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Hydraulic diversity stabilizes productivity in a large-scale subtropical tree biodiversity experiment

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Abstract

Extreme climatic events threaten forests and their climate mitigation potential globally. Understanding the drivers promoting ecosystem stability is therefore considered crucial to mitigate adverse climate change effects on forests. Here, we use structural equation models to explain how tree species richness, asynchronous species dynamics and diversity in hydraulic traits affect the stability of forest productivity along an experimentally manipulated biodiversity gradient ranging from 1 to 24 tree species. Tree species richness improved stability by increasing species asynchrony. That is, at higher species richness, inter-annual variation in productivity among tree species buffered the community against stress-related productivity declines. This effect was mediated by the diversity of species' hydraulic traits regarding drought tolerance and stomatal control, but not by the community-weighted means of these traits. The identified mechanisms by which tree species richness stabilizes forest productivity emphasize the importance of hydraulically diverse, mixed-species forests to adapt to climate change.

Introduction

Climate change is increasing the frequency and severity of droughts and other extreme events, threatening tree growth and survival globally[1], including in comparably humid tropical and subtropical forests[2]. This compromises the ability of the world's forests to act as a carbon sink[3] and as a nature-based solution to climate change[4]. Stability, the ability of forests to maintain functioning in periods of stress, is consequently emerging as a primary focus of forest management in the 21st century. One key management strategy to enhance stability may be to increase tree species richness in secondary and plantation forests[5-7]. However, we lack a comprehensive understanding of what drives biodiversity–stability relationships in forest ecosystems.

58

59   There is compelling evidence that species richness can stabilize community biomass production

60   against variable climate conditions such as droughts or extremely wet years[8–11]. However, the

61   majority of this evidence comes from grassland ecosystems. Biodiversity–stability relationships

62   likely differ between forests and grasslands because trees invest in long-lasting structures and

63   therefore community composition changes more slowly in forests[7]. The few existing studies in

64   forests support the notion that species richness stabilizes aboveground wood production, hereafter

65   referred to as 'productivity', of mixed-species tree communities[7,12–14], but the underlying

66   mechanisms remain largely unknown.

67

68   According to the insurance hypothesis[15,16] a mixture of tree species with different strategies should

69   help to maintain or increase the functioning of forests under highly variable climatic conditions,

70   thus increasing their temporal stability. This stability[17] is often quantified as temporal mean

71   productivity (μ) divided by the temporal standard deviation in productivity (σ)[e.g.8,9] and may be

72   promoted by diversity in mixed-species tree communities via two principal mechanisms[15]. First,

73   overyielding, which refers to an increased temporal mean productivity in mixtures compared to

74   monocultures, has been reported by numerous studies in natural and experimental forests[18–21].

75   Here, different species perform relatively better in mixtures than in monocultures, for example

76   through complementary resource use or facilitation and this higher performance can increase

77   stability[7]. Second, decreased temporal variation in community productivity through buffering of

78   the effects of stress may increase stability. In contrast to overyielding, little is known about this

79   buffering effect of biodiversity in forest ecosystems. Various mechanisms may decrease temporal

80   variation in productivity[15,17,22,23] but arguably the one most supported by theoretical and

81   observational studies in grasslands and increasingly also in forests is species asynchrony[8,22,24]. In

82   forests, these asynchronous inter-annual dynamics in productivity among tree species (hereafter

83   'species asynchrony'[23]) have been found to be the strongest driver of community stability[7,12–14,25].

84   Asynchronous species dynamics may result from intrinsic rhythms like phenology or mast

85   seeding[26,27], differential responses of species to extrinsic factors such as climatic conditions[23,28]

86   and species interactions in mixtures like resource partitioning or biotic feedbacks[29,30]. Species

87   asynchrony may buffer the temporal variation in community productivity during times of stress as

88   some species likely maintain functioning or compensate for the productivity losses of other species

89   (Fig. 1). This stabilizing effect may be especially important in the context of the global increase in

90   the severity and frequency of drought events[31,32]. Hence, there is an urgent need to identify the

91   characteristics that allow tree species and species mixtures to maintain functioning under future

92   drought conditions.

93

94   While the number of species may increase stability, communities also require certain hydraulic

95   characteristics to endure drought. Among other features such as non-structural carbohydrates[33],

96   two key hydraulic strategies that determine a tree's response to drought are drought tolerance and

97   stomatal control[28]. First, drought tolerance depends on xylem resistance to cavitation because

98   embolism decreases water availability and may ultimately lead to desiccation and tree death[2,28].

99   Here, we use the threshold at which 50% of xylem conductivity is lost due to cavitation (Ψ_{50};

100   measured as water potential) as key trait[2] and, in addition, classic traits of the leaf economics

101   spectrum (indicating conservative vs acquisitive resource use)[34] to quantify drought tolerance.

102   Second, tree species may follow different strategies of stomatal control. Some rely on continued

103   water extraction and keep their stomata open, i.e. they continue to transpire even though this poses

104   a high risk for cavitation-induced mortality under extreme drought (called water-spenders or

105   anisohydric species)[28,35,36]. Other tree species decrease their stomatal conductance quickly during

106   water shortage to avoid transpiration losses and xylem cavitation but may risk carbon starvation

107   under prolonged droughts (called water-savers or isohydric species). Consistent with recent

108   perspectives[36], we view stomatal control here along a gradient from water-spending to water-

109   saving species behaviour and quantify it through physiological traits such as stomatal conductance

110   and control of conductance under increasing water pressure deficits[37,38].

111

112   These different hydraulic strategies may enable mixed-species forests to stabilize community

113   productivity in two ways. First, tree species richness may increase stability indirectly via

114   promoting species asynchrony through diversity in functional traits related to hydraulic water

115   transport (hereafter 'hydraulic diversity'[39]). The importance of tree species richness and species

116   asynchrony for stability is supported by previous studies[7,12–14]. However, these studies were based

117   on observational data from naturally assembled forests (with only one exception[14]) and tree species

118   richness gradients were short. Therefore, it remains difficult to establish causal relationships

119   between tree diversity and stability. In particular, the mechanistic links between tree species

120   richness, species asynchrony and stability as well as the underlying trait-based mechanisms remain

121   unknown for forests. Second, stability could also be influenced by the community-weighted mean

122   of hydraulic traits, as indicated by findings in grassland diversity experiments where stability was

123   higher in communities dominated by species with traits associated with conservative resource use[8].

124   However, as we expect species asynchrony to be the key driver of stability in forests, we consider

125   trait diversity more important for stability than community trait means.

126

127   We use structural equation models (SEMs) to test the direct and indirect effects of species richness,

128   species asynchrony, hydraulic diversity and community-weighted means of hydraulic traits on the

129   stability of community productivity under the controlled conditions of a large-scale tree

130   biodiversity experiment (BEF-China[18,40]; biodiversity–ecosystem functioning China). Our

131   experiment is located in the highly diverse subtropical forests of China and features a gradient of

132   species richness ranging from monocultures up to mixtures of 24 tree species planted at two sites

133   using multiple species pools. All species occurred at all richness levels, thus avoiding any

134   confounding between species occurrence and richness. In our study, stomatal control and drought

135   tolerance strategies form two orthogonal species trait gradients (Supplementary Fig. 1), which

136   allows us to quantify their relative contributions to species asynchrony and stability. Specifically,

137   we tested the following hypotheses:

138

139   **H1** Tree species richness increases stability via species asynchrony.

140

141   **H2** Hydraulic diversity in stomatal control and drought tolerance strategies increases stability

142   through species asynchrony.

143

144   **H3** Stability increases through buffered temporal variation in productivity mediated by species

145   asynchrony and by overyielding.

146

Results

148   Overall, the stability of community productivity significantly increased with species richness in

149   our experimental tree communities. We found significant positive relationships between stability,

150   species asynchrony and hydraulic diversity – calculated as functional dispersion of species along

151   two trait gradients related to stomatal control (functional diversity of stomatal control) and

152   resistance to cavitation (functional diversity of drought tolerance) (Fig. 2; Supplementary Figs. 1-

153   4; Supplementary Table 1–2). In contrast, community-weighted means (CWMs) of these hydraulic

154   gradients did not influence the stability of productivity (Supplementary Fig. 5; Supplementary

155   Table 2). Specifically, we found a significant positive effect of species richness on stability

156   (t=3.98, P<0.001, n=375; Fig. 2), which was insensitive to the inclusion or exclusion of

157   monocultures into the models (Supplementary Fig. 6; Supplementary Table 2). Among the

158   analysed bivariate relationships species asynchrony had, as predicted, the strongest positive effect

159   on stability in mixtures and explained most of its variation (t=10.13, P<0.001, marginal R^2=34%,

160   n=218; Fig. 2; Supplementary Table 2). Species asynchrony significantly increased with species

161   richness (t=9.53, P<0.001), functional diversity of stomatal control (t=5.29, P<0.001) and

162   functional diversity of drought tolerance (t=5.84, P<0.001) (Supplementary Figs. 2-3). Direct

163   effects of hydraulic diversity on stability were weak: we found a marginally significant positive

164   effect of functional diversity of stomatal control on stability (t=1.92, P=0.058) but no significant

165   relationship with functional diversity of drought tolerance (t=1.12, P=0.27; Supplementary Fig. 4).

