus content, life-form, potential plant height and
32 dispersal type.

33 **3.** Monoculture plantations comprised seedlings that were more closely related than
34 would be expected by chance (i.e., phylogenetically clustered), and regenerating
35 forest contained species more distantly related than would be expected by chance (i.e.,
36 phylogenetically overdispersed). This suggests that seedlings beneath monocultures
37 assemble through environmental filtering and through the dispersal limitation of
38 predictable functional guilds. However, dispersal limitation is frequently overcome by
39 human-assisted dispersal, increasing trait diversity. Comparing SLA values revealed
40 that regenerating forests recruit seedlings with both high and low mean and variation
41 of SLA, leading to higher overall diversity.

42 **4.** Regenerating forest seedlings showed signs of environmental filtering, only based on
43 within-species variation of SLA. Regenerating forest understoreys appear to favour
44 species that show a high intra-specific variation in SLA values (e.g., *Pterocarpus*
45 *indicus* Willd.) and at the same time provided habitat for later-successional seedlings
46 that show a lower intra-specific variation in SLA (e.g., *Canarium luzonicum* (Blume)
47 A.Gray). This trait diversity suggests limiting similarity or competitive exclusion may

48 be reduced because of niche differences, allowing species with different traits to co-
49 exist.

50 **5. *Synthesis and applications.*** Phylogenetic and functionally distinct species are
51 restricted in their regeneration capacity, many of which are of conservation
52 significance (under the IUCN Red List). Reforestation projects should maximise
53 desired ecological services (including conservation value) by actively managing for
54 the recruitment of species that are phylogenetically and functionally (including intra-
55 specifically) distinct. This management aim will increase the probability of fulfilling a
56 wider array of niche spaces and potentially increase the diversity of ecosystem
57 services provided.

58 **Key-words**

59 Degraded tropical forests, emergent tree species, human dominated landscapes, intraspecific
60 variation, mechanistic, phylogenetic comparative ecology, recruitment

61 **Introduction**

62 Understanding how and why some plant species coexist is important when attempting to
63 restore degraded plant communities, particularly in areas once occupied by highly diverse
64 ecosystems, like tropical forests (Funk et al. 2016). Finding the optimal tropical forest
65 restoration strategies is not straightforward, with strategies ranging from the planting of one
66 or just a few species at a site to initiate understorey recruitment of native biodiversity, to
67 diverse ecological restoration plantings and strategies that do not require the planting of any
68 trees (e.g. regenerating secondary forest) (Lamb et al. 2005). In highly modified tropical
69 landscapes, a combination of monocultures and mixed-species plantations, high diversity
70 restoration plantings, and natural regeneration of secondary forests have been found to
71 provide different benefits for biodiversity and ecosystem function (Barlow et al. 2007, Wills

72 et al. 2017). What is not well understood is how the restoration strategy used impacts on the
73 mechanisms that drive understorey plant community assembly. Unpacking the mechanisms
74 acting on the recruitment of plant species in the understories of, for example, monocultures
75 versus more diverse restoration focused strategies may provide a mechanistic underpinning
76 for future attempts at restoring tropical forests (Hector et al. 2011, Cadotte et al. 2017).

77 Environmental filtering and interactions between species are key mechanisms acting on the
78 assembly of plant communities (Silvertown 2004). Environmental conditions, such as
79 rainfall, soil nutrient and light availability, provide conditions that potentially favour the
80 recruitment and survival of some species over others. This essentially selects for species with
81 traits that are suited to the abiotic conditions, which leads to trait similarity. Whereas biotic
82 interactions such as competition can limit how similar traits are between species presumably
83 as species are more likely to be in competition for the same niche space (Grubb 1977). The
84 relative importance of environmental filtering and competitive interactions can potentially be
85 teased apart by measuring the phylogenetic and functional structure of plant communities
86 (Ricklefs 2008, Baraloto et al. 2012).

87 If functional traits are conserved amongst related species or inherited over evolutionary
88 timescales, a community's phylogenetic and functional structure may be found to be either
89 clustered (i.e., community members are more closely related and display a higher similarity
90 in trait values than would be expected by chance alone) or overdispersed (i.e., community
91 members are more distantly related and display a higher dissimilarity than would be expected
92 by chance alone) (Webb 2000, Cavender-Bares et al. 2004, Kraft and Ackerly 2010). Niche
93 theory predicts that the assembly of clustered communities is explained by environmental
94 filtering, as a reflection of species adaptations to their shared environment (Webb et al. 2002,
95 Cornwell et al. 2006, Pausas and Verdú 2010). Overdispersed communities are explained by
96 competitive interactions between species that have similar resource requirements and

97 growing habits, potentially resulting in competitive exclusion and greater niche
98 differentiation (Pausas and Verdú 2010). However, competitive interactions may not simply
99 lead to overdispersion in either traits or phylogenetic structure, because of the opposing
100 effects of niche differences (altering the balance between intra- and inter-specific
101 competition, and tending to stabilise coexistence), versus differences in competitive ability
102 (which could involve a narrow range of trait values and actually lead to clustering), and
103 important functional traits may not be conserved phylogenetically (Mayfield and Levine
104 2010).

105 Phylogenetic approaches have been applied rarely to understanding reforestation methods
106 (but see Hipp et al. (2015), Verdú et al. (2012), Schweizer et al. (2015) and Schweizer et al.
107 (2014)) and studies of reforestation have focused more on positive biotic interactions, such as
108 facilitation that can initiate successional development (Shoener et al. 2015). Valiente-Banuet
109 and Verdú (2007) found that regeneration niches are conserved across evolutionary time.
110 They argue that positive interactions (i.e., facilitation) occur between phylogenetically distant
111 species and that facilitation can lead to phylogenetic overdispersion. Increased seedling
112 phylogenetic diversity can also have a positive influence on survival, via phylogenetically-
113 correlated pathogen susceptibilities, which can lead to density-dependent selection (Webb et
114 al. 2006). As further evidence of the importance of phylogenetic diversity, in a
115 comprehensive meta-analysis co-occurring plant species from the same life-form were more
116 likely to survive if they were distantly related (Verdú et al. 2012).

117 In this study, we measure the phylogenetic and functional diversity of seedling recruitment
118 beneath different reforestation methods across a degraded tropical forest landscape on the
119 Island of Leyte in the Philippines. The reforestation methods we compare ranged from low-to
120 high-diversity forests, in the form of monoculture plantations of the exotic species *Swietenia*
121 *macrophylla* King, mixed-species plantations and regenerating selectively logged native

122 forests. We analysed both phylogenetic and functional traits, including intraspecific
123 variability in specific leaf area (SLA). We specifically address the following three questions:

- 124 1. What is the phylogenetic and functional trait structure (SLA, leaf nutrients, life-form,
125 potential plant height and dispersal type) of seedling communities beneath different
126 reforestation types?
- 127 2. What is the intraspecific variation of SLA observed in the different forest types, and
128 between species and groups that are common or obligate across forest types?
- 129 3. What do the phylogenetic structure, functional trait structure and intraspecific
130 variation in SLA tell us about how seedling communities assemble in the understories
131 of these different forest types?

132 We expected to find a shift in the main assembly patterns between seedling communities
133 beneath the different reforestation methods, from environmental filtering under monoculture
134 forests (where species colonisation is limited by dispersal and abiotic conditions) to
135 competitive exclusion within regenerating selectively logged forest, which are more diverse
136 in terms of species and microclimates. We also expected to find that seedlings beneath
137 regenerating selectively logged forests and mixed-species plantations will show greater
138 intraspecific variation in SLA because of the greater environmental and biotic variation in
139 these forests (e.g., in light levels, topography and leaf litter composition) and potentially
140 reflecting genetic variation.

141 **Materials and methods**

142 **Study sites and Data Collection**

143 The study was undertaken on the Island of Leyte in the Philippines (between 124°17' and
144 125°18' east longitude, and between 9°55' and 11°48' north latitude). Leyte has an average

145 annual rainfall of 2753 mm and an average annual temperature of 27.5 °C. All plants below 2
146 m in height were sampled within a total of 35 circular plots (individual plot area = 78 m²) that
147 were spread across 15 sites. Most sites had between 2-3 plots, except for one (Table S1).
148 These sites included five mahogany (*Swietenia macrophylla* King) monoculture plantations,
149 five mixed-species plantations (known locally and hereafter as ‘Rainforestation’) and five
150 regenerating selectively logged native forests. On the island of Leyte and in the Philippines in
151 general it is challenging to find primary forest sites and therefore the regenerating selectively
152 logged native forests were chosen for this study as the best examples available of more intact
153 natural forests. Sites occurred at elevations of less than 600 m a.s.l. and, with one exception,
154 had soils of volcanic origin, and were previously located within the same vegetation type.
155 Plantations were between 13 and 18 years of age at the time of sampling. Regenerating
156 selectively logged native forest sites had higher average slope angles and elevations than
157 plantations, were logged relatively recently (~20 years) and, at the time of sampling, were
158 frequently used by nearby communities for the harvesting of non-timber forest products
159 (NTFPs). At each of the plantation locations the distances to potential seed sources, as the
160 regenerating selectively logged native forests, were measured using google earth imagery and
161 verified in the field. Plantations were located at similar distances from potential seed sources
162 (Appendix S1: Table S1 and Fig. S1) (Nguyen et al. 2016, Wills et al. 2017).

