1   **Biodiversity effects on seedling biomass growth are modulated by light environment across**

2   **functional groups**

3

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15   **Abstract**

16   1. Tree biodiversity has the potential to ensure consistency in the functioning of forest

17   ecosystems, not just over space, but over long-timescales by maintaining composition

18   through recruitment. However, for continued buffering in the face of global

19   environmental change, the sensitivity of biodiversity-ecosystem functioning relationships

20   to heterogeneous environments needs to be understood.

21   2. Seedling recruitment in carbon-rich tropical forests is a result of biotic and abiotic drivers

22   but their combined outcomes at the community-level remain poorly understood.

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23   Although biodiversity in seedling communities can potentially increase their growth and

24   biomass accumulation, abiotic drivers like light can alter this effect through divergent

25   effects on constituent species and functional groups. In forests with high baseline

26   heterogeneity in microclimates, these processes can enhance or constrain regeneration.

27   3. We tested the effects and interactions between species richness and canopy cover on the

28   growth of seedling communities consisting of tropical broad-leaved evergreen and

29   deciduous forest species using a fully crossed manipulated experiment in the Andaman

30   Islands, India and compared these with field observations from a long-term forest plot in

31   the same landscape.

32   4. We show that in the critical seedling establishment phase, species richness and light

33   increase community biomass independently. Accounting for variation across species,

34   individual species on average accumulated more biomass in communities with both

35   higher light and higher diversity.

36   5. We also show that overyielding in species rich communities fits expectations from a

37   model of complementarity with non-random overyielding than selection or spatial

38   insurance effects.

39   6. *Synthesis* Taken together, our results show that the potential for biodiversity to increase

40   ecosystem functioning in seedling communities is modulated by light. Further

41   understanding on the interaction of biodiversity with multiple abiotic drivers and their

42   effect on regeneration dynamics is crucial for predicting future ecosystem functioning.

43   **Keywords:** biodiversity, ecosystem functioning, tropical forests, overyielding,

44   environmental heterogeneity

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Introduction

47

48 Diverse forests consistently store more carbon than low diversity stands, but these ecosystem

49 functions can be destabilised by changing environments is less understood (Ammer, 2019;

50 Hutchison et al., 2018). At global and regional scales, higher tree diversity in forests is

51 associated with greater productivity and higher contribution towards reducing atmospheric

52 carbon (Liang et al., 2016; Osuri et al., 2020). However, with global environmental change

53 increasing spatial and temporal environmental heterogeneity and driving compositional shifts,

54 the future of forest-associated carbon storage remains uncertain (Feeley et al., 2011). In forested

55 ecosystems, where large, long-lived trees have disproportionate contributions to biomass,

56 productivity and associated ecosystem functions, future functioning depends on mortality and

57 recruitment processes that shape community composition (Bunker et al., 2005). Although the

58 responses of tree mortality to global environmental change are actively studied, recruitment

59 processes have received relatively less attention in this context (but see Zhao et al., 2018).

60 Understanding the importance of diversity to the community function of recruited tree

61 communities under heterogenous environments is crucial for understanding and predicting the

62 future of ecosystem functioning under scenarios of co-occurring environmental change and

63 biodiversity loss.

64 The contribution of species diversity to ecosystem functioning under varied environmental

65 conditions depends on how these conditions affect species performance. Diverse communities

66 could have higher yield compared to monocultures either due to increased probability of

67 selecting species that are high yielding across all conditions (selection effect), higher yield across

68 all species in mixtures across all conditions (complementarity), each species performing better in

3

69   a suitable condition (spatial insurance), or differences in species yield but species overyielding in

70   mixtures (complementarity with non-random overyielding) (Isbell et al., 2018). Trait differences

71   between species and their performance under different conditions can therefore contribute

72   significantly to the biodiversity effect, with larger spatial heterogeneity requiring higher species

73   richness to maintain biodiversity (Thompson et al., 2018, 2021). Tests of these basic theoretical

74   frameworks have mostly involved grassland communities with annuals or short-lived perennials.

75   On the other hand, tropical forests store roughly 55% of terrestrial carbon with 56% of this

76   stored in live biomass (Badgley et al., 2019; Pan et al., 2011). In these forests with long-lived

77   species, the relative importance of diversity mechanisms, fine-scale environmental heterogeneity

78   and high species richness remains unknown.

79   Intraspecific competition plays an integral role in structuring seedling communities and

80   neighbourhood biodiversity can therefore increase growth. Studies with tropical tree species

81   show that species richness and functional diversity in communities has the potential to increase

82   the relative growth rate of individual seedlings and cause overyielding in communities (Kuptz et

83   al., 2010; Sapijanskas et al., 2013; Shen et al., 2021; Van de Peer et al., 2018). Seedling diversity

84   in the neighbourhood can alter seedling root traits directly, altering resource niches and

85   acquisition patterns, and increasing growth at the community level (Madsen et al., 2020).

86   However, seedling competition occurs in an environmental context for limiting resources, and

87   the outcomes of interspecific interactions can change as the environment varies (Butterfield &

88   Callaway, 2013). Biodiversity can therefore increase spatial and temporal insurance, leading to

89   more consistent growth (lower variation over time), and higher biomass accumulation compared

90   to single-species stands (Hutchison et al., 2018; Isbell et al., 2018; Tuck et al., 2016).

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91   In diverse forests, light differentially affects growth across functional groups of tree seedlings,

92   potentially structuring local communities and affecting standing biomass along natural gradients.

93   As a result of pervasive light competition in forest understories, seedlings respond to increased

94   light intensity with increased growth (Kuptz et al., 2010; Lu et al., 2021; Sangsupan et al., 2021;

95   Sovu et al., 2010). Fundamentally, growth plasticity and the ability to utilize increased light is

96   mediated by species identity or functional identity (Kuptz et al., 2010; Tomlinson et al., 2014;

97   Tripathi et al., 2020). Deciduous species grow faster under increased light conditions while

98   evergreen species have slower growth and are sensitive to drought in high light conditions

99   (Tripathi et al., 2020). Mixed deciduous forests, a type of seasonally dry tropical forests, have

100   both broad-leaved evergreen and deciduous species in the same canopy, leading to seasonal

101   heterogeneity of microclimates in the forest floor. These differences can determine the

102   distribution of seedlings in the understory; deciduous species in the canopy increase the

103   abundance and diversity of light-demanding species in the understory by increasing light

104   availability (Souza et al., 2014). Since evergreen and deciduous species are adapted to low and

105   high light respectively, potential diversity effects under different light conditions are likely

106   driven by mechanisms of spatial insurance. However, with increased tree mortality in tropical

107   forests due to drought and extreme climatic events (Aleixo et al., 2019; Uriarte et al., 2019), light

108   environments in the understory are potentially undergoing large-scale shifts, affecting both

109   biodiversity and its effects on ecosystem functioning.