166   Hydraulic diversity explained a much higher share of variability in asynchrony than it did in

167   stability (Supplementary Table 2).

168

169   Structural equation models allowed us to disentangle the direct and indirect drivers and

170   connections behind observed diversity effects on stability (Fig. 3). Species asynchrony was the

171   principal mediator of indirect effects of species richness via hydraulic diversity on stability. Our

172   model fit the data well (Fishers' C=9.7, d.f.=8, P=0.28, n=218). The hypothesized pathways

173 explained 35% of variation in stability (fixed effects, marginal R^2), which increased to 58% if both

174 fixed and random effects (conditional R^2) were considered. Species richness, functional diversity

175 of stomatal control and functional diversity of drought tolerance explained 52% of variation in

176 species asynchrony (marginal R^2). Species asynchrony was the strongest direct driver of stability

177 (standardized path coefficient of direct effect 0.76, P<0.001). Tree species richness increased

178 stability indirectly through increasing species asynchrony (standardized path coefficient of

179 compound effect 0.35, i.e. the product of the coefficients along the path). We did not find an

180 additional independent effect of species richness on stability (P=0.31), indicating that species

181 asynchrony was the principal mediator of species richness effects on stability. Quantifying

182 hydraulic diversity allowed us to disentangle some of the functional drivers behind asynchronous

183 species responses: both functional diversity of stomatal control and functional diversity of drought

184 tolerance contributed to increased stability via positive effects on species asynchrony (standardized

185 path coefficients of direct effects on asynchrony 0.18, P=0.005 and 0.30, P<0.001, respectively).

186 Functional diversity of drought tolerance also had a direct negative effect (P=0.007) on stability,

187 that was smaller than its positive effect on asynchrony (standardized path coefficients of direct

188 effects –0.21 vs 0.30). Importantly, only functional diversity but not community-weighted means

189 of the hydraulic trait gradients explained variations in stability (effect of CWM of stomatal control

190 and CWM of drought tolerance on stability both not significant with P≥0.25; Fig. 3).

191

192 We further separated the components of our stability measure — the temporal mean (μ_{AWP}) and

193 the temporal standard deviation (σ_{AWP}) of productivity — to examine the underlying cause of the

194 observed biodiversity–stability relationships (Fig. 4). Tree species richness directly increased both

195 the mean and the standard deviation of productivity similarly (standardized path coefficients of

196   direct effects 0.23 and 0.30, respectively). Tree species richness thus increased mean productivity

197   but this was accompanied by increased variation in productivity. However, species richness also

198   decreased the standard deviation of productivity indirectly via its positive effect on species

199   asynchrony with about the same strength (indirect effect of species richness on σ_{AWP} –0.3,

200   calculated as the product of the coefficients along each significant path and their sum[41]; Fig. 4).

201   Species asynchrony, which increased with species richness and hydraulic diversity, hence

202   stabilized productivity through buffering its temporal variation (standardized path coefficient of

203   direct effect of species asynchrony on σ_{AWP} –0.47, P<0.001). The unexpected direct negative effect

204   of functional diversity of drought tolerance on stability (Fig. 3, see above) can be attributed to its

205   positive effect on the temporal standard deviation (Fig. 4, marginally significant, P=0.06). Finally,

206   the CWM of drought tolerance increased both, mean productivity and the standard deviation of

207   productivity (standardized path coefficients of direct effects 0.21 and 0.16, respectively). That is,

208   communities dominated by drought-intolerant species (those with higher trait gradient scores;

209   Supplementary Fig. 1) had a higher productivity but tended to also have a higher variation in

210   productivity. Overall, stability increased with species richness (Fig. 3) through increased mean

211   productivity (i.e. overyielding) and buffered temporal variation in productivity (Fig. 4).

212

Discussion

214   Our results provide experimental evidence that the insurance effect[15] of diversity stabilizes tree

215   productivity in forest ecosystems. We show that the stability of forest community productivity

216   increases with tree species richness and that asynchronous productivity of co-existing species in

217   response to climatic variation is the principal mediator of this diversity effect. As hypothesized,

218   both hydraulic diversity in stomatal control and drought tolerance had net positive, indirect effects

219   on stability that operated via enhanced species asynchrony. In contrast, the community-weighted

220   means of these hydraulic trait gradients did not influence stability.

221

222   **Species asynchrony and stability**

223   The controlled diversity gradient of the BEF-China experiment[40] ranging from monocultures to

224   mixtures of 24 tree species, detailed trait information and the use of structural equation models[41]

225   allowed us to disentangle the direct and indirect drivers of stability in forests in the absence of

226   confounding environmental variation typically hampering interpretations in observational studies.

227   We show here that species richness increases stability indirectly via promoting asynchronous

228   species productivity over time. Stability and species asynchrony were positively correlated with

229   tree species richness in former studies[7,12–14]. Our experimental results add support for the

230   hypothesized causality in these studies and demonstrate that species richness can drive species

231   asynchrony and thereby stability in highly diverse subtropical forests. Asynchronous productivity

232   integrates different mechanisms, such as those captured by the selected hydraulic traits that help

233   species to cope in different ways with the variable climatic conditions typical for the sites

234   (Supplementary Fig. 9). This species asynchrony due to diverse hydraulic strategies enhanced

235   stability via buffering (reducing) variation of productivity over the 10-year observation

236   period[7,8,13,15,23]. Species richness also increased temporal mean productivity directly. This finding

237   is in line with a rapidly increasing number of studies reporting that forest productivity increases

238   with increasing tree species richness[14,18–20]. However, this increased productivity by itself did not

239   increase stability because species richness also increased the temporal variation of productivity.

240   Stability only increased due to the variance buffering effect of species asynchrony on productivity

241   (Fig. 4).

242

243   The asynchronous growth dynamics of different species in our experimental tree communities

244   likely result from different, non-mutually exclusive mechanisms. First, extrinsic factors like

245   climate may increase species asynchrony. Species react differently to climatic conditions[e.g.2,28] and

246   species asynchrony is thus likely driven by differential growth responses of species in mixture to

247   climatic variability. Next, tree growth in mixtures is shaped by tree–tree interactions such as

248   resource partitioning and biotic feedbacks[21,29,30,42] which may in turn be modulated by variation in

249   climatic conditions[43–45]. Finally, intrinsic rhythms like mast seeding can influence species

250   productivity and its inter-annual variability[26] thereby inducing species asynchrony. These intrinsic

251   factors are, however, presumably less important in young forest stands. We thus expect that the

252   observed strong species asynchrony resulted from differential response strategies of species to

253   inter-annual variation in climatic conditions (the only environmental variable with strong inter-

254   annual variation during our 10-year study period; Supplementary Fig. 9) and how these strategies,

255   which we quantified via hydraulic traits, shape the nature of tree–tree interactions between years

256   with different climatic conditions.

257

258   **Hydraulic diversity and stability**

259   We used two orthogonal hydraulic trait gradients (Supplementary Fig. 1), related to species-

260   specific stomatal control and drought tolerance and explored their relative contribution to stability.

261   This allowed us to explain some of the mechanisms that induced asynchronous growth dynamics

262   and stabilized productivity in the face of highly variable climatic conditions. According to a

263   contextualization of the stress-gradient hypothesis' for forests[46], complementary species

264   interactions likely increase in frequency and intensity with decreasing resource availability. Hence,

265   while we show that species asynchrony increased with dissimilarity in hydraulic traits, we expect

266   that the relative importance of these traits for tree productivity is higher in dry years than in years

267   with ample water supply. Consistent with this expectation, we found the strongest positive tree

268   species richness effects on tree growth during severely dry years in former studies[14,43]. This

269   climate-driven biodiversity effect was modulated by a species drought tolerance at our study site

270   (quantified as in this study as resistance to cavitation; Ψ_{50})[43]. Hence, we consider the hydraulic

271   traits used here to be suitable response traits that capture inter-annual changes in productivity as

272   driven by inter-annual variation in climatic conditions. This is in line with the ubiquity of

273   vulnerability to drought across all forest ecosystems[2], including comparably humid subtropical

274   forests.

