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 ecosystems 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 in relation to drought tolerance and stomatal control, but not the community-weighted means of these traits. Our results demonstrate important mechanisms by which tree species richness stabilizes forest productivity, thus emphasizing 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]. This compromises the ability of the world's forests to act as a carbon sink[2] and as a nature-based solution to climate change[3]. 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[4–6]. 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[7–10]. However, the

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

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

63   community composition changes slower in forests[6]. The few existing studies in forests support the

64   notion that species richness stabilizes aboveground wood production, hereafter referred to as

65   'productivity', of mixed-species tree communities[6,11,12]. However, previous studies were largely

66   restricted to temperate and boreal forests and tree diversity gradients have been short so that

67   establishing causal relationships between tree diversity and the stability of productivity remains

68   difficult[13].

69

70   According to the insurance hypothesis[14,15] a mixture of tree species with different strategies should

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

72   thus increasing their temporal stability. This stability[16] has often been defined as temporal mean

73   productivity (μ) divided by the temporal standard deviation in productivity (σ)[e.g.7,8] and may be

74   promoted by diversity in mixed-species tree communities via two principal mechanisms[14]. First,

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

76   monocultures, has been reported by numerous studies in natural and experimental forests[17–20].

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

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

79   stability[6]. Second, decreased temporal variation in community productivity through buffering of

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

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

82   variation in productivity[14,16,21,22] but arguably the one most supported by theoretical and

83   observational studies in grasslands and increasingly also in forests is species asynchrony[7,21,23]. In

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

85   'species asynchrony'[22]) have been found to be the strongest driver of community stability in

86   some[6,24,25] but not all studies[11]. Asynchronous species dynamics may result from intrinsic rhythms

87   like phenology or mast seeding[26,27], extrinsic factors such as climatic conditions[22,28] and species

88   interactions in mixtures like resource partitioning or biotic feedbacks[29,30]. Species asynchrony may

89   buffer the temporal variation in community productivity during times of stress as some species

90   likely maintain functioning or compensate for the productivity losses of other species (Fig. 1). This

91   stabilizing effect may be especially important in the context of the global increase in the severity

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

93   that allow tree species and species mixtures to maintain functioning under future drought

94   conditions.

95

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

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

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

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

100   embolism decreases water availability and may ultimately lead to desiccation and tree death[28,34].

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

102   measured as water potential) as key trait[34] and, in addition, classic traits of the leaf economics

103   (indicating conservative vs acquisitive resource use)[35] to quantify drought tolerance. Second, tree

104   species may follow different strategies of stomatal control. Some rely on continued water

105   extraction and keep their stomata open, i.e. they continue to transpire even though this poses a high

106   risk for cavitation-induced mortality under extreme drought (called water-spenders or anisohydric

107   species)[28,36,37]. Other tree species decrease their stomatal conductance quickly during water

108   shortage to avoid transpiration losses and xylem cavitation but may risk carbon starvation under

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

110   perspectives[37], we view stomatal control here along a gradient from water-spending to water-

111   saving species behaviour and quantify it through physiological traits such as stomata conductance

112   and control of conductance under increasing water pressure deficits[38,39].

113

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

115   productivity in two ways. Diverse hydraulic strategies may stabilize productivity through

116   promoting species asynchrony. Stability was recently shown to strongly increase with species

117   asynchrony in experimental tree mixtures[40], but the underlying trait-based mechanisms remain

118   unknown in forests. On the other hand, stability may be influenced by the community-weighted

119   mean of hydraulic traits, as indicated by findings in grassland diversity experiments where stability

120   was higher in communities dominated by species with traits associated with conservative resource

121   use[7]. Here, we hypothesize that tree species richness increases stability via increasing species

122   asynchrony and that diversity in functional traits related to hydraulic water transport (hereafter

123   'hydraulic diversity'[41]) drives these asynchronous species responses. We thus expect trait diversity

124   to be more important for stability than community trait means.

