

 Open access • Journal Article • DOI:10.1126/SCIENCE.AAT6405

Impacts of species richness on productivity in a large-scale subtropical forest experiment. — [Source link](#)

Yuanyuan Huang, Yuxin Chen, Nadia Castro-Izaguirre, Martin Baruffol ...+65 more authors

Institutions: University of Zurich, Alexander von Humboldt Biological Resources Research Institute, Lüneburg University, Dresden University of Technology ...+16 more institutions

Published on: 05 Oct 2018 - Science (American Association for the Advancement of Science)

Topics: Species richness, Biodiversity, Shrub, Productivity (ecology) and Ecosystem

Related papers:

- [Positive biodiversity-productivity relationship predominant in global forests](#)
- [Partitioning selection and complementarity in biodiversity experiments](#)
- [Spatial complementarity in tree crowns explains overyielding in species mixtures](#)
- [The effect of biodiversity on tree productivity: from temperate to boreal forests](#)
- [Effects of biodiversity on ecosystem functioning: a consensus of current knowledge](#)

Share this paper:    

View more about this paper here: <https://typeset.io/papers/impacts-of-species-richness-on-productivity-in-a-large-scale-5d8npruek>

1 **Strong positive biodiversity–productivity relationships in a subtropical forest**
2 **experiment**

3 Yuanyuan Huang¹, Yuxin Chen¹, Nadia Castro-Izaguirre¹, Martin Baruffol^{1,2}, Matteo
4 Brezzi¹, Anne Lang³, Ying Li³, Werner Härdtle³, Goddert von Oheimb^{4,5}, Xuefei
5 Yang^{6,7}, Kequan Pei⁸, Sabine Both⁶, Xiaojuan Liu^{1,8}, Bo Yang⁹, David Eichenberg⁶,
6 ¹⁰, Thorsten Assmann³, Jürgen Bauhus¹¹, Thorsten Behrens¹², François Buscot¹³,
7 Xiao-Yong Chen¹⁴, Douglas Chesters¹⁵, Bing-Yang Ding¹⁶, Walter Durka^{17,4},
8 Alexandra Erfmeier⁶, Jingyun Fang¹⁸, Markus Fischer¹⁹, Liang-Dong Guo²⁰, Dali
9 Guo²¹, Jessica L.M. Gutknecht²², Jin-Sheng He¹⁸, Chun-Ling He¹⁵, Andy Hector²³,
10 Lydia Höning⁶, Ren-Yong Hu²⁴, Alexandra-Maria Klein²⁵, Peter Kühn¹², Yu Liang⁸,
11 Stefan Michalski¹⁷, Michael Scherer-Lorenzen²⁶, Karsten Schmidt¹², Thomas
12 Scholten¹², Andreas Schuldt^{3,4}, Xuezheng Shi²⁷, Man-Zhi Tan²⁷, Zhiyao Tang¹⁸,
13 Stefan Trogisch^{6,26}, Zhengwen Wang²⁸, Erik Welk^{6,4}, Christian Wirth^{10,4}, Tesfaye
14 Wubet^{13,4}, Wenhua Xiang²⁹, Jiye Yan³⁰, Mingjian Yu³¹, Xiao-Dong Yu¹⁵, Jiayong
15 Zhang³², Shouren Zhang⁸, Naili Zhang⁸, Hong-Zhang Zhou¹⁵, Chao-Dong Zhu¹⁵, Li
16 Zhu⁸, Helge Bruelheide^{6,4†}, Keping Ma^{8†}, Pascal A. Niklaus^{1†}, Bernhard Schmid^{1†}

17

18 ¹ Department of Evolutionary Biology and Environmental Studies, University of
19 Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

20 ² Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, calle
21 28A # 5-09, Bogotá D.C, Colombia

22 ³ Institute of Ecology, Leuphana University of Lüneburg, Scharnhorststr. 1, 21335
23 Lüneburg, Germany

24 ⁴ German Centre for Integrative Biodiversity Research (iDiv) Jena – Halle – Leipzig,
25 Deutscher Platz 5e, 04103 Leipzig, Germany