275

276   Functional diversity in stomatal control increased species asynchrony and thus indirectly stability

277   through reducing variation in productivity. This effect of hydraulic diversity on stability is

278   consistent with recent evidence that tree hydraulic diversity buffers temporal variations in forest

279   ecosystem carbon fluxes during drought[39]. Functional diversity in stomatal control may promote

280   species asynchrony among water spenders and water savers. The former keep their stomata open

281   and continue to transpire during drought. This strategy, however, likely relies on continuous water

282   uptake via roots to balance transpiration losses and carries high cavitation risks[28,36], a principle

283   mechanism behind drought-induced mortality across tree taxa[47]. Conversely, water savers can

284   reduce this risk but may face carbon starvation under prolonged droughts[28] even though starvation

285   is less ubiquitous than cavitation[47]. These contrasting stomatal control strategies themselves may

286   induce strong inter-annual changes in tree growth while also determining the water availability in

287   mixed-stands through soil water partitioning between co-existing species[48,49]. In tree

288 neighbourhoods comprising species with different stomatal control strategies, water spenders may

289 benefit from soil water left by their water-saving neighbours during drought, while water savers

290 may capitalize on improved soil water conditions after a drought due to their potentially faster

291 drought recovery[48]. Both may thus profit from neighbourhood species richness as the likelihood

292 for functional dissimilar species increases with species richness. Diversity in stomatal control is

293 therefore one potential mechanism that explains reported positive neighbourhood species richness

294 effects on individual tree growth especially during drought[14,43] but conceivably also during wetter

295 years.

296

297 Functional diversity in drought tolerance had a stronger positive influence on stability via

298 asynchronous species productivity but also a direct (albeit weaker) negative effect on stability.

299 Whereas drought-tolerant species can stabilize productivity of mixed-species communities

300 through lower risks for xylem cavitation during dry years[2,28], the latter, characterized by traits

301 associated with an acquisitive resource use strategy[37] (see Supplementary Fig. 1), can stabilize

302 productivity in wet years. This acquisitive resource use may, moreover, enable soil water

303 partitioning between neighbours during dry years in favour of drought-intolerant species[43]. The

304 reasons for the additional direct negative effect of drought tolerance diversity on stability remain

305 speculative. Nevertheless, as it resulted from increased temporal variation in community

306 productivity at higher species richness (Fig. 4), it might be related to a dieback of highly drought-

307 sensitive species in drought years destabilizing community productivity.

308

309 The direct positive effects of species richness on species asynchrony, remaining after accounting

310 for the indirect effects via hydraulic diversity, may result from dissimilarity in traits[8] that were not

311 considered here such as leaf phenology[27], storage of non-structural carbohydrates[33], traits

312 regulating biotic feedbacks[29] and below- and aboveground structural traits[50–52]. For example,

313 rooting-depth, complementary water uptake through niche differentiation[53] and facilitation via

314 hydraulic redistribution[48] between species could be important drivers of species asynchrony and

315 stability belowground.

316

317 **Community hydraulic means and stability**

318 In contrast to hydraulic diversity, we did not find effects of community-weighted means of

319 hydraulic traits on stability. Species asynchrony, the key driver of stability, depends naturally more

320 on diverse species strategies (see Fig. 1) than on the prevalence of a specific strategy within a

321 community. The absence of community mean effects on stability and the preponderance of

322 negative selection effects developing over time in our experiment[18] underlines that the observed

323 responses are not simply related to communities becoming increasingly dominated by particularly

324 stable-growing species with stand development. We found some indication for increased

325 productivity in communities dominated by rather drought-intolerant (acquisitive) species,

326 consistent with the common expectation for 'fast' growth of these species[34,54]. However, this did

327 not influence stability because the same communities also had increased variation in productivity,

328 likely because they were susceptible to drought. In the future, research should focus on how tree

329 species richness, hydraulic diversity and community-weighted means of hydraulic traits affect

330 population stability and potentially individual tree stability in addition to community stability. For

331 instance, empirical work in forests found neutral[12] or positive[7] effects of species richness on

332 population stability while studies in grasslands often reported a destabilizing effect of diversity on

333 population stability[10].

334

335 **Outlook**

336 The frequency and severity of droughts and corresponding surges of tree mortality is dramatically

337 increasing across the globe[31,32]. This situation is expected to worsen with intensifying climate

338 change[1], which threatens the climate mitigation potential of the world's forests[3]. We show that the

339 stability of forest community productivity along a 10-year observation period increases with tree

340 species richness and that the key driver behind this diversity effect are the asynchronous growth

341 dynamics of different tree species in hydraulically diverse communities. Importantly, stability did

342 not compromise productivity. Instead, reduced temporal variation in productivity coincided with

343 increased productivity in mixed-species tree communities. Hence, mixing tree species with a

344 diversity of hydraulic strategies is likely a key management strategy to increase forest stability and

345 their potential to mitigate the effects of climate change. Hydraulic traits may be used to select

346 suitable tree species and design mixtures that stabilize productivity in an increasingly variable

347 climate. Here, we examined the stability of young forest communities established as part of a large-

348 scale biodiversity experiment. At the end of the observation period, tree height reached >10m in

349 25% of the experimental communities. It is conceivable that diversity effects on stability may

350 strengthen as these stands mature, as indicated by the strengthening diversity effects on

351 productivity[18] and by results from an observational study that found stronger positive effects of

352 species asynchrony on stability in old-growth than in secondary forests[25]. Our results extend

353 research on forest stability from observational studies in relatively species-poor forests[7,12,13] to

354 species-rich subtropical tree communities growing under experimental conditions. This allowed

355 establishing causality and avoiding confounding effects of environmental variation, major issues

356 in observational studies. Stability increased consistently with tree species richness and did not

357   plateau at low levels of tree species richness, which underlines the enormous potential of species

358   richness to improve stability in many of our species-poor or mono-specific secondary and

359   plantation forests around the world. This finding has important implications; contemporary

360   forestry, and especially large-scale forest restoration initiatives[4], like the Bonn Challenge, should

361   focus on hydraulically diverse, mixed-species forests to enhance stability in a changing climate.

362

Methods

Study site and experimental design

365   In this study, we used data collected from the Tree Biodiversity–Ecosystem Functioning

366   Experiment China (BEF-China, www.bef-china.com), located at Xingangshan, Dexing, Jiangxi

367   (29° 08′–29° 11′N, 117° 90′–117°93′E). BEF-China[18,40] is a large-scale tree biodiversity

368   experiment that was established at two sites, A and B, each approximately 20 ha in size and planted

369   in 2009 (site A) and 2010 (site B). The study sites are characterized by a subtropical, seasonal

370   monsoon climate with hot and humid summers and dry and cool winters with a mean annual

371   temperature of 16.7°C and mean annual precipitation of 1821mm[55]. The sites experienced strong

372   inter-annual changes in climate-induced water availability during the 10-year observation period

373   (Supplementary Fig. 9), with annual precipitation being more variable than temperature at our

374   study sites[18]. The highly diverse native subtropical forests of the area are dominated by

375   broadleaved mixed evergreen and deciduous tree species, sometimes interspersed with some

376   conifers[40]. These forests are located in an area of overlap between tropical and temperate zones[56,57],

377   which makes them ideally suited to study diverse water use strategies and idiosyncratic species

378   asynchrony as drivers of biodiversity–stability relationships. Furthermore, the region is densely

379   populated and experiences frequent anthropogenic disturbances[56], which makes the maintenance

380   and improvement of the functioning of these forests important for the global ecosystem balance

381   and restoration efforts.

382

383   The experiment covers a richness gradient ranging from 1–24 tree species. Communities have been

384   assembled from a total pool of 40 native broadleaved evergreen and deciduous tree species (see

385   Supplementary Table 3 for detailed species information). To ensure the representation of all

386   species at each diversity level, mixture compositions were randomly allocated following a 'broken-

387   stick' design[40]. In total 226,400 individual trees were planted on 566 plots[40]. In this study, we used

388   data from six random extinction scenarios allocated to site A and B (three at each site) with a total

389   of 396 plots and 158,400 planted trees[18]. Of these, we excluded 21 plots prior to our analysis due

390   to failed establishment success, which left 375 plots (n=218 mixtures and n=157 monocultures)

391   for our analysis. Each plot had a size of 25.8×25.8 m^2 with 400 individual trees planted in $20 \times$

392   20 regular gridded positions (spacing 1.29m between trees). Tree positions and species

393   compositions were randomly assigned to plots. More detailed information about the BEF-China

394   experiment can be found in Huang *et al.* and Bruelheide *et al.*[18,40].