125

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

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

128   the stability of community productivity in a large-scale tree biodiversity experiment (BEF-

129   China[17,42]; biodiversity–ecosystem functioning China). The experiment is located in the diverse

130   subtropical forests of China and features a gradient of species richness ranging from monocultures

131   up to mixtures of 24 tree species planted at two sites with distinct species pools. In our study,

132   stomatal control and drought tolerance strategies form two orthogonal species trait gradients

133   (Supplementary Fig. 1), which allows us to quantify their relative contributions to species

134   asynchrony and stability. Specifically we tested the following hypotheses:

135

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

137

138   **H2** Hydraulic diversity in stomata control and drought tolerance strategies increases stability

139   through increasing species asynchrony.

140

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

142   asynchrony and by overyielding.

143

144   **Results**

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

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

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

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

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

150   4; Supplementary Table 1-2). In contrast, community-weighted means (CWMs) of these hydraulic

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

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

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

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

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

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

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

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

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

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

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

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

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

164   stability (Supplementary Table 2).

165

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

167   connections behind observed diversity effects on stability (Fig. 3). Species asynchrony was, as we

168   predicted, the principal mediator of indirect effects of species richness via hydraulic diversity on

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

170   pathways explained 35% of variation in stability (fixed effects, marginal R^2), which increased to

171   58% if both fixed and random effects (conditional R^2) were considered. Species richness,

172   functional diversity of stomatal control and functional diversity of drought tolerance explained

173   52% of variation in species asynchrony (marginal R^2). Species asynchrony was the strongest direct

174   driver of stability (standardized path coefficient of direct effect 0.76, P<0.001). Tree species

175   richness increased stability indirectly through increasing species asynchrony (standardized path

176   coefficient of compound effect 0.35, i.e. the product of the coefficients along the path). Note, that

177   we did not find an additional independent effect of species richness on stability (P=0.31) once we

178   had accounted for the pathway via asynchrony. Hence, most of the variation in stability was

179   explained by species asynchrony. Quantifying hydraulic diversity allowed us to disentangle some

180   of the functional drivers behind asynchronous species responses: both functional diversity of

181   stomatal control and functional diversity of drought tolerance contributed to increased stability via

182   positive effects on species asynchrony (standardized path coefficients of direct effects on

183   asynchrony 0.18, P=0.005 and 0.30, P<0.001). Functional diversity of drought tolerance, however,

184   also had a direct negative effect (P=0.007) on stability that was smaller than its positive effect on

185   asynchrony (standardized path coefficients of direct effects –0.21 vs 0.30). Importantly, only

186   functional diversity but not community-weighted means of the hydraulic trait gradients explained

187   variations in stability (effect of CWM of stomatal control and CWM of drought tolerance on

188   stability both not significant with P≥0.25; Fig. 3).

189

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

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

192   observed biodiversity-stability relationships (Fig. 4). Tree species richness directly increased both

193   the mean and the standard deviation of productivity similarly (standardized path coefficient of

194   direct effect 0.23 vs 0.30). Tree species richness thus increased mean productivity but this was

195   accompanied by increased variation in productivity. However, species richness also decreased the

196   standard deviation of productivity indirectly via its positive effect on species asynchrony with

197   about the same strength (indirect effect of species richness on σ_{AWP} –0.3, calculated as the product

198   of the coefficients along each significant path and their sum[43]; Fig. 4). Species asynchrony, which

199   increased with species richness and hydraulic diversity, hence stabilized productivity through

200   buffering its temporal variation (standardized path coefficient of direct effect of species

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

202   of drought tolerance on stability (Fig. 3, see above) can be attributed to its positive effect on the

203   temporal standard deviation (Fig. 4, marginally significant, P=0.06). Finally, the CWM of drought

204   tolerance increased both, mean productivity and the standard deviation of productivity

205   (standardized path coefficients of direct effects 0.21 vs 0.16). That is, communities dominated by

206   drought-intolerant species (those with higher trait gradient scores; Supplementary Fig. 1) had a

207   higher productivity but tended to also have a higher variation in productivity. Overall, stability

208   increased with species richness (Fig. 3) through increased mean productivity (i.e. overyielding)

209   and buffered temporal variation in productivity (Fig. 4).

210

Discussion

212   Our results provide experimental evidence that the insurance effect[14] of diversity stabilizes tree

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

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

215   response to climatic variation is the principle mediator of this diversity effect. As hypothesized,

216   both hydraulic diversity in stomatal control and drought tolerance had net positive but indirect

217   effects on stability that operated via enhanced species asynchrony. In contrast, the community-

218   weighted means of these hydraulic trait gradients did not influence stability.