- 26 ⁵ Technische Universität Dresden, Institute of General Ecology and Environmental
27 Protection, PO Box 1117; 01735 Tharandt, Germany
- 28 ⁶ Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale),
29 Germany
- 30 ⁷ Kunming Institute of Botany, Chinese Academy of Sciences, 134, Lanhei Road,
31 Kunming, 650204, China
- 32 ⁸ State Key Laboratory of Vegetation and Environmental Change, Institute of Botany,
33 Chinese Academy of Sciences, Beijing 100093, China
- 34 ⁹ Key Laboratory of Plant Resources and Biodiversity of Jiangxi Province,
35 Jingdezhen University, 838 Cidu Avenue, Jingdezhen, Jiangxi 333000, China
- 36 ¹⁰ Institut für Spezielle Botanik und Funktionelle Biodiversität, University of Leipzig,
37 04103 Leipzig, Germany
- 38 ¹¹ Chair of Silviculture, Faculty of Environment and Natural Resources, University of
39 Freiburg, Tennenbacherstr. 4, 79106 Freiburg, Germany
- 40 ¹² Department of Geosciences, Soil Science and Geomorphology, University of
41 Tübingen, Rümelinstraße 19-23, 72074, Tübingen, Germany
- 42 ¹³ Helmholtz Centre for Environmental Research – UFZ, Department of Soil Ecology,
43 Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany
- 44 ¹⁴ School of Ecological and Environmental Sciences, ECNU-UH Joint Translational
45 Science and Technology Research Institute, East China Normal University, Shanghai
46 200241, China
- 47 ¹⁵ Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road,
48 Chaoyang District, Beijing 100101, China
- 49 ¹⁶ School of Life & Environment Sciences, Wenzhou University, Wenzhou, China

- 50 ¹⁷ Helmholtz Centre for Environmental Research – UFZ, Department of Community
51 Ecology, Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany
- 52 ¹⁸ Department of Ecology, Peking University, 5 Yiheyuan Rd., Beijing 100871, China
- 53 ¹⁹ University of Bern, Altenbergrain 21, 3013 Bern, Switzerland
- 54 ²⁰ State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of
55 Sciences, Beijing 100101, China
- 56 ²¹ Institute of Geographic Sciences and Natural Resources Research, Chinese
57 Academy of Sciences, Beijing, China
- 58 ²² Department of Soil, Water, and Climate University of Minnesota, Twin Cities,
59 USA
- 60 ²³ Department of Plant Sciences, University of Oxford, South Parks Road, OX1 3RB,
61 UK
- 62 ²⁴ Department of Biology, College of Life and Environmental Sciences, Wenzhou
63 University, Wenzhou 325035 China
- 64 ²⁵ Nature Conservation and Landscape Ecology, Faculty of Earth and Environmental
65 Sciences, University of Freiburg, Germany
- 66 ²⁶ Geobotany, Faculty of Biology, University of Freiburg, Germany
- 67 ²⁷ Institute of Soil Science, the Chinese Academy of Sciences, Nanjing 210008 China
- 68 ²⁸ Institute of Applied Ecology, Chinese Academy of Sciences, 72 Wenhua Road,
69 Shenyang 110016, P.R.China
- 70 ²⁹ Faculty of Life Science and Technology, Central South University of Forestry and
71 Technology, Changsha 410004, Hunan Province, China
- 72 ³⁰ Institute of Plant and Environment Protection, Beijing Academy of Agriculture and
73 Forestry Sciences, Beijing 100079, China
- 74 ³¹ College of Life Sciences, Zhejiang University, Hangzhou, Zhejiang 310058, China

75 ³² Institute of Ecology, College of Chemistry and Life Science, Zhejiang Normal
76 University, Yingbin Road No. 688, Jinhua City, Zhejiang Province, China 321004

77

78 † Corresponding authors: Helge Bruelheide, Keping Ma, Pascal A. Niklaus, Bernhard
79 Schmid