395

Tree data collection

397   Individual tree basal diameter at 5 cm above ground level (*gd*), tree height and species identity

398   were measured annually from 2010 (site A) and 2011 (site B) onwards at the end of the growing

399   season. To avoid edge effects, the central 12×12 trees were measured for each plot in the 4-, 8-,

400   16- and 24-species mixtures, while a smaller group of the central 6×6 trees was measured for

401   monocultures and 2-species mixtures. Missing tree diameter and height values (in total 2% of

402   census data) were imputed if the increment series was otherwise logical, i.e. $value_{x+1} \geq$

403    $value_{x-1}$. To preserve climate-induced growth changes between years during imputation, we used

404   a modelled site-specific rate of growth changes for each yearly step (r) based on complete

405   increment series of trees with logical (i.e. with annual increases) and complete census data. A

406   missing tree value was imputed as: $(v_{x+1} - v_{x-1}) * r_x + v_{x-1}$, where v is the *gd* or *height*

407   measurement in a year and r the rate of change (see Supplementary Method 1 for details). Overall,

408   we used annual data of 12,852 planted trees from 2010 to 2019 at site A and of 12,204 trees from

409   2011 to 2019 at site B to estimate community- and species-level productivity.

410

411   **Calculation of aboveground wood production**

412   We used aboveground wood volume production as measure of community and species level

413   productivity. First, annual aboveground wood volume per tree (awv, m^3) was calculated with a

414   fixed form factor of 0.5 (to account for the non-cylindrical shape of trees), which is an average

415   value for the young subtropical trees in our experiment[21,58]; with

416

417    $awv = gd * h * f,$ (1)

418

419   where *gd* is the basal area at measured tree ground diameter, *h* the measured tree height and *f* the

420   form factor. Second, aboveground wood volume production (awp, m^3 year^{-1}) per tree and year was

421   calculated as

422

423    $awp = awv_{t+1} - awv_{t-1},$ (2)

424

425   where t is an index for the year of measurement. Finally, *awv* and *awp* of all trees planted as part

426   of the original design were summed per species and plot and scaled to 1 ha (based on the sampled

427   subplot areas) to derive annual estimates of aboveground wood volume and volume production

428   per species (AWV$_s$, m^3 ha^{-1}; AWP$_s$, m^3 ha^{-1} year^{-1}) and community (AWV, m^3 ha^{-1}; AWP, m^3 ha^{-}

429   ^{1} year^{-1}), referred to as species and community 'productivity'. A value of 0 was used in case of

430   species or plots with no alive tree individuals within individual years (note that completely failed

431   plots were excluded from the analysis, see above). Our annual productivity estimates thus cover a

432   complete series of forest growth over the course of 9 and 8 years for site A and B, respectively.

433

434   **Stability and asynchrony of production**

435   The temporal stability[17] of tree community productivity, hereafter 'stability', was calculated as the

436   inverse of the coefficient of variation:

437

438    $Stability = \frac{\mu_{AWP}}{\sigma_{AWP}}$ (3)

439

440   where μ_{AWP} is the temporal mean and σ_{AWP} the temporal standard deviation of annual plot

441   productivity for our observation period (2010–2019 for site A and 2011–2019 for site B). Thus,

442   any diversity effect that leads to overyielding (a higher productivity of mixtures vs monocultures)

443   increases stability through increasing temporal mean productivity μ_{AWP}. Conversely, any diversity

444   effect that buffers variations in productivity against changing climatic conditions would increase

445   stability through decreasing σ_{AWP}[15]. We hypothesize here that asynchronous species growth

446   dynamics to changing climatic conditions is the dominant mechanism that stabilizes young tree

447   communities through lowering their productivity variance. To test this we calculated community-

448   level species asynchrony using the species synchrony statistic φ[22] as $1 - \varphi$:

449

450    $$Species\ asynchrony = 1 - \frac{\sigma_{AWP}{}^2}{(\sum_{i=1}^{n} \sigma_{AWP_{s\,i}})^2} \qquad (4)$$

451

452   where $\sigma_{AWP_{s\,i}}$ is the temporal standard deviation of the annual productivity of species i in a plot of

453   n species[7,59]. Thus, species asynchrony increases if the variance in individual species productivity

454   increases relative to the variance in community productivity. Species asynchrony ranges from 0

455   (complete synchrony) to 1 (complete asynchrony) and is per definition 0 in monocultures as here

456   variations in community productivity result from variations within a single species[7]. We expect

457   here that species asynchrony increases stability through lowering the variation in community level

458   productivity[7]. Young tree communities, as the ones examined here, show a strongly increasing

459   productivity over time. As this age trend strongly masks annual variations in productivity, we

460   removed it and calculated stability as temporal mean productivity divided by its detrended standard

461   deviation. Similarly, species asynchrony was calculated based on detrended plot and species level

462   productivity. Detrending was performed for each plot and species per plot through regressing

463   annual productivity against time and then calculating the standard deviation based on the residuals

464   of this regression following Craven *et al.* and Tilman *et al.*[8,10] (see Supplementary Fig. 10 for a

465   visualization of this approach).

466

467   **Trait gradients**

468   Species employ different strategies to cope with climate induced water variability, which are likely

469   related to a set of (hydraulic) functional traits (Anderegg *et al.*[39] and citations within). We

470   assembled species-specific hydraulic trait data related to stomatal control and drought tolerance

471   that was measured within the experiment (Supplementary Table 1; refs.[37,38]). Trait data were

472   subjected to a principal component analysis (PCA). The first and second axis partitioned the

473   hydraulic traits into two orthogonal trait gradients related to stomatal control (PC1) and drought

474   tolerance (PC2) (Supplementary Fig. 1). Based on physiological and morphological leaf traits, we

475   classified species as water spenders if they decrease their stomatal conductance only at high levels

476   of water pressure deficit, and as water savers, if they already decrease stomatal conductance at low

477   water pressure deficits and have leaves characterized by high stomatal density. We used the water

478   potential at which 50% of xylem conductivity is lost (Ψ_{50}) as key physiological trait to quantify a

479   species drought tolerance[2]. Higher values of Ψ_{50} (i.e. lower absolute values Ψ_{50}) indicate a higher

480   susceptibility to drought-induced xylem cavitation. We also included specific leaf area, leaf

481   toughness and carbon to nitrogen ratio as classic traits of the leaf economics spectrum (LES[34]) in

482   our analysis, which are associated with a species drought tolerance[37], to foster the still limited

483   understanding of trait syndromes that govern forest responses to climatic stress[36]. We used trait

484   data from 39 out of the 40 planted species (*Castanopsis carlesii* was excluded due to complete

485   establishment failure) and imputed two missing trait values (Ψ_{50} and stomatal density) for one out

486   of these 39 species (*Quercus phillyreoides*) with predicted mean value matching with 500 runs

487   using the R package mice[60]. PCA was performed with the *rda* function in the vegan package

488   version 2.5-6[61].

489

490   **Quantifying hydraulic diversity and community means**

491   We used the scores of the first and second PCA axis (Supplementary Fig. 1) as measure of the

492   species stomatal control and drought tolerance strategies within each community. Functional

493   diversity in traits associated with water spending vs water saving stomatal behaviour (hereafter

494   'functional diversity of stomatal control') and functional diversity of drought tolerance was

495   calculated with the 'FD' package as abundance-weighted functional dispersion[62,63] using temporal

496   mean species wood volume per plot as measure of species abundance. Functional dispersion

497   measures the mean distance of species along each trait gradient[62] and thus represents the

498   complementarity in hydraulic strategies of co-occurring species within each community. We

499   calculated community-weighted mean (CWM) trait values for both gradients, hereafter called

500   'CWM of stomatal control' and 'CWM of drought tolerance' using temporal mean species wood

501   volume per plot as measure of species abundance.

502

503   **Modelling framework and statistical analysis**

504   First, we analysed direct relationships between stability, its hypothesized drivers and relationships

505   between these drivers. Specifically, we used linear mixed-effect models (LMM) to test for

506   bivariate relationships between species richness, species asynchrony, functional diversity of

507   stomatal control, functional diversity of drought tolerance, CWM of stomatal control and the

508   CWM of drought tolerance. We also tested the effect of species richness and hydraulic diversity

509   on species asynchrony. LMM were fit with the nlme package version 3.1-144[64] to allow for the

510   specification of variance functions with a significance level of $\alpha=0.05$. Confidence intervals (95%)

511   of LMM effects were computed with the ggeffects package[65]. Tree species richness was $\log_2$

512   transformed in all models. As the two sites were planted one year apart, we tested for a potential

513   age effect and other site-specific influences on the biodiversity–stability relationship through

514   including site and its interaction with species richness as fixed effect. Diversity effects on stability

515   did not differ between sites (P=0.46 for the interaction). We therefore accounted for site and other

516   aspects of our experimental design through a nested random effect structure of site, species

517   composition and arrangement of plots within quadrants (see Huang *et al.*[18]). Model assumptions

518   were visually checked for independence and homogeneity of variance through examining model

519   residuals and for normal distribution with quantile-quantile plots. For all response variables we

520   tested the inclusion of an exponential variance structure[64] to model heteroscedasticity (parsimony

521   evaluated via AIC) and a log/square-root transformation to normalize residuals. As results did not

522   differ for any bivariate relationship, we present only the models without variance function or

523   transformation of response variables.