219

220   **Species asynchrony and stability**

221   The controlled diversity gradient of the BEF-China experiment[42] ranging from monocultures to

222   mixtures of 24 tree species, detailed trait information and the use of structural equation models[43]

223   allowed us to disentangle the direct and indirect drivers of stability in forests. We show here that

224   species richness increases stability indirectly via promoting asynchronous species productivity

225   over time. Stability and species asynchrony were shown to increase concomitantly with tree

226   species richness in former studies[6,12,40], but here we provide experimental evidence to show that

227   species richness drives species asynchrony and thereby stability in forests. Asynchronous

228   productivity integrates different mechanisms, such as those captured by the selected hydraulic

229   traits that help species to cope with variable climatic conditions. The largest contributor to the

230   stability of productivity was species asynchrony which largely enhanced stability via buffering

231   (reducing) the variation of productivity over time[6,7,12,14,22]. Species richness also increased

232   temporal mean productivity directly. This finding is in line with a rapidly increasing number of

233   studies that support the view that forest productivity increases with increasing tree species

234   richness[17–19,40]. However, this increased productivity by itself did not increase stability because

235   species richness also increased the temporal variation of productivity. Stability only increased due

236   to the variance buffering effect of species asynchrony on productivity (Fig. 4).

237

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

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

240   climate (the variable with the likely strongest inter-annual change during our study) may increase

241   species asynchrony. Species react differently to climatic conditions[e.g.28,34] and species asynchrony

242   is thus likely driven by idiosyncratic growth responses to climatic variability. Next, tree growth in

243   mixtures is shaped by tree-tree interactions such as resource partitioning and biotic

244   feedbacks[20,29,30,44] which may in turn be modulated by changes in climatic conditions[45–47]. Finally,

245   intrinsic rhythms like mast seeding[26,27] may induce asynchronous growth dynamics. These

246   intrinsic factors are, however, presumably less important for inter-annual changes in species

247   productivity in young forest stands. We expect that the observed strong species asynchrony

248   resulted from species' response strategies to climate and how these strategies, which we quantified

249   via hydraulic traits, shape the nature of tree-tree interactions along climatic stress gradients.

250

251   **Hydraulic diversity and stability**

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

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

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

255   and stabilized productivity in the face of highly variable climatic conditions. We show that species

256   asynchrony increased with dissimilarity in hydraulic traits and expect that the relative importance

257   of these hydraulic traits for tree productivity likely depends on the prevailing climatic conditions.

258   According to the stress-gradient hypothesis[48] and its contextualisation for forests[49], traits related

259   to hydraulic functioning are likely more important for productivity in dry years, when water is the

260   limiting resource, while their importance should be lower during years with ample water.

261

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

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

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

265   ecosystem carbon fluxes during drought[41]. Functional diversity in stomatal control may promote

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

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

268   uptake via roots to balance transpiration losses and carries high cavitation risks[28,37], a principle

269   mechanism behind drought-induced mortality across tree taxa[50]. Conversely, water savers can

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

271   is less ubiquitous than cavitation[50]. These contrasting stomatal control strategies themselves may

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

273   mixed-stands through soil water partitioning between co-existing species. In tree neighbourhoods

274   comprising species with different stomatal control strategies, water spenders may benefit from the

275   water saving strategy of their neighbours through higher levels of remaining soil water[51].

276   Likewise, water savers might recover faster from (short) droughts and could thus profit from

277   spenders in their neighbourhood that cannot as quickly use improved soil water conditions. Both

278   may thus profit from neighbourhood species richness as the likelihood for functional dissimilar

279   species increases with species richness. Diversity in stomatal control is therefore one potential

280   mechanism that explains reported positive neighbourhood species richness effects on individual

281   tree growth during drought[40,45].