110   We experimentally assessed the combined influence of light and species diversity on the growth

111   of tropical forest seedling communities and compared dynamics with field communities under

112   natural regeneration in a high diversity tropical forest. We expected that (i) light would increase

113   overall seedling growth and lead to overyielding in high light treatments compared to shade

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114   treatments (ii) decreased intraspecific competition in mixed cultures would lead to higher

115   biomass with increasing species richness and combined with expectation (i), lead to higher

116   overyielding in high diversity, high light treatments (iii) light responses of evergreen and

117   deciduous species would be different, with evergreen species performing better under low light

118   and deciduous species performing better under high light environments, i.e., overyielding

119   through spatial insurance.
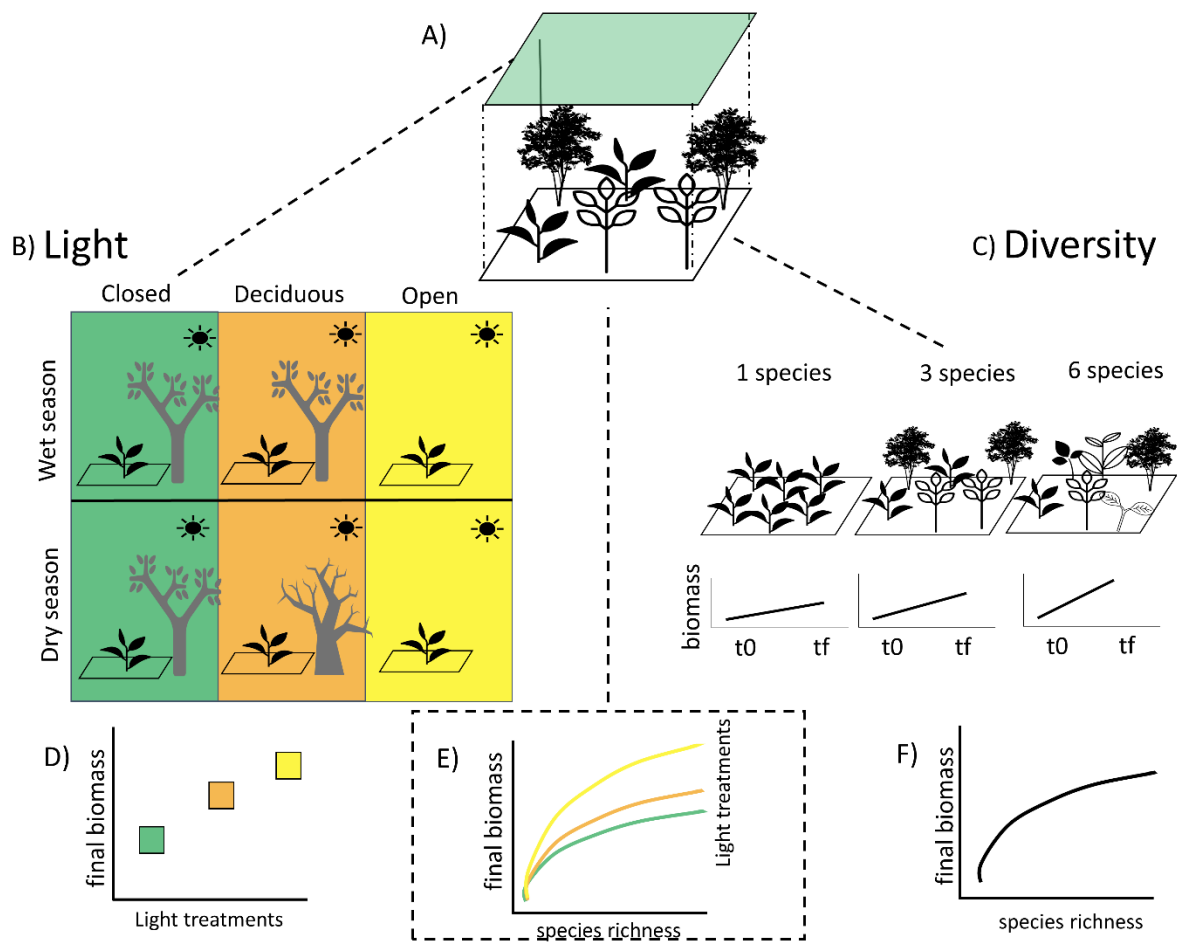
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121   <u>Figure 1</u>: Schematic of experimental and expectations A) Experimental setup with fully crossed

122   light and diversity treatments B) Light treatments in detail – closed, deciduous and open canopy

123   treatments and with colour codes – in the wet and dry season and D) final biomass expectations

124   for each of these based on increased growth in the presence of light. C) Three levels of diversity

6

125   treatments – 1, 3 and 6 species and biomass expectations between initial and final communities

126   and F) expectations for final biomass between the three treatments – an increasing, saturating

127   curve. And finally, E) combined expectations for community biomass under the combined

128   influence of light and diversity treatments; the influence of species diversity on growth is

129   expected to be modulated by light conditions. Icons from The Noun Project.

130   **Methods**

131   We measured the combined influences of two key factors structuring forests – light and species

132   diversity – through experimental methods and long-term data from a tropical forest landscape.

133   The study was conducted in the Andaman Islands, India, an archipelago in the Bay of Bengal. It

134   is part of the Indo-Burma biodiversity hotspot with high species diversity, high endemism and

135   >80% forest cover. Many forests in the archipelago are mixed deciduous forests, where tropical

136   evergreen and tropical deciduous tree species co-exist in the canopy. This has the potential to

137   create heterogeneity in microclimate in the understory. A shadehouse experiment was conducted

138   at the Silviculture Research nursery, Nayashahar, maintained by the Department of Environment

139   and Forest, Andaman and Nicobar Islands. We matched the design of the experimental plots

140   (plot size, range of species richness, abundance) and census methods closely with seedling plots

141   at a permanent forest dynamics plot at Alexandra Island, about 10 km from the experiment site

142   and with mixed deciduous forest type. This plot is part of the Long-term Ecosystem Monitoring

143   Network (LEMoN) in India established to set baselines for forest dynamics and carbon storage

144   across various biomes in India.