524

525   Second, we developed a hypothesis driven structural equation model (SEM) framework to

526   disentangle direct and indirect drivers of stability based on *a priori* knowledge of mechanisms

527   driving biodiversity–stability relationships (Supplementary Fig. 7). We explored whether the data

528   supported our first and second hypothesis through including indirect pathways that tested for

529   effects of the multiple diversity facets species richness, functional diversity of stomatal control

530   and functional diversity of drought tolerance on stability through effects mediated via species

531   asynchrony. We also included direct pathways from these diversity facets to stability, to test for

532   mechanisms not mediated by species asynchrony such as performance enhancing effects that

533   increase temporal mean productivity in mixtures[8,14,18]. To test for the effects of community trait

534   means we included direct pathways from the CWM of stomatal control and the CWM of drought

535   tolerance to stability[8,39]. As the experimental manipulation of species richness may directly affect

536   the functional diversity of a community[40], we included pathways from species richness to

537   functional diversity of stomatal control and functional diversity of drought tolerance. Piecewise

538   SEMs[41] were used to test the support for and relative importance of these hypothesized pathways.

539   To understand whether diversity effects on stability result from overyielding (increased μ_{AWP}), a

540   buffered variation (decreased σ_{AWP}) or both, we fit a separate SEM with these two components of

541   our temporal stability measure as response. In this second SEM, we tested all hypothesized effects

542   of diversity on stability for each of its two components (Supplementary Fig. 8).

543

544   Global model fit was assessed via Fisher's C statistic ($P>0.05$). We assessed the independence of

545   variables and included partial, non-directional correlations if these improved model fit based on

546   tests of directed separations ($P<0.05$ for violation of independence claims)[41]. For each SEM we

547   calculated standardized path coefficients, which allowed us to compare the strength of paths within

548   and among models and of indirect pathways (calculated as product of the coefficients along the

549   path)[41]. We fitted individual pathways with LMM using the same random structure and model

550   evaluation as for our analysis of bivariate relationships detailed above. In all SEMs stability,

551   species asynchrony, the temporal mean (μ_{AWP}) and the temporal standard deviation of productivity

552   (σ_{AWP}) were square-root transformed to best meet model assumptions. Our analysis focuses on the

553   role of species asynchrony and hydraulic diversity as drivers of biodiversity–stability relationships.

554   As species asynchrony and functional diversity in monocultures are per definition 0, we analysed

555   their effects within 2-, 4-, 8-, 16- and 24-species mixtures only to avoid many observations without

556   variation. Alternative models including monocultures yielded the same results for effects reported

557   here (Supplementary Figs. 6, 11–12). To further test the sensitivity of our models, we ran

558   alternative SEMs without response transformation but with an exponential variance structure for

559   log2 species richness. These yielded the same results (Supplementary Figs. 13–14). SEMs had low

560   variance inflation (Variance Inflation Factor < 5, a conservative threshold choice[66]). All analyses

561   were performed in R 3.6.2[67].

562

Author contributions

F.S. and X.L. are co-first authors. H.B., W.H., B.S., Z.T., B.Y., J.B., G.v.O., K.M. and C.W. designed the project; F.S., X.L., K.E.B., J.A.S., J.B. and C.W. conceived the idea for the manuscript; X.L., M.K., G.v.O., H.B., F.J.B., A.F., S.L., C.T.P. and F.S. collected and compiled data; F.S. analysed and interpreted the data and wrote the manuscript with support from X.L., K.E.B. and C.W.; F.S. and K.E.B. created figures; All authors discussed the results and contributed substantially to revisions.

583

584 **Data availability statement**

585 Data supporting the findings of this study have been deposited on the BEF-China project database

586 (https://data.botanik.uni-halle.de/bef-china/datasets/634) and are available upon reasonable

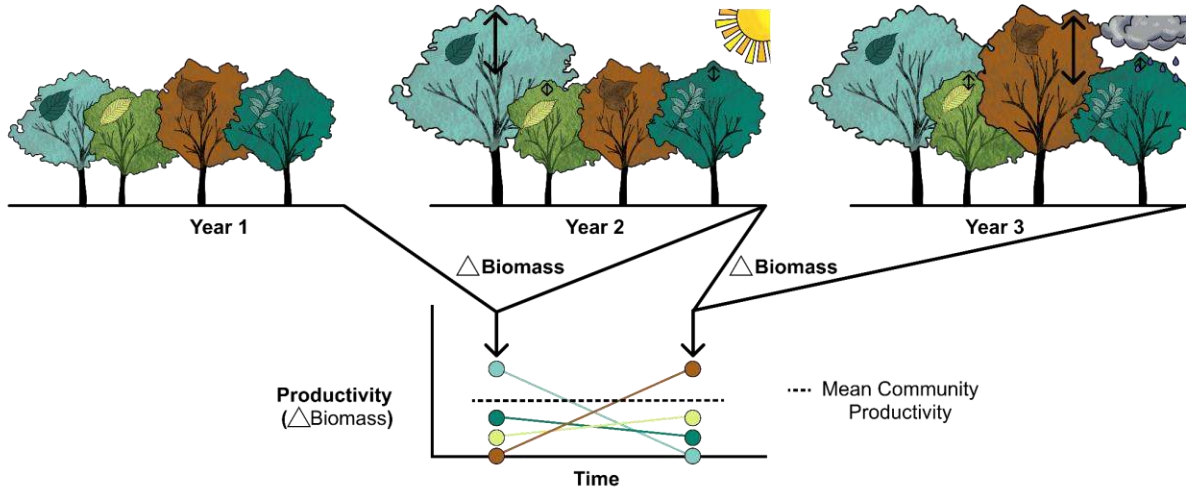587 request from the corresponding authors.

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Fig. 1 Graphical illustration of asynchronous species responses in mixed-species tree communities to contrasting climatic conditions over a period of three years. The tree community experiences a 'normal' (year 1), an exceptionally dry (year 2) and an exceptionally wet (year 3) year, which result in distinctly different growth responses of the participating species but the same community productivity due to compensatory dynamics. In our hypothetical example taken from a four species mixture in the BEF-China experiment, one species (*Nyssa sinensis*, light turquoise) does not close its stomata fast during water shortage (water-spender) and might grow well during drought, a second species (*Liquidambar formosana*, brown) exhibits a fast downregulation of stomatal conductance at increasing water pressure deficits and its productivity is thus more strongly reduced during drought (water-saver), while the two other species (*Castanea henryi*, *Sapindus mukorossi*) do not show strong reactions to the changing climatic conditions. The reverse response pattern is found during an exceptionally wet year. We hypothesize here that such asynchronous species dynamics are the key driver behind stabilizing effects of species richness on productivity in mixed-species forests and that the functional traits of co-existing species — especially those associated with hydraulic functioning — may help to elucidate the mechanisms that produce this species asynchrony.