163 Plant identification was verified with several local experts at Visayas State University, Leyte
164 Island. A CID Bio-Science CI-110 Plant Canopy Imager was used to measure Leaf Area
165 Index (LAI) and the average of three readings per plot measured at 1.3m above ground level
166 were used in the analysis; where higher values represent more closed canopies.

167 **Functional traits**

168 Three continuous traits were measured: SLA (cm^2/g), leaf nitrogen concentration (hereafter,
169 LNC, % dry leaf mass) and leaf phosphorus concentration (hereafter, LPC, % dry leaf mass),
170 generally following the protocols set out by Pérez-Harguindeguy et al. (2013). We collected a
171 minimum of two leaves per seedling for all tree and shrub species recorded in the plots. The
172 youngest mature fully expanded leaves were collected, but leaf traits were not collected if it
173 were judged to be detrimental to the individual's survival because of only a few leaves being
174 available. Collected leaves were placed into a paper bag, labelled and scanned using a CID
175 Bio-Science CI-203 Laser Area Meter. Leaf area scanning was conducted either onsite or in
176 the afternoon of the same day. Leaf samples were oven dried at 65 °C for 48 hours and
177 weighed to calculate SLA. To determine LNC and LPC (see Appendix S1: Section S1 for soil
178 N and P methods), samples were prepared with a single digestion method and analysed with a
179 colorimetric determination of LNC using the salicylate-hypochlorite method developed by
180 Baethgen and Alley (1989) and LPC using an adaptation of Murphy and Riley (1962) single
181 solution method (Anderson and Ingram 1989).

182 SLA was sampled for 856 individual plants, representing 91 identified species from a
183 sampled total of 2899 individuals from 219 species. LNC and LPC were analysed on a subset
184 of the species used for the calculation of SLA, which included 127 individual plants
185 representing 53 species. For intraspecific variation of SLA, initially all species with more
186 than one SLA measurement were used, and a minimum of five individuals per species are
187 presented within the results, limiting the number of species that were analysed to 39.

188 Data on three categorical traits, which were scored on an ordinal scale were extracted from
189 open databases and primary literature for a total of 123 species; dispersal type (abiotic or
190 biotic), potential plant height was coded with 4 levels (**1** = understory "0 m-5 m", **2** = mid-
191 canopy "6 m-15 m", **3** = canopy "16 m-30 m", **4** = emergent "30 m +"), and life-form was
192 also coded with 5 levels (**1** = herb, **2** = vine/liana, **3** = palm, **4** = shrub, **5** = tree). The species

193 were comprised of 13 herbaceous species, one palm species, 13 shrub species, 93 trees
194 species and 3 vine/liana species.

195 **Community phylogeny**

196 The regional species pool can have significant influences on the local phylogenetic structure
197 (Lessard et al. 2012), statistical inferences and subsequent conclusions regarding community
198 assembly processes (Pigot and Etienne 2015). Therefore, we contextualize the present study
199 within broader evolutionary temporal and spatial scales. The Philippine flora, in particular the
200 Mindanao-Eastern Visayas tropical forest (that includes the island of Leyte) has a dominant
201 affiliation with the Asia/Malesia floristic province, but also includes Gondwanan relicts such
202 as the southern gymnosperms (e.g. *Podocarpus rumphii* Blume and *Agathis philippinensis*
203 Warb) (Langenberger et al. 2006, Sniderman and Jordan 2011). These Gondwanan lineages
204 have extremely long divergence times relative to all other lineages.

205 The community phylogeny was constructed using a regional species pool consisting of all
206 125 seed-plant species recorded in the understorey of all forest types. (Five non-seed plants
207 were excluded due to their extremely early divergence relative to all other species, which
208 would have eclipsed the phylogenetic distances among seed plants). The 125 seed plants
209 consisted of 124 angiosperms and one gymnosperm (*Agathis philippinensis*). This
210 gymnosperm was included in traits analyses, but excluded from phylogenetic diversity
211 analysis due to its long phylogenetic distance compared to other species (Cavender-Bares et
212 al. 2006, Cadotte 2014). Of the total 125 species used (124 angiosperms for phylogenetic
213 diversity), 95 were native and 30 were classified as recently introduced. The phylogenetic
214 structure was analysed using three taxonomic subsets: (1) all angiosperm species (i.e.,
215 excluding the gymnosperm), (2) all angiosperm species excluding recently introduced
216 species, and (3) all angiosperm species excluding monocot species (i.e., tree, shrub and

217 herbaceous species). Chronograms are approximate or ‘pseudo’ chronograms because single
218 fixed points were assigned for ‘known’ ages, and all other divergences were assumed to be
219 evenly distributed between them (see Appendix S1: Section S1). These subsets were used to
220 decipher their influence on the phylogenetic structure of the different seedling communities
221 (Appendix S1: Table S1).

222 For a detailed description of the methods used to age the phylogenetic tree refer to the
223 community phylogeny section within Appendix S1: Section S1.

224 **Data analysis**

225 Analyses were conducted using R statistical computing version 3.1.1 (R Core Team 2013)
226 and Phylomatic command Version 3 (Webb et al. 2008).

227 Phylogenetic structure was quantified using phylogenetic diversity (PD), mean pairwise
228 phylogenetic distance (MPD) and mean nearest taxon phylogenetic distance (MNTD) for
229 both incidence- and abundance- based methods (Webb et al. 2002). The patterns of
230 phylogenetic structure between forest types were analysed using nodesigl command from
231 Phylocom 4.2 (Appendix S1: Section S1) (Webb et al. 2008). The functional structure was
232 quantified using the same metrics as the phylogenetic structure; mean pairwise functional
233 traits distance (MFD) and mean nearest functional traits distance (MNFD) (Li et al. 2015).
234 Trait distances were constructed using a Euclidian distance matrix for continuous traits both
235 individually and together. For categorical traits (that included missing data) a Gower distance
236 matrix was constructed within the FD package in R (Gower 1971, Laliberté and Legendre
237 2010, Laliberté 2014). To test for differences in the seedling phylogenetic and functional
238 structure beneath different forest types, taking into consideration unequal sample sizes and
239 species richness, we compared analyses to a null model that randomized the species identity
240 at the plot level with species drawn from the regional species pool, using 1000 null iterations.

241 To do this, we created standard effect sizes (SES) in the picante R package (Kembel et al.
242 2010). Traits were analysed both in isolation and including all traits, and when limited to
243 native species.

244 We used linear mixed effect models (LMEMs), estimated using maximum likelihood, to
245 compare the phylogenetic and functional structure between forest types and how this varied
246 depending on the abiotic conditions (e.g. soil phosphorus, soil nitrogen and LAI). To account
247 for our sampling design, random effects were structured as plots nested within sites. The R
248 package nLME was used to fit all LMEMs and because the experimental design is largely
249 balanced, Wald F-statistics were used to assess the significance of the fixed effects (Pinheiro
250 et al. 2016). The effects package (Fox 2016) from R was used to display the higher-order
251 fixed effects.

252 For more details on how we identified patterns of phylogenetic structure between forest
253 types, how we tested relationships between traits (SLA, LNC and LPC) taking into
254 consideration phylogenetic covariance and how we tested for phylogenetic signal of both
255 continuous and discrete traits see Appendix S1: Section S1.

256 **Results**

257 **What is the phylogenetic and functional trait structure of seedling communities beneath** 258 **the different forest types?**

259 Phylogenetic diversity

260 Overall, seedling communities were phylogenetically overdispersed within regenerating
261 selectively logged forests and clustered within monoculture forest types (Fig. 1 and 2).
262 However, this pattern could not be differentiated in some cases from random assembly
263 processes. In general this pattern was robust to different null models, species pools (e.g. all

264 species, natives, trees and shrubs) and pseudo-chronograms, i.e., one pseudo-chronogram
265 based solely on Wikström et al. (2001) ages and one incorporating Bayesian estimates
266 (Appendix S1: Table S1).