145   Experimental Methods

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146 In a fully crossed experiment, we planted similarly sized evergreen and deciduous seedlings

147 under 3 shade conditions (simulating an evergreen canopy that is closed throughout the year –

148 "closed", a deciduous canopy that is closed in the wet season and open in the dry season -

149 "deciduous" and a consistently open condition – "open") and in 3 levels of diversity (1 species, 3

150 species and 6 species from a pool of 10 species) and measured growth for 1 year (Fig 1). Each

151 treatment had 6 replicates each, totalling 54 plots. Each plot of 1 m x 1 m plot was planted with

152 18 individually tagged seedlings belonging to 1, 3 or 6 species from a pool of 10 species in

153 March 2019. Seedling plots of $1m^2$ in the landscape contained an average of 16 seedlings and

154 had a maximum of 7 species and the planting numbers were matched to these naturally occurring

155 values. Experimental plots were set up using natural, well-mixed soil from an abandoned plot

156 nearby and demarcated as regular rows using bamboo and other locally available building

157 material. Over each plot, standard shade nets of 50% shade were used to cover the canopy at 6ft

158 height to mimic either a closed canopy (closed throughout the year) or a deciduous canopy

159 (closed in the wet season and open in the dry season) or they were left fully open throughout the

160 year. The plots were arranged in regular rows with a spacing of 30 cm between adjacent plots

161 and the 9 treatments were randomly distributed spatially among the 54 plots in the experiment.

162 We used seedlings of ten native forest tree species germinated by ANI forest department

163 nurseries from seeds collected from nearby forests and for the purpose of replanting into

164 selectively logged forests in the area. Six common species – 3 evergreen (*Dipterocarpus*

165 *griffithii*, *Myristica andamanica* and *Mangifera andamanica*) and 3 deciduous (*Terminalia*

166 *procera*, *Pterocarpus dalbergioides* and *Planchonia valida*) were chosen as the primary

167 experimental species to make up the monocultures, while the other 4 species (*Artocarpus*

168 *chaplasha*, *Diospyros sp.*, *Planchonella longipetiolata*, *Walsura* sp.) were planted in a few of the

8

169   3 and 6 species plots, to increase variation in species combinations in polycultures. For the 6

170   primary species, monocultures were planted under each of the 3 canopy treatments. Seedlings

171   were planted into the experiment when approximately 30 cm tall and within the height range in

172   which these are usually replanted into forests. During transplanting, we removed the plants from

173   the potting soil and measured root length, shoot length, basal area and total biomass, allowing us

174   to create allometric equations of this life history stage. Eighteen individually tagged seedlings

175   were planted into each plot in a random order but with equal spacing, 15 cm apart. After

176   transplanting, we watered the plots for two weeks to reduce mortality specifically from

177   transplanting. Other than weeding every month to maintain planting conditions, the plots were

178   left unmanaged until the end of the experiment.

179   Two months after replanting, we initiated monthly censuses of the plots for 11 iterations. During

180   each census, the height and basal area of every tagged individual seedling was measured. Height

181   of the seedlings were measured using a standard measuring tape (carpentry tape) with an

182   accuracy of 1 mm. Basal area of seedlings was measured using an Insize digital calliper with an

183   accuracy of 0.01 mm. We report values from the final census, conducted in June 2020

184   throughout this study.

185   Observational data

186   Seedling data from long-term plots with comparable species composition and microclimate

187   heterogeneity in the landscape were analysed to validate experimental results. Under the LEMoN

188   network, a 1-hectare long-term monitoring plot was set up at Alexandra Island in the Andaman

189   archipelago. This site is in a mixed deciduous forest with no recent logging history and protected

190   as part of the Mahatma Gandhi Marine National Park. Within the 1 ha plot, 25 seedling plots of 1

191   m^2 have been set up on a uniform grid covering the extent of the plot. Within these subplots,

192   naturally regenerating seedlings are tagged, identified to the best possible degree and measured

193   at monthly intervals. For comparing the light environments of the 25 different seedling plots, the

194   canopy cover at each location was measured in December 2020, using a Forestry Suppliers

195   Spherical Crown Densiometer, Convex Model A. At each seedling plot, the percent of canopy

196   cover was calculated as the number of grid cells in the densiometer with canopy cover as an

197   average over four replicate measures. Since much of the canopy cover in these plots is

198   determined by the upper canopy where dynamics are slow, these light environments were

199   assumed to be stable through the years of measurements.

200   Data on basal diameter and height of individual seedlings in these plots measured using similar

201   equipment and methods as the experiment from three censuses done in June 2016, 2017 and

202   2018 were used for comparison. Height was measured for all individuals in the seedling plot,

203   while basal diameter was measured only for seedlings with height > 1m. For those instances

204   where basal area was not recorded as part of monitoring protocol, basal area was calculated as a

205   function of height using a fit for basal area to height from experimental communities. The

206   allometric equation was $basal\ diameter = 2.34 + 0.08 * height$. Being under natural

207   regeneration, the abundance, species richness and species composition varied across these plots.

208   Over the three censuses, 585 seedlings were recorded, out of which 310 were unique individuals,

209   while the rest were repeated encounters. Gaps in species IDs within the data were filled to the

210   best possible extent using other information in the data sheet – like local names and remarks, but

211   unidentified individuals with no further information were considered as a single species to avoid

212   overcounting of richness. 254 of these individuals remained unassigned to species. Identified

213   species belonged to genera that were used in the manipulated experiment, including *Myristica*

214   *spp.*, *Terminalia bialata*, *Diospyros spp.*, *Dipterocarpus spp.*, and *Planchonia andamanica*.

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215

216   Statistical methods

217   All statistical analyses were performed in R with R Studio (R Core Team 2020). For both

218   experimental communities and field communities, we analysed the effects of experimental

219   treatments of light and species richness on basal area and height using generalized linear models

220   using the *lme4* package. To avoid the confounding effects of differential survival on total final

221   biomass, we modelled treatment effects on the mean values of surviving individuals in the

222   experiment (n=651) and on observed individuals in the field. Mean basal area and height being

223   continuous, non-zero variables were modelled with gamma errors for continuous, non-zero

224   variables, and because it best fit the distribution.

225   For the final communities, we assessed the degree of overyielding with species richness and the

226   relative contribution of complementarity and selection effects using methodology from Loreau

227   M. & Hector. A., 2001. We used data from the tenth census of the experiment as one of the

228   monocultures (of *D. griffithii*) had all died by the last census. We used 49 of 54 replicates for this

229   analysis, excluding mixed communities planted with species for which monocultures were not

230   planted in the experiment (see above section). For each species, we calculated the average basal

231   area in a monoculture across all three light treatments (*M*). We calculated relative yield (*ΔY*) in

232   mixed communities as the difference of the observed yield (*Y*) from the expected simple sum.