615
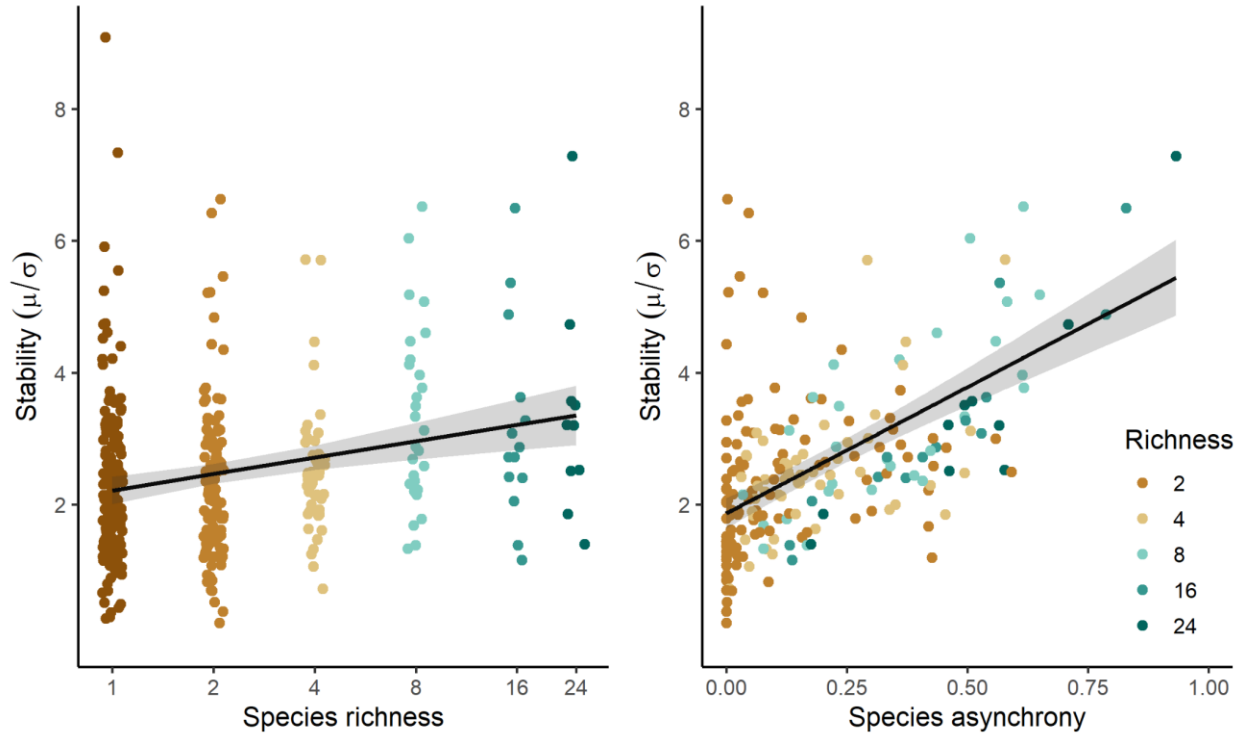
Fig. 2 Effects of species richness and species asynchrony on stability. Lines are linear mixed-effect model fits that show (a) significant increases in stability with species richness (P<0.001) along a planted diversity gradient ranging from monocultures up to mixtures of 24 tree species and (b) significant increases in stability with species asynchrony (P<0.001) in mixtures. Species asynchrony ranges from 0 to 1, where 0 represents complete synchrony and 1 complete asynchrony. Grey bands represent a 95% confidence interval. See Supplementary Table 2 for details on the fitted models.

624
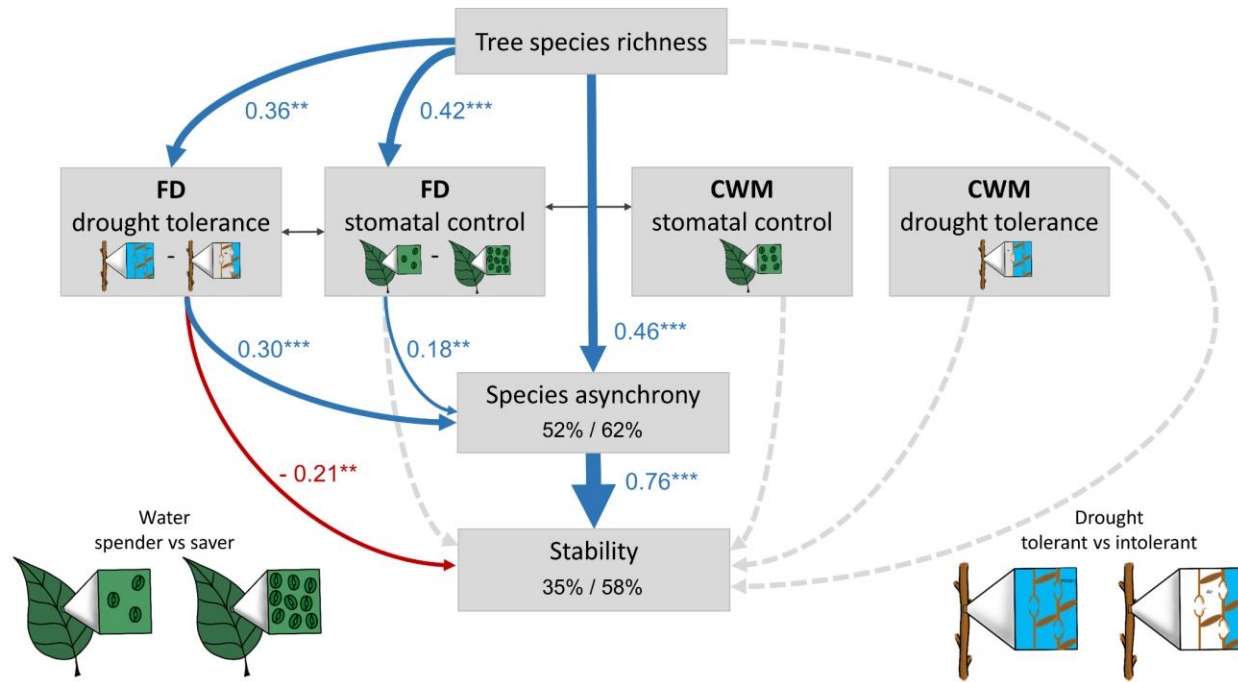
Fig. 3 Direct and indirect effects of species richness, hydraulic diversity and community hydraulic means on stability. The structural equation model (SEM) tests the direct effects of tree species richness, functional diversity of stomatal control (FD stomatal control) and functional diversity of drought tolerance (FD drought tolerance) as well as their indirect effects mediated via species asynchrony on stability. Effects of community-weighted mean (CWM) traits are explored through testing the effect of the CWM of stomatal control (CWM stomatal control) and the CWM of drought tolerance (CWM drought tolerance) on stability. The sketches schematically illustrate the trait gradients: water-spending vs water-saving stomatal control (few vs abundant stomata) and drought tolerance (high vs low cavitation resistance). Functional diversity was calculated as abundance-weighted functional dispersion. The SEM fit the data well (Fisher's C=9.7, P =0.28, d.f.=8, n=218 plots). Data is based on a long, experimental species richness gradient with mixtures of 2, 4, 8, 16 and 24 tree species. Examined variables are shown as boxes and relationships as directional arrows with significant positive effects in blue, significant negative effects in red and non-significant paths in dotted grey based on a hypothesis driven SEM framework (Supplementary Fig. 7). Standardized (significant) path-coefficients are shown next to each path with asterisks indicating significance (* P<0.05, ** P<0.01, *** P<0.001), path-width is scaled by coefficient size. Significant partial correlations[41] are

640   shown through grey, bi-directional arrows. The variation in species asynchrony and stability explained by

641   fixed (left, marginal R^2) and fixed together with random model effects (right, conditional R^2) is shown in

642   the corresponding boxes.

643
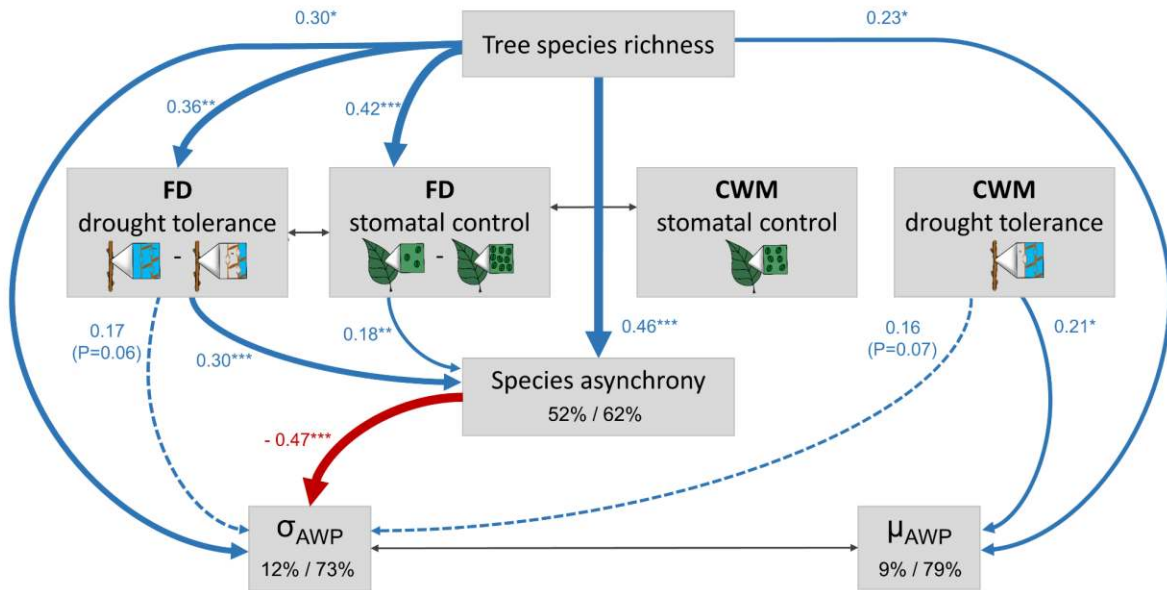
644

645   Fig. 4 Structural equation model (SEM) of direct and indirect effects of species richness, species

646   asynchrony, hydraulic diversity and community hydraulic means on the two components of stability, the

647   temporal mean (μ_{AWP}) and the temporal standard deviation of productivity (σ_{AWP}), which represent

648   overyielding and variance buffering effects, respectively. Increases in μ_{AWP} enhance stability through

649   overyielding — a higher productivity in mixtures vs monocultures — and decreases in σ_{AWP} enhance

650   stability through buffered variations in productivity. All drivers hypothesized to influence stability, i.e.