267 Observed PD was higher within the regenerating selectively logged forest sites ($F_{2,12} = 9.0$, P
268 $= 0.03$) and differed depending on soil nitrogen ($F_{1,17} = 5.51$, $P = 0.031$). PD between forest
269 types also differed from the null model expectations when all species were included in the
270 models ($F_{2,12} = 4.6$, $P > 0.033$), and varied depending on soil phosphorus ($F_{1,17} = 4.9$, $P =$
271 0.041) (Fig. 1). The PD of tree and shrub species differed from null expectations between
272 forest types ($F_{2,12} = 9.26$, $P > 0.004$) and LAI ($F_{1,17} = 6.62$, $P = 0.02$). The abundance-
273 weighted and non-weighted MPD and weighted MNTD did not differ from the null model
274 expectations between forest types, soil nitrogen, soil phosphorus or LAI (Appendix S1: Table
275 S2), using the entire species pool (i.e. including exotics and natives, and all growth forms).
276 The non-weighted MNTD for all species, and when restricted to trees and shrubs, and
277 natives, differed from the null model expectations (all species: $F_{2,12} = 3.95$, $P = 0.048$, tree
278 and shrub: $F_{2,12} = 9.74$, $P = 0.003$ and natives: $F_{2,12} = 6.56$, $P = 0.012$), with regenerating
279 selectively logged forest seedlings being overdispersed and monoculture and Rainforestation
280 plantations being more similar and clustered (Fig. 2).

281 Associations between phylogenetic groups and forest types

282 Using the *nodesigl* function from Phylocom 4.2, the family Meliaceae (*Swietenia*
283 *macrophylla*, *Sandoricum koetjape* (Burm.f.) Merr., *Lansium domesticum* Correa and
284 *Dysoxylum gaudichaudianum* (A.Juss.) Miq. contributed significantly more taxa to seedling
285 communities beneath the monoculture forest types than by chance. The family Moraceae
286 (*Ficus septica* Burm.f., *F. pseudopalma* Blanco, *F. nota* (Blanco) Merr., *Artocarpus*
287 *odoratissimus* Blanco and *A. blancoi* (Elmer) Merr.) also contributed more taxa than by

288 chance within monoculture forest types, when restricting the analysis to native species. There
289 was also an overabundance of seedlings from the genus *Ficus* (that included seven species)
290 within regenerating selectively logged forests.

291 Functional diversity

292 Generally, functional diversity showed weaker trends across forest types, compared to
293 phylogenetic diversity and did not differ from the null model expectations, except in the case
294 of the mean SLA values per plot ($F_{2, 12} = 9.0, P = 0.004$) (Appendix S1: Table S3). Using
295 SLA, abundance-weighted and non-weighted MFD displayed overdispersion for regenerating
296 selectively logged forests, while monoculture and Rainforestation sites were similar and
297 clustered (Fig. 2). However, this trend was not evident using MNFD of SLA seedling values.
298 Using seedling LNC, abundance-weighted and non-weighted MFD, and MNFD displayed a
299 similar trend to SLA. Abundance-weighted and non-weighted MFD and MNFD of seedling
300 SLA, LPC and LNC displayed random patterns, where forest types had similar SES values.
301 The non-weighted MNFD for SLA and LNC varied depending on soil nitrogen (SLA: $F_{1, 17} =$
302 $4.7, P = 0.044$ and LNC: $F_{1, 17} = 6.47, P = 0.021$). Overall, understory leaf traits suggest
303 weaker trends to phylogenetic structure, with some evidence of overdispersion under the
304 regenerating selectively logged forest and clustering within monoculture forest seedling
305 communities. However, this relationship was weak, and could not be statistically
306 differentiated from random patterns.

307 In contrast, analysis of the functional structure incorporating categorical traits of potential
308 plant height, dispersal type and life-form suggests a reverse in the patterns generally found
309 using phylogenies and to a lesser extent leaf traits. The weighted SES.MFD using all traits
310 tended towards overdispersion within monoculture forests and random to clustering within
311 the Rainforestation and regenerating selectively logged forests (Fig. 3a). When restricting the

312 analysis to native species, the Rainforestation forest type switched from random to
313 overdispersed (Fig. 3b). Within the monoculture forests, weighting by species' relative
314 abundances using the MFD and MNFD of all traits resulted in an increase towards
315 overdispersion compared to the null model.

316 Phylogenetic and functional trait relationships

317 Considering phylogenetic covariance, the tallest trees and native species were significantly
318 more likely to be wind-dispersed (trees: $z = 2.98$, $P = 0.003$ and natives: $z = 2.289$, $P = 0.02$).
319 However, this trend was not detected when using the entire species pool (all species: $z =$
320 0.958 , $p = 0.34$). SLA had a positive relationship with LNC after accounting for phylogenetic
321 covariance ($F_{1, 51} = 24.47$, $P = < 0.0001$). SLA and LPC were not significantly correlated after
322 accounting for phylogenetic covariance ($F_{1, 51} = 0.5$, $P = 0.48$).

323 LPC and LNC exhibited significant phylogenetic signals compared to a Brownian motion
324 model of evolution ($P < 0.05$), with LPC showing higher K values ($K = 0.528$) than both
325 LNC ($K = 0.419$) and SLA ($K = 0.285$, non-significant). Due to the high number of replicates
326 for SLA, we analysed phylogenetic signal considering sampling error and/or intraspecific
327 variation, and this increased the K value for SLA considerably ($K = 0.436$). Significant
328 phylogenetic signals ($P < 0.05$) were also found for life-form, dispersal type and potential
329 plant height (Appendix S1: Table S4).

330 **SLA mean and variation beneath the different forest types and between common or** 331 **obligate clades**

332 Average seedling SLA values at the plot level were significantly higher in the monoculture
333 forest type than in the regenerating selectively logged forests, while the Rainforestation forest
334 types were intermediate ($F_{2, 12} = 10.3$, $P = 0.003$). The weighted community mean SLA

335 values showed a similar trend; however, evidence of this relationship was not significant ($F_{2, 12} = 1.02, P = 0.4$). The plot level CV was significantly higher within regenerating selectively
336 logged forests than monoculture forests and the Rainforestation forest type was again
337 intermediate ($F_{2, 12} = 6.59, P = 0.012$) (Fig. 4a).

339 Taking into account differences in species richness and only using species with adequate
340 replication (≥ 5 individuals per species) for SLA measurements; we found regenerating
341 selectively logged forests included species with both high and low intraspecific variation in
342 SLA (e.g., higher variation in SLA: *Pterocarpus indicus* Willd, *Koordersiodendron pinnatum*
343 Merr. and *Neolitsea vidalii* Merr, lower variation in SLA: *Canarium luzonicum* (Blume)
344 A.Gray, *Diplodiscus paniculatus* Turcz, *Ficus baletae* and *Shorea contorta* S.Vidal)
345 (Appendix S1: Fig. S2 and S3). This resulted in a significant overdispersion of CV in the
346 weighted SESMNF ($F_{2, 12} = 15.32, P = <0.001$) and SESMFD ($F_{2, 12} = 14.91, P = <0.007$)
347 (Fig. 4b and c), and non-weighted SESMNF ($F_{2, 12} = 5.99, P = 0.016$) and SESMFD ($F_{2, 12} =$
348 $5.82, P = 0.017$) within regenerating selectively logged forest seedling communities, and
349 clustering within the monoculture and Rainforestation forest types. Weighted SESMNF and
350 SESMFD also varied depending on soil nitrogen (Appendix S1: Table S5).

351 The Moraceae family was common across forest types and generally showed higher than
352 average CV values for SLA (~18 to ~34). The monoculture grown species *Swietenia*
353 *macrophylla* showed a relatively lower than average CV in SLA (~16). Species within the
354 family Dipterocarpaceae that were absent within the monoculture forests showed a relatively
355 low CV in SLA (~14-16). Wind-dispersed species had representatives that showed both a
356 higher variation in SLA (e.g. *Pterocarpus indicus*) and a lower variation in SLA (e.g.
357 Dipterocarpaceae species) (Table 1 and Appendix S1: Table S5).

358 Discussion

359 Overall, we found that seedling communities beneath mahogany monocultures were likely
360 recruited because of environmental filtering as these seedling communities were found to be
361 more closely related than by chance. In contrast, seedling communities within regenerating
362 selectively logged forest, this studies more “natural” baseline communities, showed evidence
363 of competitive processes explaining their compositional make-up as these seedling
364 communities were more distantly related than would be expected by chance. Further analyses
365 that also considered intraspecific variation in SLA, found that the assembly of seedling
366 communities beneath regenerating selectively logged forests was likely explained by both
367 environmental filtering and competitive interactions (see Fig. 5 for a summary conceptual
368 diagram of community assembly processes).