282

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

284   asynchrony but also a direct (albeit weaker) negative effect on stability. Species asynchrony my

285   result from drought intolerant species facing a higher risk for xylem cavitation or even death under

286   drought while tolerant species are less affected[28,34]. Drought induced cavitation may lead to a lower

287   productivity of drought intolerant species through damage or dieback and this effect may last for

288   years after the drought event as the repair of damaged xylem vessels may require resources at the

289   expense of productivity[28]. Conversely, drought-intolerant species also have relative advantages, as

290   positive neighbourhood diversity effects on tree growth during drought were found to be stronger

291   for drought intolerant species in our study system[45]. Drought-intolerant species are also

292   characterized by traits associated with an acquisitive resource use strategy[38] (see Supplementary

293   Fig. 1). This acquisitiveness may enable soil water partitioning between neighbours in favour of

294   the less drought-tolerant species in the community during drought[45]. At the same time, however,

295   the likelihood for highly drought-sensitive species to occur within a community increases with

296   diversity, which in the face of drought may reduce community productivity and therefore also its

297   stability through damage or dieback of the most vulnerable individuals or species. This may

298   explain the direct negative effect of drought tolerance diversity on stability that we found in

299   addition to its positive effect on stability mediated by species asynchrony.

300

301   The direct positive effects of species richness on species asynchrony may result from dissimilarity

302   in traits[7] that were not considered here; these may include leaf phenology[27], storage of non-

303   structural carbohydrates[33], traits regulating biotic feedbacks[29] and below- and aboveground

304   structural traits[52–54]. For example, rooting-depth, complementary water uptake through niche

305   differentiation[55] and facilitation via hydraulic redistribution[51] between species could be important

306   drivers of species asynchrony and stability belowground. Considering such traits in addition to the

307   hydraulic traits used here may help to decrease the amount of unexplained variance in stability and

308   species asynchrony.

309

310   **Community hydraulic means and stability**

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

312   hydraulic traits on stability. Species asynchrony, the principle driver of stability, depends naturally

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

314   a community. The absence of community mean effects on stability underlines that the observed

315   responses are not simply related to communities being dominated by particularly stable-growing

316   species. We found some indication for increased productivity in communities dominated by rather

317   drought-intolerant (acquisitive) species, consistent with the common expectation for 'fast' growth

318   of these species[35,56]. However, this did not influence stability because the same communities also

319   had increased variation in productivity, likely because they were susceptible to drought. In contrast

320   to drought tolerance, stomatal control is not related to the leaf economic spectrum, which may

321   explain why we did not find an effect of the CWM of stomatal control on stability.

322

323   **Outlook**

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

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

326   change[1], which threatens the climate mitigation potential of the world's forests[2]. We show that the

327   stability of forest community productivity increases with tree species richness and that the

328   principal driver behind this diversity effect are the asynchronous growth dynamics of different tree

329   species in hydraulically diverse communities. Hence, mixing tree species with a diversity of

330   hydraulic strategies is likely a key management strategy to increase forest stability and their

331   potential to mitigate the effects of climate change. Hydraulic traits may be used to select suitable

332   tree species and design mixtures that stabilize productivity in an increasingly variable climate

333   through diverse response strategies, while excluding those that would succumb to drought or

334   competition. Here, we examined stability over the first decade since establishment of a large-scale

335   tree biodiversity experiment. Yet, the biodiversity-stability relationships we report may strengthen

336   with stand development[25]. Importantly, stability did not compromise productivity. Instead, reduced

337   temporal variation in productivity coincided with increased productivity in mixed-species tree

338   communities. Our results extend research on forest stability from comparably species-poor

339   forests[6,11,12,40] to species-rich subtropical communities with up to 24 co-existing tree species.

340   Stability increased consistently with tree species richness and did not plateau at low levels of tree

341   species richness, which underlines the enormous potential of species richness to improve stability

342   in many of our species-poor or mono-specific secondary and plantation forests around the world.

343   This finding has important implications; contemporary forestry, and especially large-scale forest

344   restoration initiatives[3], like the Bonn Challenge, should focus on hydraulically diverse, mixed-

345   species stands to enhance stability in a changing climate.

346

Methods

Study site and experimental design

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

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

351   (29° 08′–29° 11′N, 117° 90′–117°93′E). BEF-China[17,42] is a large-scale tree biodiversity

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

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

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

355   temperature of 16.7°C and mean annual precipitation of 1821mm[57]. The sites experienced strong

356   inter-annual changes in climate-induced water availability during the 11-year observation period

357   (Supplementary Fig. 9). The diverse native subtropical forests of the area are dominated by

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

359   conifers[42]. These forests are located in an area of overlap between tropical and temperate zones[58,59],

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

361   asynchrony as drivers of biodiversity-stability relationships. Furthermore, the region is densely

362   populated and experiences frequent anthropogenic disturbances[58], which makes the maintenance

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

364   and restoration efforts.