233   Further, for each plot, we partitioned this difference into selection effects ($cov(\Delta RY, M)$, where

234   $\Delta RY = \frac{Y}{M} - \frac{1}{N}$) and complementarity effects ($N\overline{\Delta RY}\,\overline{M}$), where *N* is the planted species

235   diversity.

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236   For observed communities on field, we modelled total basal area and height of individuals as a

237   generalized linear mixed effects model with a gamma family of errors. We modelled each of

238   these with separate quadratic models of species richness and canopy openness, with intercepts

239   allowed to vary with the year of observation. We compared models with the linear only model

240   (without the quadratic term) using AIC values.

241   All figures were created using *ggplot2* and *sjPlot*.

242   **Results**

243   <u>Growth at the community level</u>

244   Seedlings in experimental communities with greater species richness and greater light levels

245   accumulated more biomass on average. Individual wet weight at the initial time point was more

246   strongly associated with basal diameter than height (linear model for weight adjusted R^2 with

247   height=0.26, basal diameter=0.40). Mean basal area in the plant community, indicative of

248   biomass, significantly increased with increasing levels of light and species richness; the 6 species

249   treatment and the deciduous canopy treatment had significantly higher mean basal area than the

250   closed, monocultures (Fig 2). Mean height of the seedlings, however, was only influenced by

251   light; the deciduous treatment significantly increased mean height, while other treatments were

252   not significantly different from the closed canopy monocultures (Fig 2). Moreover, there were no

253   significant interaction effects of light and species richness treatments on either mean basal area

254   or mean height of the seedlings (Fig 2). The differences between communities also persisted

255   through time when analysed at the monthly timescale (repeated measures ANOVA, Fig S2).

256   More trivially, regardless of treatment, higher values of final abundance were strongly associated

257   with higher mean basal area and mean height in these communities (Fig 2). Summed across all

12

258   individuals in a 1m^2 plot, total height and basal area in final communities were highly correlated

259   (Pearson's correlation coefficient r=0.96). The survival of seedlings in plots was not significantly

260   predicted by either planted species richness or by canopy treatment, but communities with higher

261   proportion of evergreen species had significantly lower survival at the end of the experiment (Fig

262   S1).

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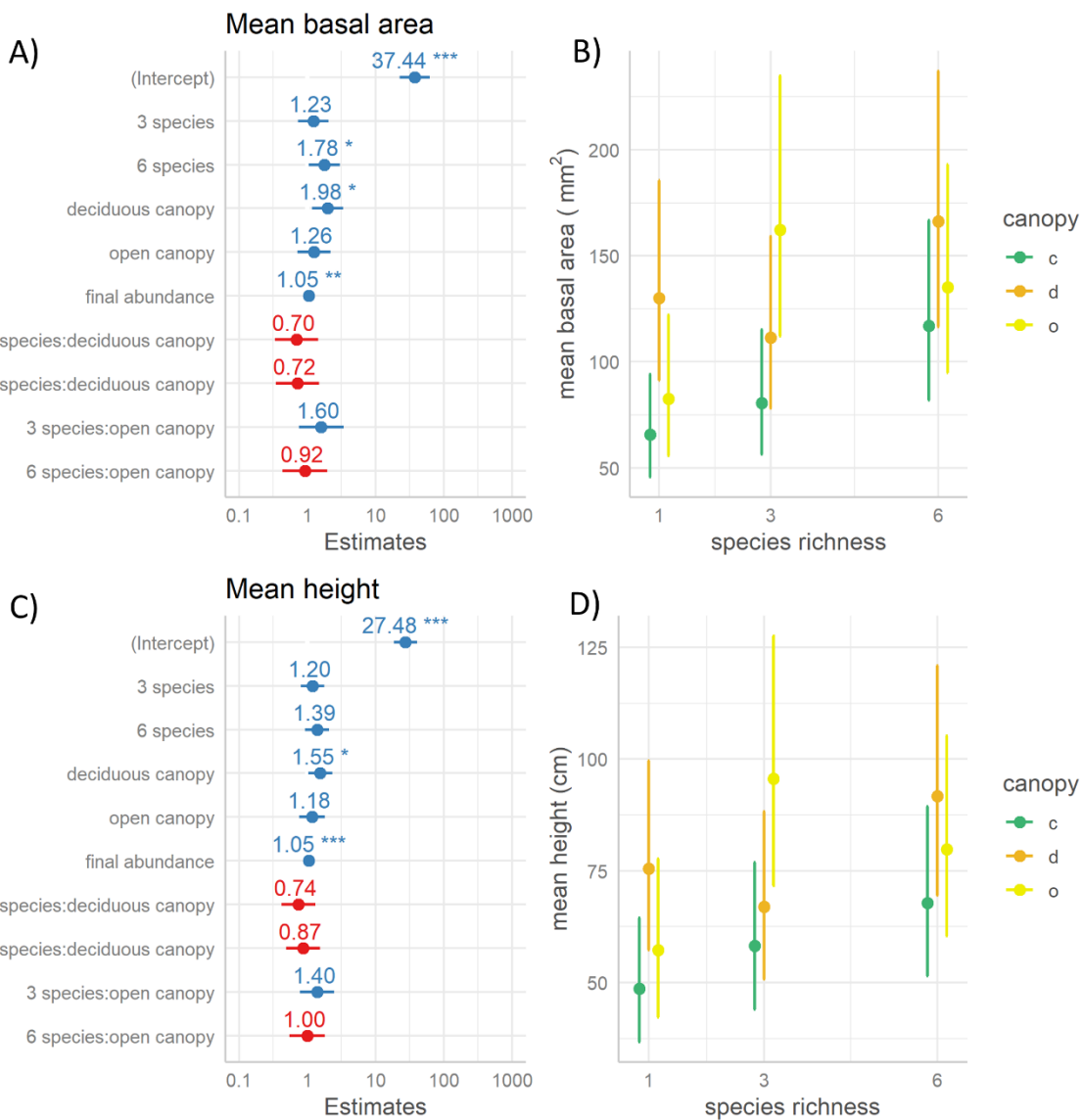
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265 **Figure 2**: Generalized linear model of mean basal area and mean height of a seedling in a 1m x

266 1m plot in the experiment. For mean basal area, deviance is 12.96, df=47, p=0.999, R2=0.41. For

267 mean height, deviance =8.24, df=47, p=1, R2=0.48. For mean basal and mean height in a

268 community A) and C) show model estimates of the parameters, B) and D) show model

269 predictions for species richness and canopy treatments. Colour codes for canopy treatment,

270 c=closed, d=deciduous and o=open treatments as specified in Fig1.