369 As expected, the more structurally complex and diverse regenerating selectively logged
370 forests likely showed a greater fulfilment of niche space within seedling communities when
371 compared to monocultures. The Rainforestation forests showed intermediate fulfilment of
372 niche space between the other forest types, suggesting that more diverse plantations may not
373 necessarily in the short-term capture true differences in species effects on ecosystem
374 functions (Lamb et al. 2005). Within the regenerating selectively logged forests there is a
375 greater occurrence of more phylogenetically- and functionally- divergent seedling species,
376 and these species show both high and low abilities to adjust their SLA values.

377 These results highlight the need for incorporating greater phylogenetic and functional
378 diversity in reforestation projects, which may not equate to increasing pure species numbers,
379 but also provides for surrogate measures of differences in how species potentially influence
380 ecosystem function. This could result in reforestation interventions that lead to a greater niche
381 fulfilment by seedling communities regenerating under planted forests, and therefore more
382 functionally rich future forests that can better adapt to future environmental conditions and
383 provide a different range of ecosystem services. To do this, we recommend the promotion of

384 phylogenetically and functionally broader ranges of seed or seedling stocks in reforestation
385 schemes across degraded tropical landscapes. In particular, efforts should be made to include
386 native emergent, wind-dispersed tree species (Wills et al. 2017), species from other limited
387 functional groups (e.g., large-seeded species), and species with a broader range of mean SLA
388 values and levels of intraspecific variation in SLA.

389 Reforestation sites, although planted with a much higher number of species than
390 monocultures, were generally not statistically different phylogenetically or functionally from
391 the other forest types and from random assembly processes. These results partly support our
392 initial predictions that community assembly in monoculture seedling communities is more
393 strongly influenced by environmental filtering and dispersal limitation. Regenerating
394 selectively logged forest, which had higher-diversity and more complex canopies and
395 understorey's that have assembled for considerably longer time periods, showed evidence of
396 more phylogenetically and functionally diverse seedling communities, likely indicating
397 stronger competitive interactions. Lower stem densities within the monoculture forest type
398 compared to the regenerating selectively logged forest likely reduced the competitive
399 interactions between monoculture seedling communities, irrespective of phylogenetic or
400 functional relatedness.

401 When we considered potential plant height, life-form and dispersal type, Reforestation and
402 regenerating selectively logged forest seedling communities could not be differentiated from
403 random, which means these traits are less variable in the higher diversity forest types
404 compared to a random subset of the species pool. Unexpectedly monocultures displayed
405 higher overdispersion when considering these same traits. Examining the identity of the
406 seedling species found in the monoculture, this finding is likely explained by the introduction
407 of functionally distinct species that are readily eaten and dispersed by local people or weed
408 species that are favoured by disturbance, such as wind-dispersed herbs and shrubs; *Crotalaria*

409 *spp.*, *Chromolaena odorata* (L.) R.M.King & H.Rob. (Siam weed), *Sphagneticola trilobata*
410 (L.) Pruski (Singapore daisy), and smaller stature trees; *Theobroma cacao* L. (cacao),
411 *Psidium guajava* L. (guava).

412 When restricting the analysis to native species or just tree species, taking phylogenetic
413 covariance into consideration, we found that wind-dispersed tree species displayed the tallest
414 potential heights. This result is consistent with a previous study on the same forest types,
415 where we found that native wind-dispersed tree species are limited across the studied forest
416 types and are the tallest trees at maturity, further supporting their occurrence as important
417 emergent tree species within tropical forests (Wills et al. 2017). It is clear from both studies
418 that wind-dispersed tree species are recruitment-limited within these monoculture forests and
419 have narrowed the range of traits available within these communities.

420 We expected the regenerating selectively logged forest seedling communities to show a
421 higher within species variation in SLA, due to more complex canopy structures and therefore
422 understory species being exposed to varied environmental and biotic conditions. This was
423 supported with the regenerating selectively logged forest seedlings comprising species with a
424 high SLA variation (e.g., *Pterocarpus indicus*, *Neolitsea vidalii* and *Palaquium foxworthyi*
425 Merr.), but also species with a lower variation in SLA (e.g., *Canarium luzonicum*,
426 *Diplodiscus paniculatus*, *Ficus baletae* and *Shorea contorta*). These results extend our initial
427 predictions, indicating that both environmental filtering and competitive exclusion may be
428 operating within regenerating selectively logged forest seedling communities; whereas within
429 monoculture seedling communities, environmental filtering and dispersal limitation are likely
430 more prominent, but human-assisted recruitment appears to overcome this filtering in some
431 cases (Fig. 5).

432 **Phylogenetic and functional structure beneath forest types**

433 The mechanism behind the overdispersion in categorical traits (potential plant height, life-
434 form and dispersal type) within monoculture seedling communities is driven by the
435 introduction of functionally distinct exotic species, both directly (via human-dispersal of
436 seeds) and indirectly (invasion of species/traits due to habitat modification and vacant niche
437 space). The understories within the monoculture forest type contained related species that
438 possess traits that enable them to overcome dispersal limitations. For example, the family
439 Moraceae typically have very small seeds and are dispersed by habitat-generalist bird species.
440 This role for dispersal limitation has been illustrated across the tropics (Corlett 2006). Our
441 results revealed that the family Meliaceae also exhibited an overabundance within the
442 monoculture forest type, likely from human-assisted dispersal of edible species with a large
443 fruit size (e.g. *Sandoricum koetjape* and *Lansium domesticum*). Primates are known to be
444 important dispersal agents in tropical forests and are responsible for the dispersal of many
445 large-fruited species' (Chapman 1989). Here, we find that humans are also key dispersal
446 agents for functionally distinct exotic species due to the close physical relationship these
447 small-scale community-managed forests have with local people.

448 Assessing the value of seedling biodiversity beneath monoculture forest types depends
449 largely on the desires of landholders and the relative importance of conservation and socio-
450 economic values. Non-native understorey species contribute to ecosystem function and
451 subsequent services. However, if dominated by few species these understoreys may lack the
452 ecological complexity and ecosystem services associated with increased leaf trait and
453 phylogenetic diversity (e.g., ecosystem resilience to invasion and to a changing climate).

454 **Intraspecific variation in SLA**

455 It is now widely recognised that there is a large amount of intraspecific variation in key plant
456 functional traits including SLA (Cavender-Bares et al. 2006, Swenson and Enquist 2009,

457 Messier et al. 2010), and that this variation can have implications for coexistence and
458 improvements in detecting underlying community assembly processes (Ashton et al. 2010,
459 Jung et al. 2010, Burns and Strauss 2012). Our results suggest that incorporating information
460 on intraspecific variation in SLA can extend our understanding of seedling community
461 assembly. Our findings showed that regenerating selectively logged forests recruit species
462 with both high and low variation in SLA. Therefore, these forests appear to provide habitat
463 for later successional species with conservative leaf economies and low variation in SLA
464 (Walters and Reich 1999), as well as, species that have higher variation in SLA, due to
465 genetic diversity or environmental acclimation.

466 Previous studies have found variation in SLA is due to both abiotic conditions (e.g., soil and
467 light) and competitive interactions (Bloor and Grubb 2004, Burns and Strauss 2012). Our
468 results support these findings, and with this relationship likely explained by the more varied
469 abiotic and biotic conditions found in the understory of regenerating selectively logged
470 forests compared to the other forest types.

471 Species in the Moraceae family, and particularly the genus *Ficus*, were abundant across all of
472 the studied forest types. Members of the Moraceae family, and particularly the genus *Ficus*
473 showed a larger than average variation in SLA, in all forest types. Native wind-dispersed
474 species, which are limited in their recruitment ability across the studied forest types (Wills et
475 al. 2017), show both relatively high and low variation in SLA. The leguminous wind-
476 dispersed species *Pterocarpus indicus* showed a very high SLA variation. In contrast, other
477 wind-dispersed native species including species within the family Dipterocarpaceae all
478 showed relatively below-average species-specific mean SLA and variation in SLA. This
479 likely reflects their later successional status and a more conservative resource acquisition
480 strategy on the leaf economic spectrum (Walters and Reich 1999, Wright et al. 2004).

481 **Conclusion**

482 Analysing the phylogenetic and functional diversity beneath different reforestation methods
483 and comparing these to relatively more intact native forests has identified evolutionary
484 lineages and functional groups that are restricted in their regeneration capacity and will
485 influence future ecosystem functioning across the Island of Leyte. These include several
486 species listed under The International Union for Conservation of Nature Red List of
487 Threatened Species, including the Vulnerable *Canarium luzonicum*, *Pterocarpus indicus*,
488 *Agathis philippinensis*, and *Neolitsea vidalii*, and the Critically Endangered *Hopea plagata*,
489 *S.Vidal* and *Shorea contorta*. Our findings provide direct evidence that the design of forest
490 plantations should consider species diversity, functional diversity and phylogenetic- distance
491 but in the short-term even plantations with highly diverse overstories may lack key functional
492 and phylogenetic groups found in remnant native forests, particularly in tropical rainforests
493 ecosystems.