651   species richness, functional diversity of stomatal control (FD stomatal control), functional diversity of

652   drought tolerance (FD drought tolerance), CWM of stomatal control (CWM stomatal control), CWM of

653   drought tolerance (CWM drought tolerance) and species asynchrony, were tested for their effects on μ_{AWP}

654   and σ_{AWP}. Only significant pathways ($P<0.05$) are shown here to avoid overplotting (see Supplementary

655   Fig. 8 for the full model). The sketches schematically illustrate the trait gradients: water-spending vs water-

656   saving stomatal control (few versus abundant stomata) and drought tolerance (high versus low cavitation

657   resistance). The SEM fit the data well (Fisher's C=9.7, global P=0.28, d.f.=8, n=218 plots). Data is based

658   on a long, experimental species richness gradient with mixtures of 2, 4, 8, 16 and 24 tree species. Examined

659   variables are shown as boxes and relationships as directional arrows with significant positive effects in

660   blue, significant negative effects in red and non-significant paths in dotted grey. Standardized (significant)

661   path-coefficients are shown next to each path with asterisks indicating significance (* P<0.05, ** P<0.01,

662   *** P<0.001), path-width is scaled by coefficient size. Significant partial correlations[41] are shown through

663   grey, bi-directional arrows. The variation in species asynchrony, μ_{AWP} and σ_{AWP} explained by fixed (left,

664   marginal R^2) and fixed together with random model effects (right, conditional R^2) is shown in the

665   corresponding boxes.

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References

668   1. IPCC. *Climate change 2014. Impacts, Adaptation, and Vulnerability. Part A: Global and*

669   *Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the*

670   *Intergovernmental Panel on Climate Change* (Cambridge University Press, New York, NY,

671   2014).

672   2. Choat, B. *et al.* Global convergence in the vulnerability of forests to drought. *Nature* **491,** 752–

673   755; 10.1038/nature11688 (2012).

674   3. Anderegg, W. R. L. *et al.* Climate-driven risks to the climate mitigation potential of forests.

675   *Science* **368**; 10.1126/science.aaz7005 (2020).

676   4. Griscom, B. W. *et al.* Natural climate solutions. *PNAS* **114,** 11645–11650;

677   10.1073/pnas.1710465114 (2017).

678   5. Bauhus, J. *et al.* Ecological Stability of Mixed-Species Forests. In *Mixed-species forests.*

679   *Ecology and management,* edited by H. Pretzsch, D. I. Forrester & J. Bauhus (Springer Nature,

680   Berlin, Germany, 2017), pp. 337–382.

681   6. Verheyen, K. *et al.* Contributions of a global network of tree diversity experiments to

682   sustainable forest plantations. *Ambio* **45,** 29–41; 10.1007/s13280-015-0685-1 (2016).

683   7. Jucker, T., Bouriaud, O., Avacaritei, D. & Coomes, D. A. Stabilizing effects of diversity on

684   aboveground wood production in forest ecosystems: linking patterns and processes. *Ecol. Lett.*

685   **17,** 1560–1569; 10.1111/ele.12382 (2014).

686   8. Craven, D. *et al.* Multiple facets of biodiversity drive the diversity–stability relationship. *Nat.*

687   *Ecol. Evol.* **2,** 1579–1587; 10.1038/s41559-018-0647-7 (2018).

688   9. Isbell, F. *et al.* Biodiversity increases the resistance of ecosystem productivity to climate

689   extremes. *Nature* **526,** 574-577; 10.1038/nature15374 (2015).

690   10. Tilman, D., Reich, P. B. & Knops, J. M. H. Biodiversity and ecosystem stability in a decade-

691   long grassland experiment. *Nature* **441,** 629–632; 10.1038/nature04742 (2006).

692   11. Hector, A. *et al.* General stabilizing effects of plant diversity on grassland productivity through

693   population asynchrony and overyielding. *Ecology* **91,** 2213–2220; 10.1890/09-1162.1 (2010).

694   12. del Río, M. *et al.* Species interactions increase the temporal stability of community productivity

695   in Pinus sylvestris–Fagus sylvatica mixtures across Europe. *J. Ecol.* **105,** 1032–1043;

696   10.1111/1365-2745.12727 (2017).

697   13. Morin, X., Fahse, L., de Mazancourt, C., Scherer-Lorenzen, M. & Bugmann, H. Temporal

698   stability in forest productivity increases with tree diversity due to asynchrony in species

699   dynamics. *Ecol. Lett.* **17,** 1526–1535; 10.1111/ele.12357 (2014).

700   14. Schnabel, F. *et al.* Drivers of productivity and its temporal stability in a tropical tree diversity

701   experiment. *Global Change Biol.* **25,** 4257-4272; 10.1111/gcb.14792 (2019).

702   15. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment:

703   the insurance hypothesis. *PNAS* **96,** 1463–1468; 10.1073/pnas.96.4.1463 (1999).

704   16. Bertness, M. D. & Callaway, R. Positive interactions in communities. *Trends Ecol. Evol.* **9,**

705   191–193; 10.1016/0169-5347(94)90088-4 (1994).

706   17. Tilman, D. The ecological consequences of changes in biodiversity. a search for general

707   principles. *Ecology* **80,** 1455–1474 (1999).

708   18. Huang, Y. *et al.* Impacts of species richness on productivity in a large-scale subtropical forest

709   experiment. *Science* **362,** 80–83; 10.1126/science.aat6405 (2018).

710   19. van der Plas, F. Biodiversity and ecosystem functioning in naturally assembled communities.

711   *Biol. Rev.* **94,** 1220–1245; 10.1111/brv.12499 (2019).

712   20. Forrester, D. I. & Pretzsch, H. Tamm Review: On the strength of evidence when comparing

713   ecosystem functions of mixtures with monocultures. *For. Ecol. Manage.* **356,** 41–53;

714   10.1016/j.foreco.2015.08.016 (2015).

715   21. Fichtner, A. *et al.* From competition to facilitation. How tree species respond to neighbourhood

716   diversity. *Ecol. Lett.* **20,** 892–900; 10.1111/ele.12786 (2017).

717   22. Loreau, M. & de Mazancourt, C. Species synchrony and its drivers. Neutral and nonneutral

718   community dynamics in fluctuating environments. *Am. Nat.* **172,** E48-66; 10.1086/589746

719   (2008).

720   23. Loreau, M. & de Mazancourt, C. Biodiversity and ecosystem stability. A synthesis of

721   underlying mechanisms. *Ecol. Lett.* **16,** 106–115; 10.1111/ele.12073 (2013).

722   24. Valencia, E. *et al.* Synchrony matters more than species richness in plant community stability

723   at a global scale. *PNAS*; 10.1073/pnas.1920405117 (2020).

724   25. Yuan, Z. *et al.* Temporal stability of aboveground biomass is governed by species asynchrony

725   in temperate forests. *Ecol. Indic.* **107**; 10.1016/j.ecolind.2019.105661 (2019).

726   26. Mund, M. *et al.* The influence of climate and fructification on the inter-annual variability of

727   stem growth and net primary productivity in an old-growth, mixed beech forest. *Tree*

728   *physiology* **30,** 689–704; 10.1093/treephys/tpq027 (2010).

729   27. Du, Y., Yang, B., Chen, S.-C. & Ma, K. Diverging shifts in spring phenology in response to

730   biodiversity loss in a subtropical forest. *J. Veg. Sci.* **30,** 1175–1183; 10.1111/jvs.12806 (2019).