365

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

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

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

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

370   stick' design[42]. In total 226,400 individual trees were planted on 566 plots[42]. In this study, we used

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

372   of 396 plots and 158,400 planted trees[17]. Of these, we excluded 21 plots prior to our analysis due

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

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

375   20 regular gridded positions (spacing 1.29m between trees). Tree positions and species

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

377   experiment can be found in Huang *et al.* and Bruelheide *et al.*[17,42].

378

379   **Tree data collection**

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

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

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

383   16- and 24-species mixtures, while a smaller group of the central 6×6 trees was measured for

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

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

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

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

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

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

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

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

392   2011 to 2019 at site B to estimate community- and species-level productivity.

393

394   **Calculation of aboveground wood production**

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

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

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

398   value for the young subtropical trees in our experiment[20,60]; with

399

400 $$awv = gd * h * f,$$ (1)

401

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

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

404 calculated as

405

406 $$awp = awv_{t+1} - awv_{t-1},$$ (2)

407

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

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

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

411 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^{-1}

412 ^{1} year^{-1}), referred to as species and community 'productivity'. A value of 0 was used in case of

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

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

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

416

417 **Stability and asynchrony of production**

418 The temporal stability[16] of tree community productivity, hereafter 'stability', was calculated as the

419 inverse of the coefficient of variation:

420

421 $$Stability = \frac{\mu_{AWP}}{\sigma_{AWP}}$$ (3)

422

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

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

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

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

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

428   stability through decreasing σ_{AWP}[14]. We hypothesize here that asynchronous species growth

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

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

431   level species asynchrony using the species synchrony statistic φ[21] as $1 - \varphi$:

432

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

434

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

436   n species[6,61]. Thus, species asynchrony increases if the variance in individual species productivity

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

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

439   variations in community productivity result from variations within a single species[6]. We expect

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

441   productivity[6]. Young tree communities, as the ones examined here, show a strongly increasing

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

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

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

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

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

447   of this regression following Craven *et al.* and Tilman *et al.*[7,9] (see Supplementary Fig. 10 for a

448   visualization of this approach).

449

450   **Trait gradients**

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

452   related to a set of (hydraulic) functional traits (Anderegg *et al.*[41] and citations within). We

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

454   that was measured within the experiment (Supplementary Table 1; refs.[38,39]). Trait data were

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

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

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

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

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

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

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

462   species drought tolerance[34]. Higher values of Ψ_{50} (i.e. lower absolute values Ψ_{50}) indicate a higher

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

464   toughness and carbon to nitrogen ratio as classic traits of the leaf economics spectrum (LES[35]) in

465   our analysis, which are associated with a species drought tolerance[38], to foster the still limited

466   understanding of trait syndromes that govern forest responses to climatic stress[37]. We used trait

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

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

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

470   using the R package mice[62]. PCA was performed with the *rda* function in the vegan package

471   version 2.5-6[63].

472

473   **Quantifying hydraulic diversity and community means**

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

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

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

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

478   calculated with the 'FD' package as abundance-weighted functional dispersion[64,65] using temporal

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

480   measures the mean distance of species along each trait gradient[64] and thus represents the

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

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

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

484   volume per plot as measure of species abundance.

485

486   **Modelling framework and statistical analysis**

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

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

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

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

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

492   on species asynchrony. LMM were fit with the nlme package version 3.1-144[66] to allow for the

493   specification of variance functions with a significance level of α=0.05. Confidence intervals (95%)

494   of LMM effects were computed with the ggeffects package[67]. Tree species richness was $\log_2$

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

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

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

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

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

500   composition and arrangement of plots within quadrants (see Huang *et al.*[17]). Model assumptions

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

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

503   tested the inclusion of an exponential variance structure[66] to model heteroscedasticity (parsimony

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

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

506   transformation of response variables.