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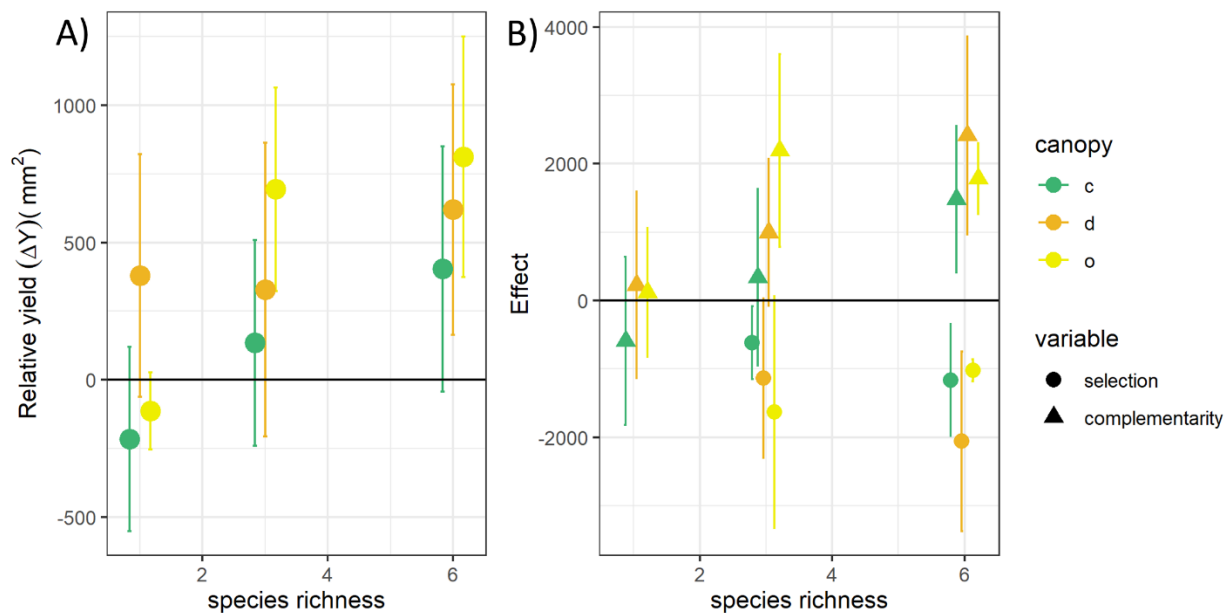
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273 **Figure 3:** Relative contributions of complementarity and selection effect to relative yield (ΔY) of

274 multispecies communities. A) Plot of the relative yield (ΔY) for different treatments, based on

275 basal area measurements. B) The magnitude of complementarity and selection effects, as

276 calculated by the Loreau-Hector method (details in methods). Points represent means and errors

277 bars represent 95% confidence intervals.

278

14

279   Species richness in communities increased overyielding and complementarity effect and

280   decreased the magnitude of selection effect across light environments (Fig 3). At the end of 10

281   months of the experiment, observed total basal area in many plots was higher than from the

282   expectation from monoculture averages; relative yield was largely positive. The relative yield

283   increased with both light and diversity treatments; two-way ANOVA of observed – expected

284   total basal area was significant for both species richness treatments (F=13.6, df=1, p<0.001***)

285   and canopy treatments (F=3.4, df=2, p=0.04*). Further, the effect of complementarity increased

286   and selection effect decreased with increasing species richness (Fig 3). At the highest level of

287   species diversity, the six species treatment, the magnitude of complementarity effect across all

288   light treatments in all communities were positive while selection effect was negative for all

289   communities. The magnitude of the complementarity effect was significantly different across

290   light and diversity treatments (two-way ANOVA: species richness F=24.23, df=1, p<0.001***,

291   canopy treatment F=3.74, df=2, p=0.03*), while selection effect was significantly different only

292   with species richness (F=23.3, df=1, p<0.001***, canopy treatment F=1.121, df=2, p=0.33).

293   Predictors of growth at the individual level

294   Accounting for differences in species identity, individual seedlings that survived until the end of

295   the experiment showed higher gain in basal diameter and height in mixed communities and in the

296   deciduous treatment as compared to counterparts in closed monocultures (n=651, RMSE=3.21,

297   marginal R2=0.11; Fig 4). However, the open canopy treatment was not significantly different

298   from the closed treatment. Models also revealed significant negative interactions between the

299   species richness and light treatments for individual seedling growth (Fig 4). Although species

300   richness increased basal diameter and height across light treatments, this gain was lower in the

301   deciduous treatment than in the closed treatment. Basal area and height at planting significantly

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302   increased corresponding gains in these response variables within a year of the experiment (Fig

303   4).