731   28. McDowell, N. *et al.* Mechanisms of plant survival and mortality during drought: why do some

732   plants survive while others succumb to drought? *New Phytol.* **178,** 719–739; 10.1111/j.1469-

733   8137.2008.02436.x (2008).

734   29. Barry, K. E. *et al.* The Future of Complementarity: Disentangling Causes from Consequences.

735   *Trends Ecol. Evol.* **34,** 167–180 (2019).

736   30. Grossiord, C. Having the right neighbors: how tree species diversity modulates drought impacts

737   on forests. *New Phytol.* **228,** 42–49; 10.1111/nph.15667 (2020).

738   31. Allen, C. D. *et al.* A global overview of drought and heat-induced tree mortality reveals

739   emerging climate change risks for forests. *For. Ecol. Manage.* **259,** 660–684;

740   10.1016/j.foreco.2009.09.001 (2010).

741   32. Schuldt, B. *et al.* A first assessment of the impact of the extreme 2018 summer drought on

742   Central European forests. *Basic Appl. Ecol.* **45,** 86–103; 10.1016/j.baae.2020.04.003 (2020).

743   33. O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J. & Hector, A. Drought survival of

744   tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change*

745   **4,** 710–714; 10.1038/nclimate2281 (2014).

746   34. Reich, P. B. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol.*

747   **102,** 275–301; 10.1111/1365-2745.12211 (2014).

748   35. Tardieu, F. & Simonneau, T. Variability among species of stomatal control under fluctuating

749   soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J.*

750   *Exp. Bot.* **49,** 419–432; 10.1093/jxb/49.Special_Issue.419 (1998).

751   36. Martínez-Vilalta, J. & Garcia-Forner, N. Water potential regulation, stomatal behaviour and

752   hydraulic transport under drought: deconstructing the iso/anisohydric concept. *Plant Cell*

753   *Environ.* **40,** 962–976; 10.1111/pce.12846 (2017).

754   37. Kröber, W., Zhang, S., Ehmig, M. & Bruelheide, H. Linking xylem hydraulic conductivity and

755   vulnerability to the leaf economics spectrum--a cross-species study of 39 evergreen and

756   deciduous broadleaved subtropical tree species. *PLoS ONE* **9,** e109211;

757   10.1371/journal.pone.0109211 (2014).

758   38. Kröber, W. & Bruelheide, H. Transpiration and stomatal control: a cross-species study of leaf

759   traits in 39 evergreen and deciduous broadleaved subtropical tree species. *Trees* **28,** 901–914;

760   10.1007/s00468-014-1004-3 (2014).

761   39. Anderegg, W. R. L. *et al.* Hydraulic diversity of forests regulates ecosystem resilience during

762   drought. *Nature* **561,** 538–541 (2018).

763   40. Bruelheide, H. *et al.* Designing forest biodiversity experiments: general considerations
764   illustrated by a new large experiment in subtropical China. *Methods Ecol. Evol.* **5,** 74–89;
765   10.1111/2041-210X.12126 (2014).

766   41. Lefcheck, J. S. piecewiseSEM: Piecewise structural equation modelling in r for ecology,
767   evolution, and systematics. *Methods Ecol. Evol.* **7,** 573–579; 10.1111/2041-210X.12512
768   (2016).

769   42. Trogisch, S. *et al.* The significance of tree-tree interactions for forest ecosystem functioning.
770   *Basic Appl. Ecol.*; 10.1016/j.baae.2021.02.003 (2021).

771   43. Fichtner, A. *et al.* Neighbourhood diversity mitigates drought impacts on tree growth. *J. Ecol.*
772   **108,** 865–875; 10.1111/1365-2745.13353 (2020).

773   44. Jactel, H., Moreira, X. & Castagneyrol, B. Tree Diversity and Forest Resistance to Insect Pests:
774   Patterns, Mechanisms and Prospects. *Annu. Rev. Entomol.* **66**; 10.1146/annurev-ento-041720-
775   075234 (2021).

776   45. O'Brien, M. J., Reynolds, G., Ong, R. & Hector, A. Resistance of tropical seedlings to drought
777   is mediated by neighbourhood diversity. *Nat Ecol Evol* **1,** 1643–1648; 10.1038/s41559-017-
778   0326-0 (2017).

779   46. Forrester, D. I. & Bauhus, J. A Review of Processes Behind Diversity—Productivity
780   Relationships in Forests. *Curr. Forestry Rep.* **2,** 45–61; 10.1007/s40725-016-0031-2 (2016).

781   47. Adams, H. D. *et al.* A multi-species synthesis of physiological mechanisms in drought-induced
782   tree mortality. *Nat. Ecol. Evol.* **1,** 1285–1291; 10.1038/s41559-017-0248-x (2017).

48. Forrester, D. I. Ecological and Physiological Processes in Mixed Versus Monospecific Stands. In *Mixed-species forests. Ecology and management,* edited by H. Pretzsch, D. I. Forrester & J. Bauhus (Springer Nature, Berlin, Germany, 2017), pp. 73–115.

49. Salmon, Y. *et al.* Surrounding species diversity improves subtropical seedlings' carbon dynamics. *Ecol Evol* **8,** 7055–7067; 10.1002/ece3.4225 (2018).

50. Kunz, M. *et al.* Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. *Ecol. Lett.* **22,** 2130–2140; 10.1111/ele.13400 (2019).

51. Guillemot, J. *et al.* Neighbourhood-mediated shifts in tree biomass allocation drive overyielding in tropical species mixtures. *New Phytol.* **228,** 1256–1268; 10.1111/nph.16722 (2020).

52. Bu, W. *et al.* Interspecific and intraspecific variation in specific root length drives aboveground biodiversity effects in young experimental forest stands. *Journal of Plant Ecology* **10,** 158–169; 10.1093/jpe/rtw096 (2017).

53. Schwendenmann, L., Pendall, E., Sanchez-Bragado, R., Kunert, N. & Hölscher, D. Tree water uptake in a tropical plantation varying in tree diversity. Interspecific differences, seasonal shifts and complementarity. *Ecohydrology* **8,** 1–12; 10.1002/eco.1479 (2015).

54. Lasky, J. R. *et al.* The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecol. Lett.* **17,** 1158–1167; 10.1111/ele.12322 (2014).

55. Yang, X. *et al.* Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). *Eur. J. Forest. Res.* **132,** 593–606; 10.1007/s10342-013-0696-z (2013).

805   56. Wang, X.-H., Kent, M. & Fang, X.-F. Evergreen broad-leaved forest in Eastern China: Its

806   ecology and conservation and the importance of resprouting in forest restoration. *For. Ecol.*

807   *Manage.* **245,** 76–87; 10.1016/j.foreco.2007.03.043 (2007).

808   57. Shi, M.-M., Michalski, S. G., Welk, E., Chen, X.-Y. & Durka, W. Phylogeography of a

809   widespread Asian subtropical tree: genetic east-west differentiation and climate envelope

810   modelling suggest multiple glacial refugia. *J. Biogeogr.* **41,** 1710–1720; 10.1111/jbi.12322

811   (2014).

812   58. Fichtner, A. *et al.* Neighbourhood interactions drive overyielding in mixed-species tree

813   communities. *Nat. Commun.* **9,** 1144; 10.1038/s41467-018-03529-w (2018).

814   59. Hautier, Y. *et al.* Eutrophication weakens stabilizing effects of diversity in natural grasslands.

815   *Nature* **508,** 521–525; 10.1038/nature13014 (2014).

816   60. van Buuren, S. & Groothuis-Oudshoorn, K. mice: Multivariate Imputation by Chained

817   Equations in R. *J. Stat. Softw.* **45,** 1–67 (2011).

818   61. Oksanen, J. *et al. vegan: Community Ecology Package* (2019).

819   62. Laliberté, E. & Legendre, P. A distance-based framework for measuring functional diversity

820   from multiple traits. *Ecology* **91,** 299–305; 10.1890/08-2244.1 (2010).

821   63. Laliberté, E., Legendre, P. & Shipley, B. FD: measuring functional diversity from multiple

822   traits, and other tools for functional ecology. R package version 1.0-12. (2014).

823   64. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. *nlme. Linear and Nonlinear*

824   *Mixed Effects Models* (2020).

825   65. Lüdecke, D. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *J.*

826   *Open Source Softw.* **3,** 772; 10.21105/joss.00772 (2018).

827   66. Dormann, C. F. *et al.* Collinearity. A review of methods to deal with it and a simulation study

828   evaluating their performance. *Ecography* **36,** 27–46; 10.1111/j.1600-0587.2012.07348.x

829   (2013).

830   67. R Core Team. *R: A Language and Environment for Statistical Computing* (Vienna, Austria,

831   2019).

832