494 **Acknowledgments**

495 We would like to thank staff and students at Visayas State University for their knowledge,
496 and expertise. This project was conducted as part of an ACIAR Project ASEM/2010/050;
497 Improving watershed rehabilitation outcomes in the Philippines using a systems approach.

498 **Declarations**

499 JW and JF designed the study; JW performed the research, analysed and wrote the
500 manuscript; JF and JWells contributed to the analysis and writing; JH contributed to the
501 writing and provided logistical support and knowledge of Philippine forests. MOMM and AF
502 contributed to the data collection and provided expert knowledge of Philippine forests.

503 **Data Accessibility**

504 Reforestation methods influence seedling diversity in tropical forest understoreys. *DataDryad*

505 **Reference List**

506 Anderson, S. E., and J. S. I. Ingram. 1989. *Tropical Soil Biology and Fertility: A handbook of*
507 *Methods*. p. 171. C.A.B. International, Aberystwyth.

508 Ashton, I. W., A. E. Miller, W. D. Bowman, and K. N. Suding. 2010. Niche complementarity
509 due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology*
510 **91**:3252-3260.

511 Baethgen, W. E., and M. M. Alley. 1989. A manual colorimetric procedure for measuring
512 ammonium nitrogen in soil and plant Kjeldahl digests. *Communications in Soil*
513 *Science and Plant Analysis* **20**:961-969.

514 Baraloto, C., O. J. Hardy, C. E. T. Paine, K. G. Dexter, C. Cruaud, L. T. Dunning, M.-A.
515 Gonzalez, J.-F. Molino, D. Sabatier, V. Savolainen, and J. Chave. 2012. Using
516 functional traits and phylogenetic trees to examine the assembly of tropical tree
517 communities. *Journal of Ecology* **100**:690-701.

518 Barlow, J., T. A. Gardner, I. S. Araujo, T. C. Ávila-Pires, A. B. Bonaldo, J. E. Costa, M. C.
519 Esposito, L. V. Ferreira, J. Hawes, M. I. M. Hernandez, M. S. Hoogmoed, R. N. Leite,
520 N. F. Lo-Man-Hung, J. R. Malcolm, M. B. Martins, L. A. M. Mestre, R. Miranda-
521 Santos, A. L. Nunes-Gutjahr, W. L. Overal, L. Parry, S. L. Peters, M. A. Ribeiro-
522 Junior, M. N. F. da Silva, C. da Silva Motta, and C. A. Peres. 2007. Quantifying the
523 biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings*
524 *of the National Academy of Sciences* **104**:18555-18560.

525 Bloor, J. M. G., and P. J. Grubb. 2004. Morphological Plasticity of Shade-Tolerant Tropical
526 Rainforest Tree Seedlings Exposed to Light Changes. *Functional Ecology* **18**:337-
527 348.

- 528 Burns, J. H., and S. Y. Strauss. 2012. Effects of competition on phylogenetic signal and
529 phenotypic plasticity in plant functional traits. *Ecology* **93**:S126-S137.
- 530 Cadotte, M. W. 2014. Including distantly related taxa can bias phylogenetic tests.
531 *Proceedings of the National Academy of Sciences* **111**:E536.
- 532 Cadotte, M. W., J. Barlow, M. A. Nuñez, N. Pettorelli, and P. A. Stephens. 2017. Solving
533 environmental problems in the Anthropocene: the need to bring novel theoretical
534 advances into the applied ecology fold. *Journal of Applied Ecology* **54**:1-6.
- 535 Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic
536 Overdispersion in Floridian Oak Communities. *The American Naturalist* **163**:823-
537 843.
- 538 Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic Structure of Floridian Plant
539 Communities Depends on Taxonomic and Spatial Scale. *Ecology* **87**:S109-S122.
- 540 Chapman, C. A. 1989. Primate Seed Dispersal: The Fate of Dispersed Seeds. *Biotropica*
541 **21**:148-154.
- 542 Corlett, R. T. 2006. Figs (*Ficus*, Moraceae) in Urban Hong Kong, South China. *Biotropica*
543 **38**:116-121.
- 544 Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. A Trait-Based Test for Habitat
545 Filtering: Convex Hull Volume. *Ecology* **87**:1465-1471.
- 546 Fox, J. 2016. Effect Displays for Linear, Generalized Linear, and Other Models. .
547 <http://www.r-project.org>, <http://socserv.socsci.mcmaster.ca/jfox/>.
- 548 Funk, J. L., J. E. Larson, G. M. Ames, B. J. Butterfield, J. Cavender-Bares, J. Firn, D. C.
549 Laughlin, A. E. Sutton-Grier, L. Williams, and J. Wright. 2016. Revisiting the Holy
550 Grail: using plant functional traits to understand ecological processes. *Biological*
551 *Reviews* **92**:1156-1173.

- 552 Gower, J. C. 1971. A General Coefficient of Similarity and Some of Its Properties.
553 *Biometrics* **27**:857-871.
- 554 Grubb, P. J. 1977. The Maintenance of Species-richness in Plant Communities: the
555 importance of the Regeneration Niche. *Biological Reviews* **52**:107-145.
- 556 Hector, A., C. Philipson, P. Saner, J. Chamagne, D. Dzulkipli, M. O'Brien, J. L. Snaddon, P.
557 Ulok, M. Weilenmann, G. Reynolds, and H. C. J. Godfray. 2011. The Sabah
558 Biodiversity Experiment: a long-term test of the role of tree diversity in restoring
559 tropical forest structure and functioning. *Philosophical Transactions of the Royal
560 Society B: Biological Sciences* **366**:3303-3315.
- 561 Hipp, A. L., D. J. Larkin, R. S. Barak, M. L. Bowles, M. W. Cadotte, S. K. Jacobi, E.
562 Lonsdorf, B. C. Scharenbroch, E. Williams, and E. Weiher. 2015. Phylogeny in the
563 Service of Ecological Restoration. *American Journal of Botany* **102**:647-648.
- 564 Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography* Princeton
565 University Press Princeton, NJ.
- 566 Jung, V., C. Violle, C. Mondy, L. Hoffmann, and S. Muller. 2010. Intraspecific variability
567 and trait-based community assembly. *Journal of Ecology* **98**:1134-1140.
- 568 Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S.
569 P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and
570 ecology. *Bioinformatics* **26**:1463-1464.
- 571 Kraft, N. J. B., and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of
572 community assembly across spatial scales in an Amazonian forest. *Ecological
573 Monographs* **80**:401-422.
- 574 Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional
575 diversity from multiple traits. *Ecology* **91**:299-305.

- 576 Laliberté, E., Legendre, P., and Shipley, B. 2014. FD: measuring functional diversity from
577 multiple traits, and other tools for functional ecology. R package version 1.0-12.
- 578 Lamb, D., P. D. Erskine, and J. A. Parrotta. 2005. Restoration of Degraded Tropical Forest
579 Landscapes. *Science* **310**:1628-1632.
- 580 Langenberger, G., K. Martin, and J. Sauerborn. 2006. Vascular Plant Species Inventory of a
581 Philippine Lowland Rain Forest and its Conservation Value. *Biodiversity &*
582 *Conservation* **15**:1271-1301.
- 583 Lessard, J.-P., J. Belmaker, J. A. Myers, J. M. Chase, and C. Rahbek. 2012. Inferring local
584 ecological processes amid species pool influences. *Trends in Ecology & Evolution*
585 **27**:600-607.
- 586 Li, S.-p., M. W. Cadotte, S. J. Meiners, Z.-s. Hua, L. Jiang, and W.-s. Shu. 2015. Species
587 colonisation, not competitive exclusion, drives community overdispersion over long-
588 term succession. *Ecology Letters* **18**:964-973.
- 589 Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the
590 phylogenetic structure of communities. *Ecology Letters* **13**:1085-1093.
- 591 Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological
592 scales? A case for trait-based ecology. *Ecology Letters* **13**:838-848.
- 593 Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of
594 phosphate in natural waters. *Analytica Chimica Acta* **27**:31-36.
- 595 Nguyen, H., J. Vanclay, J. Herbohn, and J. Firn. 2016. Drivers of Tree Growth, Mortality and
596 Harvest Preferences in Species-Rich Plantations for Smallholders and Communities in
597 the Tropics. *PLoS One* **11**:e0164957.
- 598 Pausas, J. G., and M. Verdú. 2010. The Jungle of Methods for Evaluating Phenotypic and
599 Phylogenetic Structure of Communities. *BioScience* **60**:614-625.