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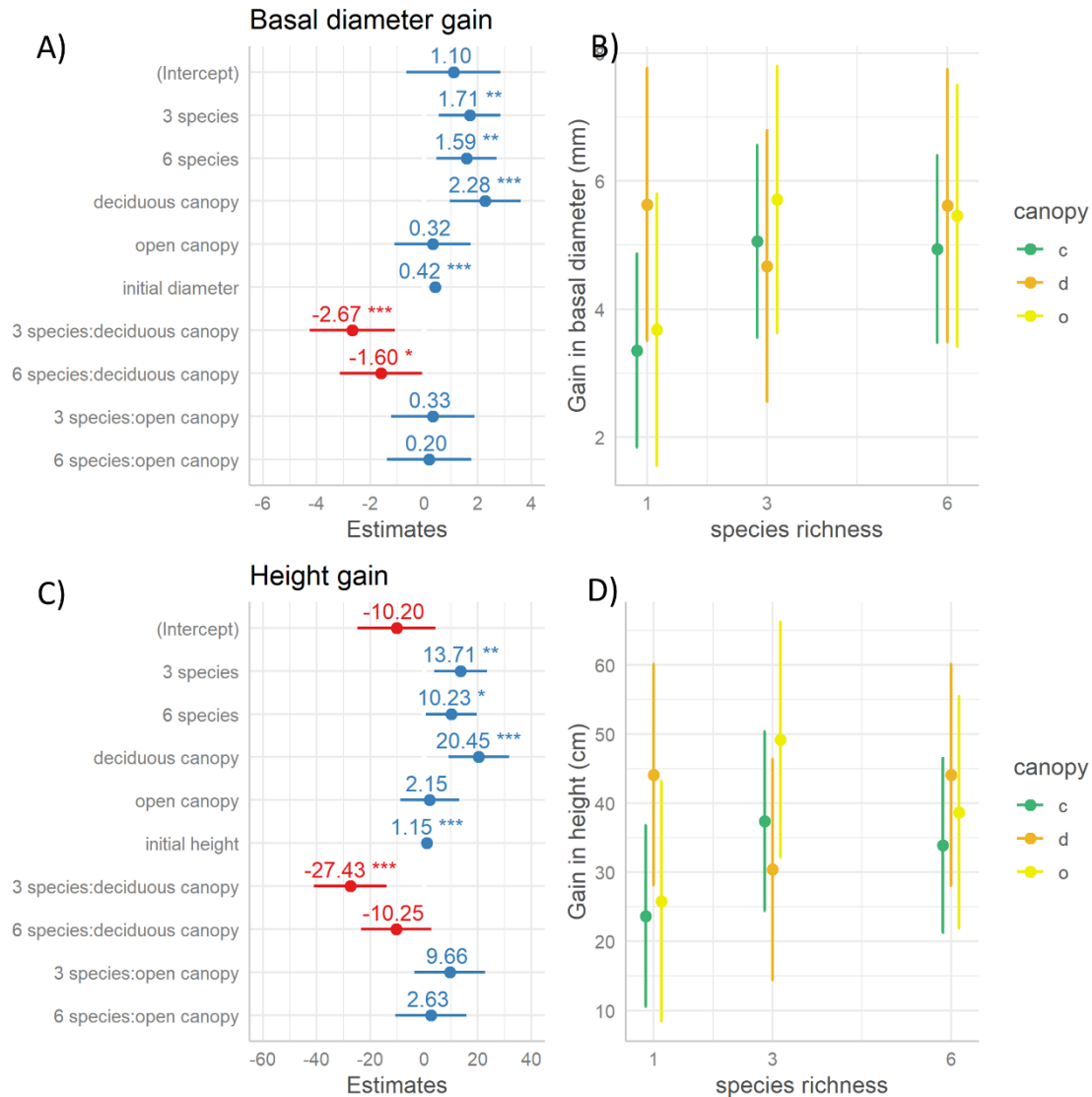
Figure 4: Linear mixed effects models for gain in basal diameter and height between the first

and the last census for individual seedlings; random slope model with variable slopes for each

species with canopy treatment. For basal diameter, deviance=3414, total R^2=0.44, fixed effect

R^2=0.16; for height, deviance=6200, total R^2=0.50, fixed effect R^2=0.29. For basal diameter and

16

309 height respectively, A) and C) represent estimated effects of different predictors, B) and D) show

310 predicted responses from the model for species richness and canopy conditions
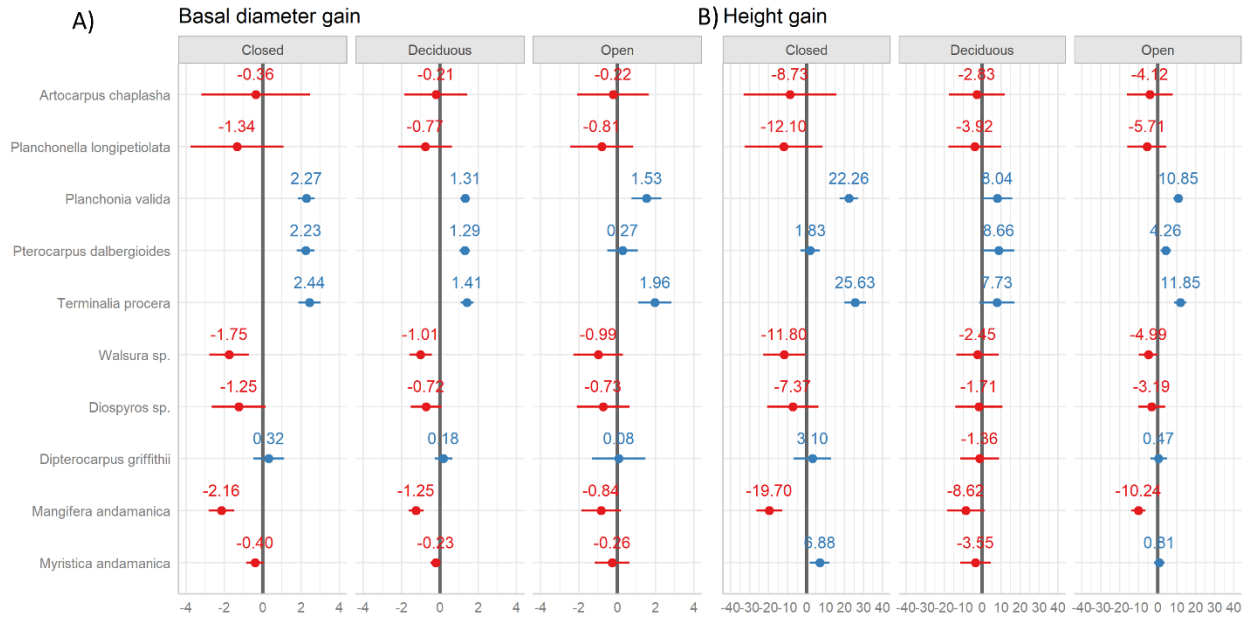
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312 **Figure 5**: Random slopes of species under different canopy conditions; A) shows random effects

313 for each species for gain in basal diameter and B) for height gain. The top six species represent

314 fast-growing, deciduous species, followed by slower growing, evergreen species towards the

315 bottom.

316

317 Individual growth varied with species in the experiment and under different canopy conditions,

318 but the differences remained consistent across light treatments. The model with species specific

319 slopes, varying with canopy, had the lowest AIC, lower than the random intercept model (ΔAIC

320 (for df=17 and df=12) =2.05). All other models - with no random effects and with only random

321 effects – performed much worse. The response of biomass to species diversity and light

322 dependent on species identity; in the full model with species richness, canopy treatment and

17

323   slopes varying with species, the random effect of species on slopes was significant (SD of

324   random effect species identity at closed canopy = 1.89; deciduous canopy = 1.09, open canopy =

325   1.20, residual =3.26). Deciduous species – *T. procera*, *P. valida*, *P. dalbergioides* and the

326   evergreen *D. griffithii* had higher than average growth rates, demonstrated by positive values of

327   the random effect, while *Myristica andamanica* and *Mangifera andamanica* were slower

328   growing species (Fig 5). These patterns were consistent between basal diameter and height.

329   Moreover, these differences were consistent across light treatments, although starker under lower

330   light.