507

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

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

510   driving biodiversity-stability relationships (Supplementary Fig. 7). We explored whether the data

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

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

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

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

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

516   increase temporal mean productivity in mixtures[7,17,40]. To test for the effects of community trait

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

518   tolerance to stability[7,41]. As the experimental manipulation of species richness may directly affect

519   the functional diversity of a community[42], we included pathways from species richness to

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

521   SEMs[43] were used to test the support for and relative importance of these hypothesized pathways.

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

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

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

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

526

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

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

529   tests of directed separations (P<0.05 for violation of independence claims)[43]. For each SEM we

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

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

532   path)[43]. We fitted individual pathways with LMM using the same random structure and model

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

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

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

536   role of species asynchrony and hydraulic diversity as drivers of biodiversity-stability relationships.

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

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

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

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

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

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

543   variance inflation (Variance Inflation Factor < 5, a conservative threshold choice[68]). All analyses

544   were performed in R 3.6.2[69].

545

557

Author contributions

558

559 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.

560 designed the project; F.S., X.L., K.E.B., J.A.S., J.B. and C.W. conceived the idea for the

561 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

562 data; F.S. analysed and interpreted the data and wrote the manuscript with support from X.L.,

563 K.E.B. and C.W.; F.S. and K.E.B. created figures; All authors discussed the results and contributed
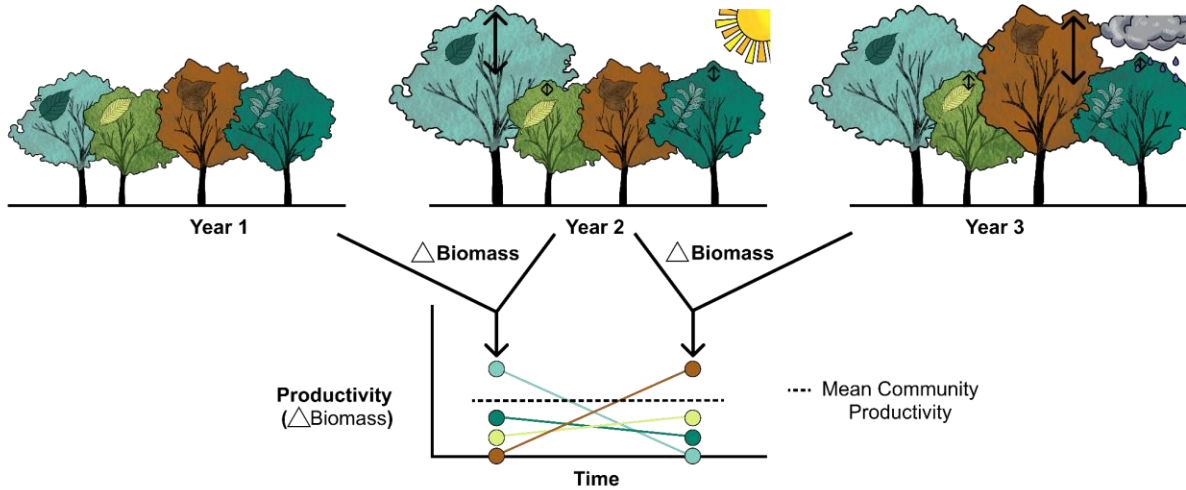
564 substantially to revisions.

565

Data availability statement

566

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

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

569 request from the corresponding authors.

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572

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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) has traits associated with water-spending behaviour 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, 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 principal drivers 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.