- 600 Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S.
601 Bret-Harte, W. K. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas,
602 P. B. Reich, L. Poorter, I. J. Wright, P. Ray, L. Enrico, J. G. Pausas, A. C. de Vos, N.
603 Buchmann, G. Funes, F. Quétier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter
604 Steege, M. G. A. van der Heijden, L. Sack, B. Blonder, P. Poschlod, M. V. Vaieretti,
605 G. Conti, A. C. Staver, S. Aquino, and J. H. C. Cornelissen. 2013. New handbook for
606 standardised measurement of plant functional traits worldwide. *Australian Journal of*
607 *Botany* **61**:167-234.
- 608 Pigot, A. L., and R. S. Etienne. 2015. A new dynamic null model for phylogenetic
609 community structure. *Ecology Letters* **18**:153-163.
- 610 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. Team. 2016. nlme: Linear and
611 Nonlinear Mixed Effects Models. R package version 3.1-124, [http://CRAN.R-](http://CRAN.R-project.org/package=nlme)
612 [project.org/package=nlme](http://CRAN.R-project.org/package=nlme).
- 613 R Core Team. 2013. R: A language and environment for statistical
614 computing., R Foundation for Statistical Computing, Vienna, Austria.
- 615 Ricklefs, Robert E. 2008. Disintegration of the Ecological Community. *The American*
616 *Naturalist* **172**:741-750.
- 617 Schweizer, D., G. S. Gilbert, and R. Aizprua. 2014. Do young tropical restoration plantations
618 exhibit a phylogenetic pattern that suggests the influence of biotic processes affecting
619 species composition? *PeerJ PrePrints* **2**:e625v621.
- 620 Schweizer, D., R. Machado, G. Durigan, and P. H. S. Brancalion. 2015. Phylogenetic patterns
621 of Atlantic forest restoration communities are mainly driven by stochastic, dispersal
622 related factors. *Forest Ecology and Management* **354**:300-308.

- 623 Shoener, S., C. Chisholm, and T. J. Davies. 2015. The phylogenetics of succession can guide
624 restoration: an example from abandoned mine sites in the subarctic. *J Appl Ecol*, 52:
625 1509–1517. doi:10.1111/1365-2664.12517.
- 626 Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution* **19**:605-
627 611.
- 628 Sniderman, J. M. K., and G. J. Jordan. 2011. Extent and timing of floristic exchange between
629 Australian and Asian rain forests. *Journal of Biogeography* **38**:1445-1455.
- 630 Swenson, N. G., and B. J. Enquist. 2009. Opposing Assembly Mechanisms in a Neotropical
631 Dry Forest: Implications for Phylogenetic and Functional Community Ecology.
632 *Ecology* **90**:2161-2170.
- 633 Valiente-Banuet, A., and M. Verdú. 2007. Facilitation can increase the phylogenetic diversity
634 of plant communities. *Ecology Letters* **10**:1029-1036.
- 635 Verdú, M., L. Gómez-Aparicio, and A. Valiente-Banuet. 2012. Phylogenetic relatedness as a
636 tool in restoration ecology: a meta-analysis. *Proceedings of the Royal Society B:*
637 *Biological Sciences* **279**:1761-1767.
- 638 Walters, M. B., and P. B. Reich. 1999. Low-light carbon balance and shade tolerance in the
639 seedlings of woody plants: do winter deciduous and broad-leaved evergreen species
640 differ? *New Phytologist* **143**:143-154.
- 641 Webb, C. O. 2000. Exploring the Phylogenetic Structure of Ecological Communities: An
642 Example for Rain Forest Trees. *The American Naturalist* **156**:145-155.
- 643 Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of
644 phylogenetic community structure and trait evolution. *Bioinformatics* **24**:2098-2100.
- 645 Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and
646 Community Ecology. *Annual Review of Ecology and Systematics* **33**:475-505.

647 Webb, C. O., G. S. Gilbert, and M. J. Donoghue. 2006. Phylodiversity-Dependent Seedling
648 Mortality, Size Structure, and Disease in a Bornean Rain Forest. *Ecology* **87**:S123-
649 S131.

650 Wikström, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms:
651 calibrating the family tree. *Proceedings of the Royal Society B: Biological Sciences*
652 **268**:2211-2220.

653 Wills, J., J. Herbohn, M. O. M. Moreno, M. S. Avela, and J. Firn. 2017. Next-generation
654 tropical forests: reforestation type affects recruitment of species and functional
655 diversity in a human-dominated landscape. *J Appl Ecol.* **54**:772-783.

656 Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, and et al. 2004. The worldwide leaf
657 economics spectrum. *Nature* **428**:821-827.

658

659

660

661

662

663

664

665

666

667

668 **Table 1.** The coefficient of variation (CV) for clades that represent common and obligate
 669 groups between monoculture (M), Rainforestation (R) and regenerating selectively logged
 670 forest types (S). Plus (+) signs represent a statistical overabundance of those clades within the
 671 corresponding community compared to a null model that randomly assigned the same number
 672 of species from the same species pool (*nodesig* statistic) (Webb et al. 2008). Minus (-) signs
 673 represent a lack of that species or family within the corresponding forest type.

674

675 **Table 1. Intra-specific variation of SLA for common and obligate species.**

Forest type present	Family	Species	SLA-n	Species CV
Common	Moraceae (+M)	<i>Ficus septica</i>	21	18.4
		(+S)		
Common		<i>Ficus pseudopalma</i>	25	33.8
		(+S)		
Common		<i>Ficus nota</i> (+S)	20	28.1
Common		<i>Artocarpus odoratissimus</i>	39	18.4
Common		<i>Artocarpus blancoi</i>	24	23.5
Obligate (M)	Meliaceae (+M)	<i>Swietenia macrophylla</i>	49	16.2
Common		<i>Sandoricum koetjape</i>	5	23.9
Obligate (M and R)		<i>Lansium domesticum</i>	5	35

Activity 1.5. Pilot test designs for multi-species, multiple product uneven-aged woodlots, agroforestry systems, and woodlot/crop livelihood systems suited to smallholders and communities.

Obligate (M and S)		<i>Dysoxylum gaudichaudianum</i>	6	10.8
Obligate (R and S)	Dipterocarpaceae (-M)	<i>Shorea contorta</i>	43	13.6
Obligate (R and S)		<i>Hopea plagata</i>	21	15.9
Obligate (R and S)	Fabaceae	<i>Pterocarpus indicus (-M)</i>	16	36.5
Obligate (S)	Clusiaceae	<i>Calophyllum inophyllum(-M)</i>	6	15.7
Obligate (S)	Burseraceae	<i>Canarium luzonicum(-M)</i>	7	7.9

676

677

678

679

680

681

682

683

684

685

686 **Figure 1.** Phylogenetic diversity in different forest types. Phylogenetic diversity (PD) was
687 compared to null model distributions (SES) of understories beneath monoculture,
688 Rainforestation and regenerating selectively logged forests. Positive values indicate
689 overdispersion whereas negative values indicate clustering. This model was statistically
690 significant ($P < 0.05$), using F-statistics.

691 **Figure 2.** Understorey phylogenetic and leaf trait diversity beneath monoculture,
692 Rainforestation and regenerating selectively logged forests. Phylogenetic and leaf trait
693 structure were measured against standardised effect sizes (SES) for (a) non-weighted mean
694 nearest taxon phylogenetic distance (MNTD) for all species, (b) non-weighted mean pairwise
695 phylogenetic distance (MPD) for tree and shrub species in isolation, (c) weighted mean
696 pairwise phylogenetic distance (MPD) for tree and shrub species in isolation, (d) non-
697 weighted mean pairwise functional distances (MFD) of SLA, (e) non-weighted MFD of LNC
698 and (f) non-weighted MFD of log transformed LPC. The phylogeny incorporating Bayesian
699 estimates of divergence times and a functional trait dendrogram were used as the basis of the
700 displayed metrics. Positive values indicate overdispersion and negative values indicate
701 clustering compared to the null model expectations that used species richness to randomise
702 the phylogeny and dendrogram.

703 **Figure 3.** Higher order fixed effects from LMEMs for understorey functional diversity (life-
704 form, potential plant height, dispersal type, SLA, LNC and LPC), measured as standard effect
705 sizes of abundance weighted MFD, for all species (a) and for native species in isolation (b),
706 beneath the different forest types. A Gower distance matrix was constructed as it allows for
707 categorical and missing data.