331   Species functional identities affect total basal area and total height of the community. Although

332   functional diversity levels were not fully replicated in the experimental design, the proportion of

333   evergreen species in the community affected the final biomass across all experimental

334   treatments. Overall, increased proportion of evergreen species was associated with lower total

335   basal area and total height across different light treatments (Fig S3). In the open canopy

336   treatment, however, a 0.3 proportional abundance of evergreen species had the highest total basal

337   area and total height. Due to a lack of replication of this combination in the closed and deciduous

338   treatments, further tests of this pattern are not possible.

339   Convergence with observational data

340   Higher values of biomass accumulation in seedling communities in observational plots was

341   associated with higher species richness and canopy openness. For 25 plots across a range of light

342   conditions and species richness, separate models of total basal area and height in seedling

343   communities showed significant non-linear effects of canopy openness and species richness on

344   these variables. AIC values of all quadratic models were lower than for models with linear terms

345   alone; except for height and species richness, where there was no clear best-fit model (Table S1).

18

346   Total basal area in communities increased with species richness, but peaked at intermediate

347   levels; for a model with observation year as a random effect, the positive linear and negative

348   quadratic term were significant (RMSE=0.5, marginal R^2=0.99, Fig 6A). Total basal area had a

349   quadratic relationship with canopy openness (RMSE=0.50, marginal R^2=0.89, Fig 6B).

350   Similarly, total height of seedling communities was highest at intermediate openness; a quadratic

351   model of canopy openness was significant (RMSE=0.49, marginal R^2=0.94, conditional R^2=0.99,

352   Fig 6D). However, a quadratic model of total height with species richness only showed marginal

353   effect of the linear term of species richness (RMSE=0.51, marginal R^2=0.99. Fig 6C). Across all

354   treatments, the values of total basal area and total height in the field observations were lower

355   than the experimental communities, but total height was closer in magnitude (Fig 6).

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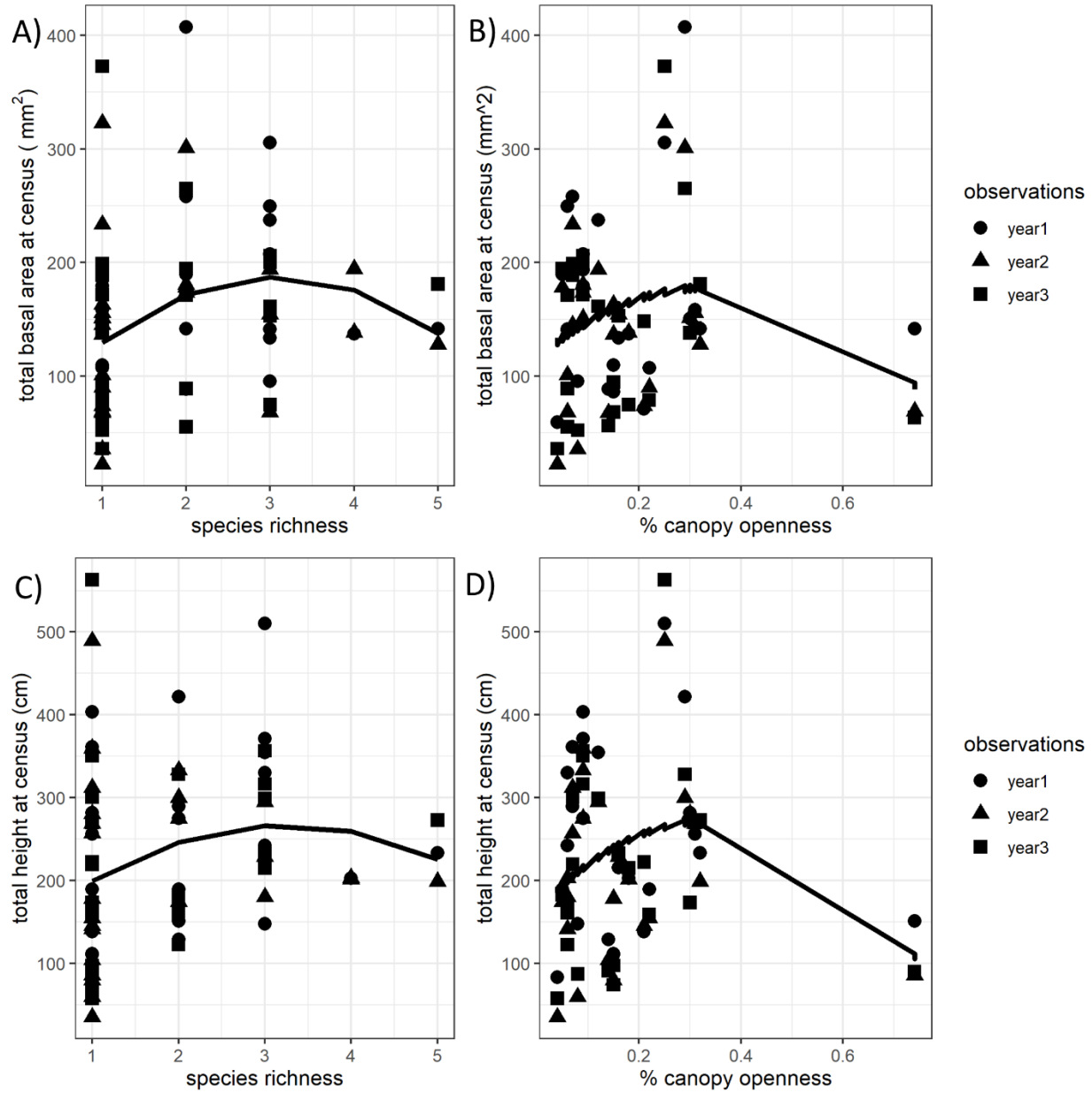
Figure 6: Observational data from long term plots. Generalised linear models of total basal area as a function of A) species richness and B) canopy openness and total height as a function of C) species richness and D) canopy openness.

Discussion

363 We found that light modulates the positive effect of species diversity on biomass accumulation in

364 seedling communities. In even-aged, experimental tree seedling communities, representing the

365 onset of regeneration, community growth was increased by both light levels and species

366 diversity. Further, we show that this increase in growth at the community level is mirrored at the

367 individual seedling level as well, even across species varying in functional types and growth

368 rates. Ultimately, we show that complementarity with non-random overyielding likely drives

369 biomass accumulation in seedling communities under combined biotic and abiotic influences in

370 seedling communities. Taken together, our results demonstrate a critical need to integrate biotic

371 and abiotic factors that structure diversity and ecosystem functioning. Our results lay

372 groundwork to further understanding of future forest diversity and ecosystem functioning by

373 disentangling processes that structure tree communities under regeneration.