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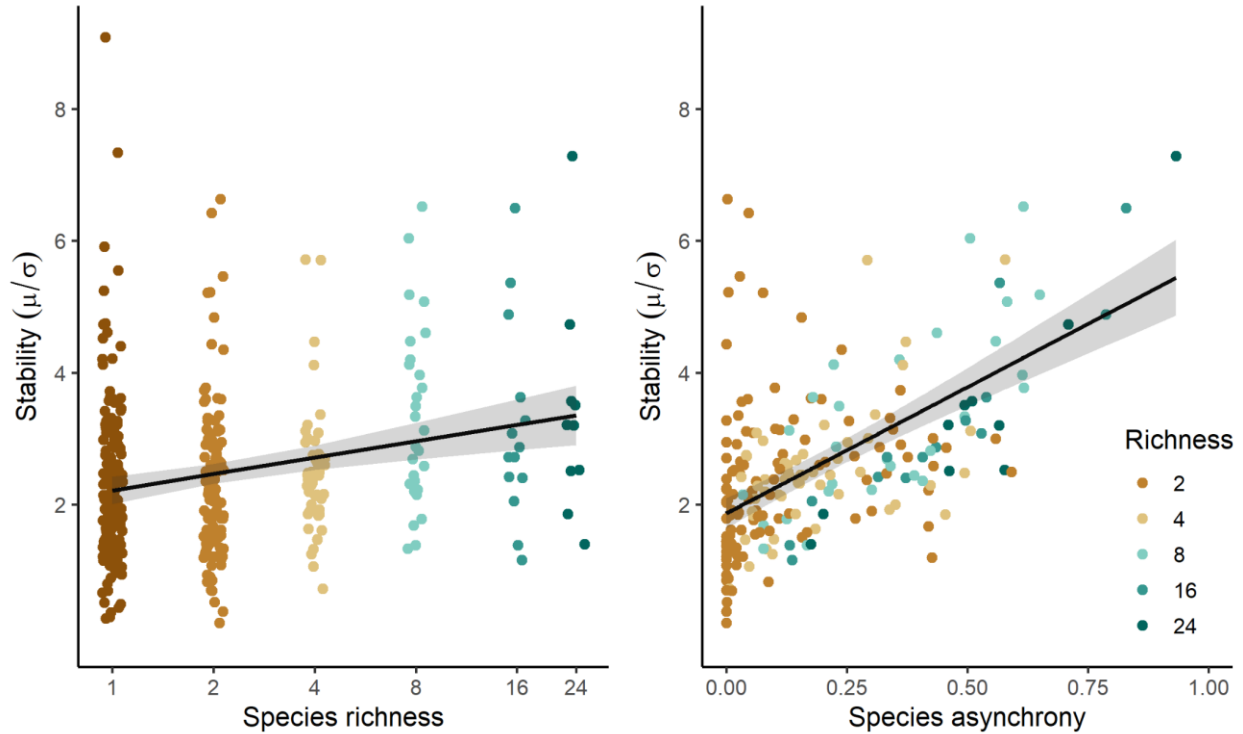
589

590   Fig. 2 Effects of species richness and species asynchrony on stability. Lines are linear mixed-effect model

591   fits that show (a) significant increases in stability with species richness (P<0.001) along a planted diversity

592   gradient ranging from monocultures up to mixtures of 24 tree species and (b) significant increases in

593   stability with species asynchrony (P<0.001) in mixtures. Species asynchrony ranges from 0 to 1, where 0

594   represents complete synchrony and 1 complete asynchrony. Grey bands represent a 95% confidence

595   interval. See Supplementary Table 2 for details on the fitted models.