708 **Figure 4.** Higher order fixed effects for mean coefficient of variation (CV) for SLA values of
709 all individuals at the plot level (a), MFD and MNFD weighted by abundances for species

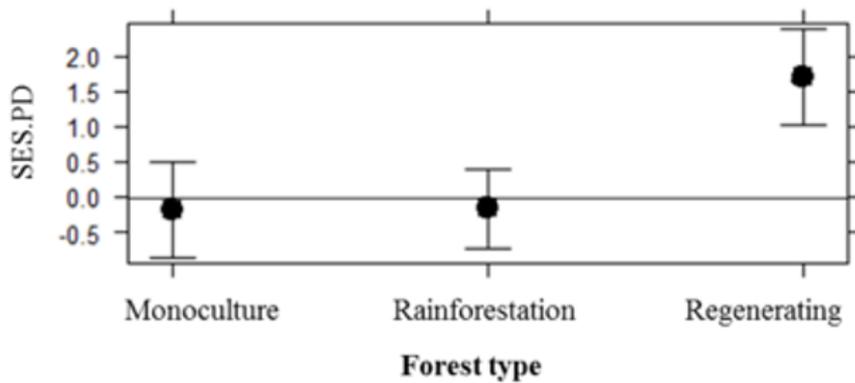
710 with 5 or greater SLA replicates (b, c), between monoculture, Rainforestation and
711 regenerating selectively logged forests seedling communities. * denotes a significant
712 relationship overall ($P < 0.05$).

713 **Figure 5.** Summarizing community assembly processes indicated by analysing evolutionary,
714 leaf trait (SLA, LNC and LPC), discrete trait (potential height, dispersal and life-form) and
715 within-species SLA data, for regenerating selectively logged forest (Regenerating),
716 Rainforestation and monoculture forest types. Species richness (SR) and phylogenetic
717 diversity (PD) were highest within regenerating selectively logged forest and lowest within
718 monoculture forest types, Rainforestation was intermediate. Species within the family
719 Moraceae (green) were common across forest types and tall, wind-dispersed native species
720 (red) were limited to regenerating selectively logged forest and Rainforestation forest types.
721 Species that exhibited high and low variation in SLA (brown gradient) were also restricted to
722 regenerating selectively logged forest seedling communities. Exotic human-dispersed herbs,
723 shrubs and trees (blue) increased all measures of seedling diversity within monoculture forest
724 types.

725

726

727



728

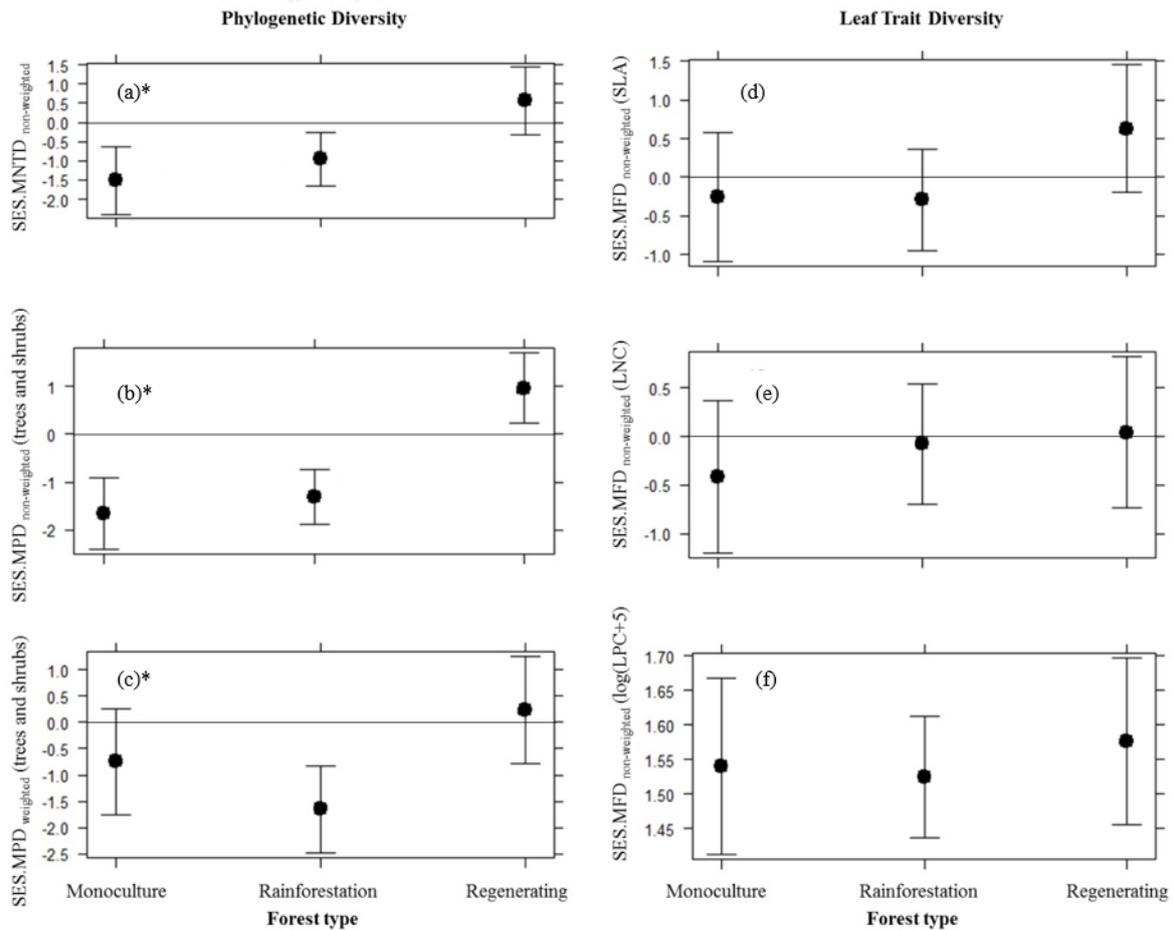
729 **Figure 1.** Phylogenetic diversity in different forest types. Phylogenetic diversity (PD) was
730 compared to null model distributions (SES) of understories beneath monoculture,
731 Rainforestation and regenerating selectively logged forests. Positive values indicate
732 overdispersion whereas negative values indicate clustering. This model was statistically
733 significant ($P < 0.05$), using F-statistics.

734

735

736

737



738

739 **Figure 2.** Understorey phylogenetic and leaf trait diversity beneath monoculture,
 740 Rainforestation and regenerating selectively logged forests. Phylogenetic and leaf trait
 741 structure were measured against standardised effect sizes (SES) for (a) non-weighted mean
 742 nearest taxon phylogenetic distance (MNTD) for all species, (b) non-weighted mean pairwise
 743 phylogenetic distance (MPD) for tree and shrub species in isolation, (c) weighted mean
 744 pairwise phylogenetic distance (MPD) for tree and shrub species in isolation, (d) non-
 745 weighted mean pairwise functional distances (MFD) of SLA, (e) non-weighted MFD of LNC
 746 and (f) non-weighted MFD of log transformed LPC. The phylogeny incorporating Bayesian
 747 estimates of divergence times and a functional trait dendrogram were used as the basis of the
 748 displayed metrics. Positive values indicate overdispersion and negative values indicate

749 clustering compared to the null model expectations that used species richness to randomise
750 the phylogeny and dendrogram.