374 Our results show that in the first and most crucial year of growth, biomass accumulation in

375 seedling communities can be influenced independently and additively by light and species

376 diversity. Seedling communities planted with higher species richness and under canopies with

377 higher light had higher values of basal area and height after a year of the experiment (Fig. 2)

378 (Sapijanskas et al., 2013; Shen et al., 2021). This demonstrates a potential additive influence of

379 diversity and light on community level seedling growth. However, the increase in biomass was

380 clearly observable only at the higher level of species richness or in the deciduous canopy

381 treatment indicating that growth responses to these factors are not linear at the community level

382 (Fig 2). Lending weight to experimental results, such non-linear responses of plot-level biomass

383 to light were also observed in the naturally regenerating communities; although light increased

384 standing biomass of seedlings, a single plot with the most open canopy had low values of

385 biomass (Fig 6). Although there were clear biomass gains with species richness in experimental

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386   plots, standing biomass increased weakly along the observed species diversity gradient (Fig 2,

387   Fig 6). Under natural regeneration, species composition varies with microclimate conditions; for

388   example, deciduous canopies with higher light have higher abundances of deciduous seedlings

389   below them (Souza et al., 2014). Such niche partitioning by these functional groups and

390   associated differences in growth rates could potentially explain weak relationships with species

391   richness in natural communities.

392   We show that in seedling communities, overyielding with increasing richness can be explained

393   by species complementarity rather than the increased probability of sampling faster growing or

394   higher yielding species (Fig 3). Increasing diversity led to overyielding in communities (Fig 3),

395   as expected from other studies on forest ecosystems (H. Pretzsch et al., 2015; Sapijanskas et al.,

396   2013; Van de Peer et al., 2018). Beyond species richness, species functional composition

397   influenced the survival and growth of communities (Fig S1, Fig S2) (Potvin & Gotelli, 2008;

398   Salisbury & Potvin, 2015; Shen et al., 2020; Yang et al., 2013). However, despite considerable

399   differences in growth rates among experimental species, inclusion of fast-growing species alone

400   did not explain the observed increase in biomass in high-diversity treatments (Fig 3). In fact,

401   selection effects decreased progressively from low to high species treatments, while

402   complementarity effects increased (Fig 3). Such evidence about biodiversity-driven mechanisms

403   in early life history stages of trees is lacking, but our results extend emerging evidence of

404   complementarity in seedlings of forest species under constant environments (Bastias et al., 2021)

405   and suggest that under heterogeneous environments, too, complementarity drives regeneration

406   dynamics.

407   Deviating from purely competition-driven (complementarity) or probabilistic (selection) effects,

408   our results indicate that the positive effect of biodiversity in heterogeneous environments can be

409   driven by complementarity with non-random overyielding (Isbell et al., 2018). Contrary to

410   expectations of differential responses by functional groups across different light conditions,

411   individuals across species, on average gained more biomass with higher light and higher species

412   richness in the community (Fig 4). In other words, fast-growing, high yielding, deciduous

413   species continued to outperform slower growing evergreen species across all conditions, but

414   species diversity and light increased yield for all species, leading to higher biomass in high light,

415   high diversity treatments (Fig 5). Light and diversity-mediated increases in individual growth

416   across species suggests strong resource and light competition within these communities, in

417   agreement with other studies on tree seedlings (Lu et al., 2021; Madsen et al., 2020; Promis &

418   Allen, 2017).

419   Grassland species as well as mature trees show significant spatial and temporal insurance effects,

420   which we did not detect on tree seedlings (Bunker et al., 2005; Isbell et al., 2018; and as

421   reviewed in Loreau et al., 2021). This implies that although functional differences in mature trees

422   might stabilise production through differential growth under heterogenous environments, these

423   differences do not produce similar asynchrony in seedling communities. Instead, strong

424   complementarity in seedling communities is a possible consequence of high intraspecific

425   competition in these stages or growth suppression by plant enemies (Inman-Narahari et al.,

426   2016). Our initial results indicate the need to explore these mechanisms further across diverse

427   ecosystems and life history stages.

428   Broadly, we show that the potential for diversity to maintain ecosystem functioning is affected

429   by changing environmental conditions. In the highest light conditions in our experiment, biomass

430   at the community level was not improved significantly or consistently with increasing diversity

431   (Fig 2). Moreover, for individual seedlings, the proportional gain with increasing light was

432   lower in high diversity treatments, indicating the limits of these positive outcomes, potentially

433   due to other competitive interactions (Fig 4) (Rüger et al., 2011). These patterns may be driven

434   by altered aboveground competition for light in high diversity communities, resulting from fast

435   growth by some species and rapid vertical stratification observed during the experiment (Lu et

436   al., 2021; Sapijanskas et al., 2014). Further, although light treatments in our study represent a

437   strong driver of community structure in these forest understories, increased light could lead to

438   both increased photosynthesis and increased water stress with consequent divergent effects on

439   growth, that could interact with species diversity (O'Brien et al., 2017). While our results hold

440   for both these processes acting together and represent realism to understand within-stand

441   dynamics, these effects may be dissociated across forest stands and need further disentangling.

442   More generally, multiple abiotic factors, including light, soil nutrients and soil moisture affect

443   seedling dynamics in these forests. The strength of the biodiversity effect and the mechanisms

444   through which it affects yield are likely to vary across forests structured by different

445   environmental factors (García et al., 2018; Thompson et al., 2018, 2021).

446   Our findings have broad implications for understanding the interaction between multiple drivers

447   and their influence on ecosystem functioning. Altered environmental conditions through global

448   and local drivers combined with biodiversity loss across biomes have heightened the

449   vulnerability of several ecosystem functions and services (Delzon et al., 2012; Heilpern et al.,

450   2018). However, many mechanistic and simulation models that quantify forest futures continue

451   to deal with single-species stands, simplified dynamics with light and focus largely on tree

452   mortality than regeneration (Hans Pretzsch et al., 2015; Strigul et al., 2008). Our study adds to

453   the understanding of future forest composition through by experimentally disentangling

454   mechanisms that affect early growth stages (Shen et al., 2021; Uriarte et al., 2018). We show that

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455 biodiversity effects on biomass gain in early growing stages of long-lived tree species can be

456 modulated by abiotic factors. In the light of renewed understanding from this study, predictions

457 of future composition and ecosystem functioning need to include community-based approaches

458 and regeneration dynamics. Updated models for regeneration that include interactions between

459 biotic and abiotic drivers and outcomes at the community level are crucial for predictions of

460 ecosystem functioning in a changing world.

461

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