596

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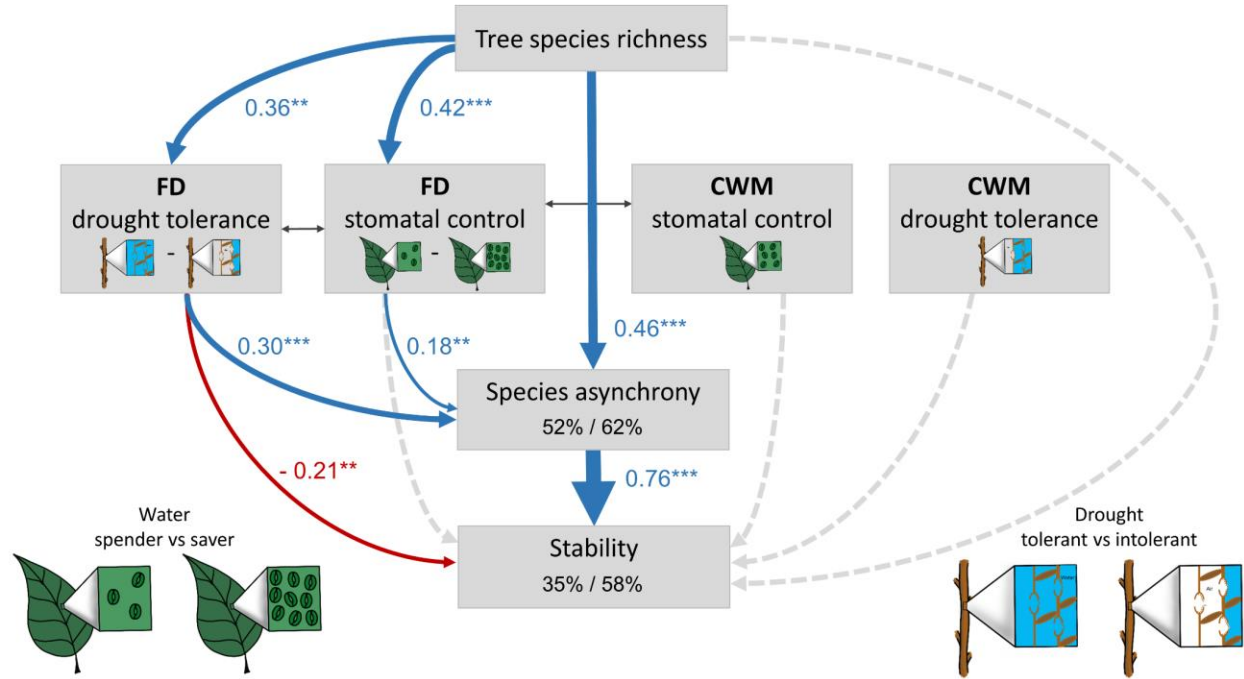
Fig. 3 Direct and indirect effects of species richness, hydraulic diversity and community hydraulic means on stability. The structural equation model (SEM) tests the direct effects of tree species richness, functional diversity of stomatal control (FD stomatal control) and functional diversity of drought 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[43] are

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

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

615   the corresponding boxes.

616
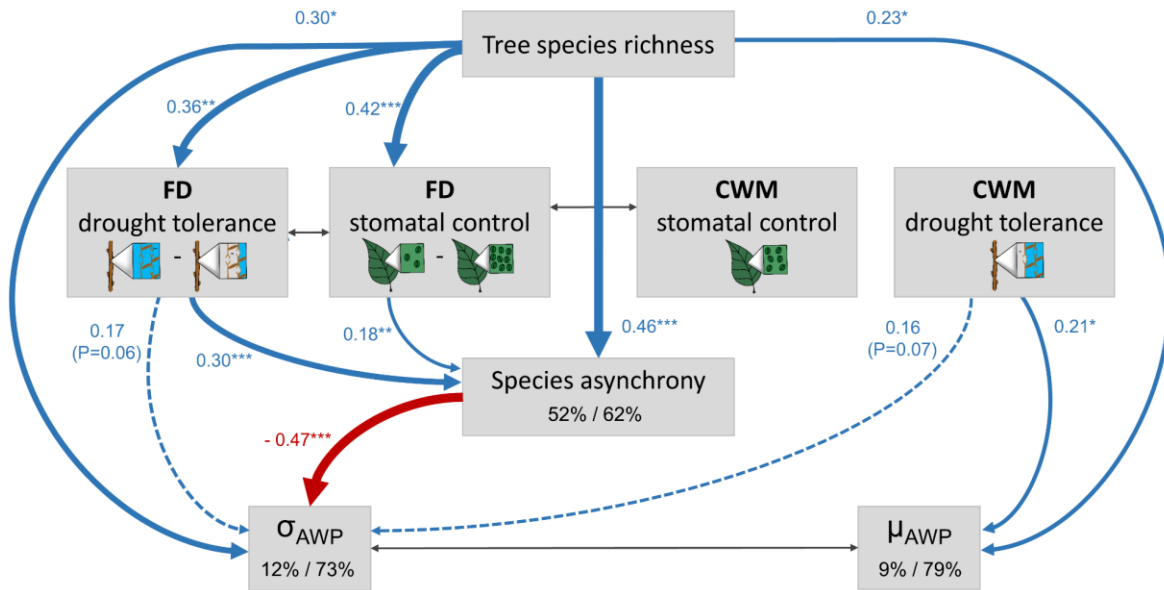
617

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

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

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

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

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

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

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

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

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

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

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

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

630   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

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

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

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

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

635   *** P<0.001), path-width is scaled by coefficient size. Significant partial correlations[43] are shown through

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

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

638   corresponding boxes.

639

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