751

752

753

754

755

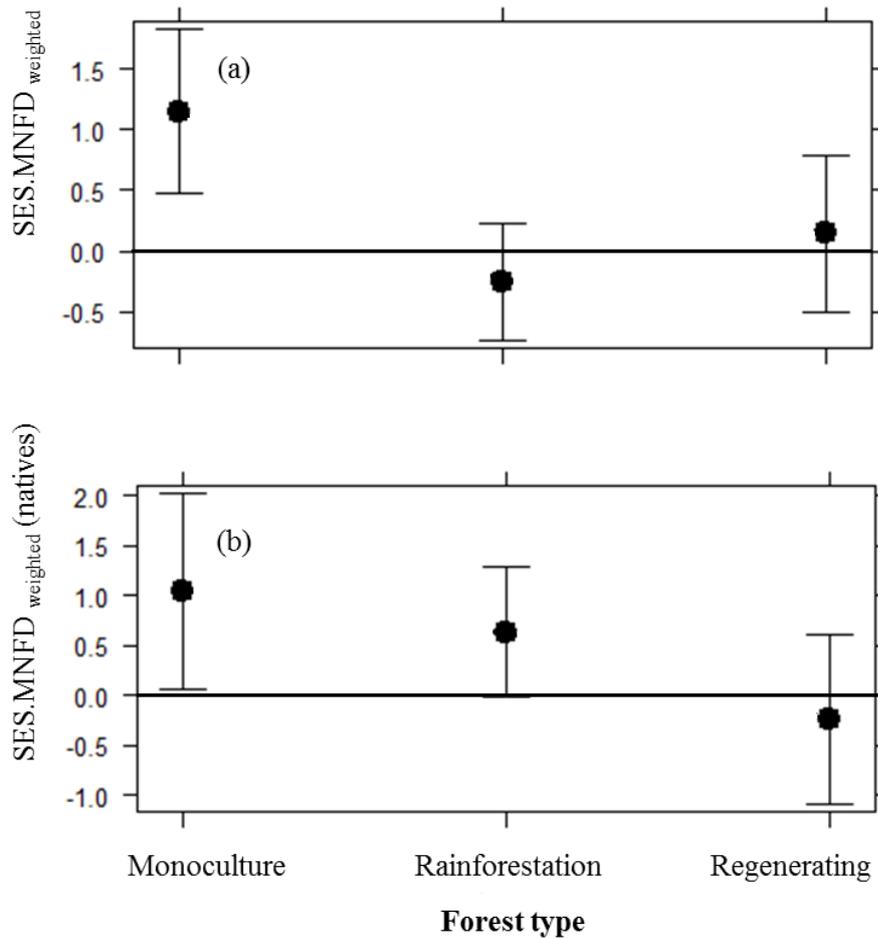
756

757

758

759

DRAFT



760

761

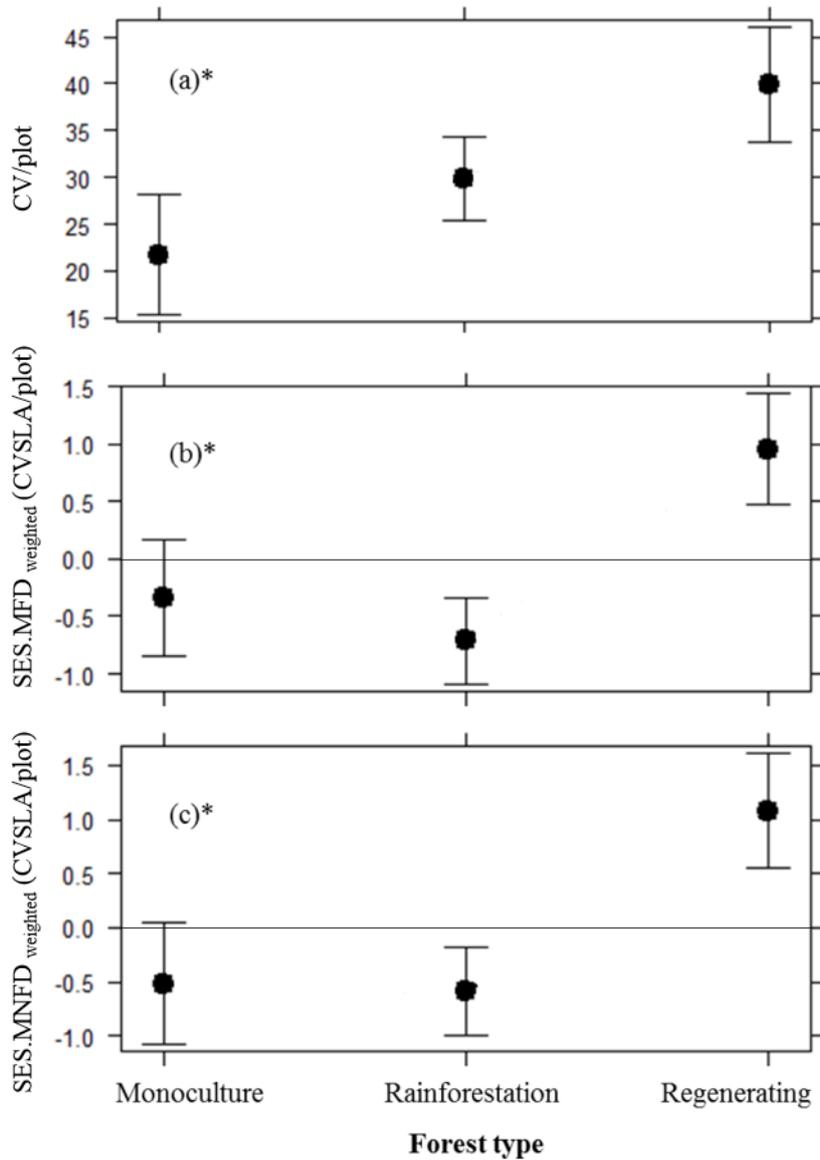
762 **Figure 3.** Higher order fixed effects from LMEMs for understorey functional diversity (life-
763 form, potential plant height, dispersal type, SLA, LNC and LPC), measured as standard effect
764 sizes of abundance weighted MFD, for all species (a) and for native species in isolation (b),
765 beneath the different forest types. A Gower distance matrix was constructed as it allows for
766 categorical and missing data.

767

768

769

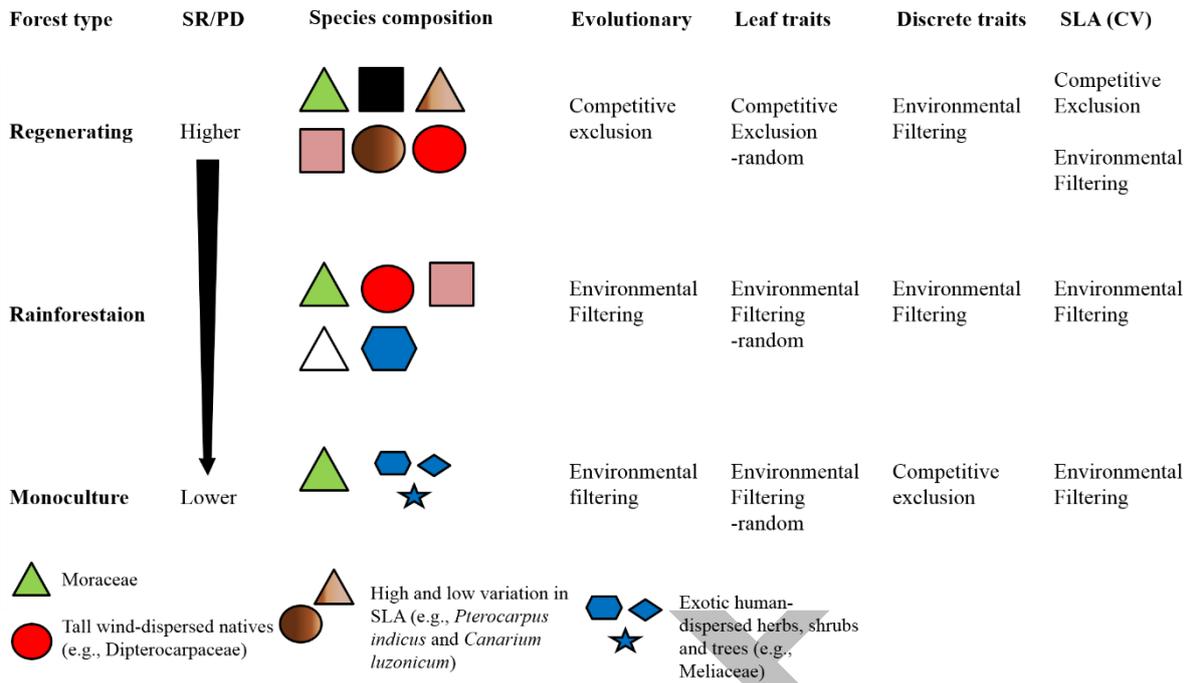
770



771

772 **Figure 4.** Higher order fixed effects for mean coefficient of variation (CV) for SLA values of
773 all individuals at the plot level (a), MFD and MNFD weighted by abundances for species
774 with 5 or greater SLA replicates (b, c), between monoculture, Rainforestation and
775 regenerating selectively logged forests seedling communities. * denotes a significant
776 relationship overall ($P < 0.05$).

777



778

779 **Figure 5.** Summarizing community assembly processes indicated by analysing evolutionary,
 780 leaf trait (SLA, LNC and LPC), discrete trait (potential height, dispersal and life-form) and
 781 within-species SLA data, for regenerating selectively logged forest (Regenerating),
 782 Rainforestation and monoculture forest types. Species richness (SR) and phylogenetic
 783 diversity (PD) were highest within regenerating selectively logged forest and lowest within
 784 monoculture forest types, Rainforestation was intermediate. Species within the family
 785 Moraceae (green) were common across forest types and tall, wind-dispersed native species
 786 (red) were limited to regenerating selectively logged forest and Rainforestation forest types.
 787 Species that exhibited high and low variation in SLA (brown gradient) were also restricted to
 788 regenerating selectively logged forest seedling communities. Exotic human-dispersed herbs,
 789 shrubs and trees (blue) increased all measures of seedling diversity within monoculture forest
 790 types.

791