80 Email: helge.bruehlheide@botanik.uni-halle.de, kpma@ibcas.ac.cn,

81 pascal.niklaus@ieu.uzh.ch, Bernhard.schmid@ieu.uzh.ch

82

83 Emails of other authors:

84 Yuanyuan Huang <yuansjob@gmail.com>;

85 Yuxin Chen <yuxin.chen@ieu.uzh.ch>;

86 Nadia Castro-Izaguirre <nadia.cci@gmail.com>;

87 Martin Baruffol <martin.baruffol@gmail.com>;

88 Matteo Brezzi <Matteo.brezzi@gmail.com>;

89 Anne Lang <anne.lang@gutaltenoythe.de>;

90 Ying Li <yingli8441@hotmail.com>;

91 Werner Härdtle <haerdtle@uni-lueneburg.de>;

92 Goddert von Oheimb <Goddert_v_Oheimb@tu-dresden.de>;

93 Xuefei Yang <xuefei@mail.kib.ac.cn>;

94 Kequan Pei <peikequan@ibcas.ac.cn>;

95 Sabine Both <s.both@abdn.ac.uk>;

96 Xiaojuan Liu <liuxiaojuan06@ibcas.ac.cn>;

97 Bo Yang <yangbomvp@aliyun.com>;

98 David Eichenberg <david.eichenberg@idiv.de>;

99 Thorsten Assmann <thorsten.assmann@leuphana.de>;

- 100 Jürgen Bauhus <juergen.bauhus@waldbau.uni-freiburg.de>;
- 101 Thorsten Behrens <thorsten.behrens@uni-tuebingen.de>;
- 102 François Buscot <francois.buscot@ufz.de>;
- 103 Xiao-Yong Chen <xychen@des.ecnu.edu.cn>;
- 104 Douglas Chesters <dchesters@ioz.ac.cn>;
- 105 Bing-Yang Ding <dingby2005@126.com>;
- 106 Walter Durka <walter.durka@ufz.de>;
- 107 Alexandra Erfmeier <aerfmeier@ecology.uni-kiel.de>;
- 108 Jingyun Fang <jyfang@urban.pku.edu.cn>;
- 109 Markus Fischer <markus.fischer@ips.unibe.ch>;
- 110 Liang-Dong Guo <guold@im.ac.cn>;
- 111 Dali Guo <guodl@igsrr.ac.cn>;
- 112 Jessica L.M. Gutknecht <jgut@umn.edu>;
- 113 Jin-Sheng He <jshe@pku.edu.cn>;
- 114 Chun-Ling He <hechunling68@126.com>;
- 115 Andy Hector <andrew.hector@plants.ox.ac.uk>;
- 116 Lydia Hönic <lydia.hoenig@botanik.uni-halle.de>;
- 117 Ren-Yong Hu <wzryhu@163.com>;
- 118 Alexandra-Maria Klein <alexandra.klein@nature.uni-freiburg.de>;
- 119 Peter Kühn <peter.kuehn@uni-tuebingen.de>;
- 120 Yu Liang <coolrain@ibcas.ac.cn>;
- 121 Stefan Michalski <stefan.michalski@ufz.de>;
- 122 Michael Scherer-Lorenzen <michael.scherer@biologie.uni-freiburg.de>;
- 123 Karsten Schmidt <karsten.schmidt@uni-tuebingen.de>;
- 124 Thomas Scholten <thomas.scholten@uni-tuebingen.de>;

- 125 Andreas Schuldt <andreas.schuldt@idiv.de>;
- 126 Xuezheng Shi <xzshi@issas.ac.cn>;
- 127 Man-Zhi Tan <mzhtan@issas.ac.cn>;
- 128 Zhiyao Tang <zytang@urban.pku.edu.cn>;
- 129 Stefan Trogisch <stefan.trogisch@botanik.uni-halle.de>;
- 130 Zhengwen Wang <wangzw@iae.ac.cn>;
- 131 Erik Welk <erik.welk@botanik.uni-halle.de>;
- 132 Christian Wirth <cwirth@uni-leipzig.de>;
- 133 Tesfaye Wubet <tesfaye.wubet@ufz.de>;
- 134 Wenhua Xiang <xiangwh2005@163.com>;
- 135 Jiye Yan <yanjiye@baafs.net.cn>;
- 136 Mingjian Yu <fishmj@zju.edu.cn>;
- 137 Xiao-Dong Yu <yuxd@ioz.ac.cn>;
- 138 Jiayong Zhang <zhangjiayong@zjnu.cn>;
- 139 Shouren Zhang <zsr@ibcas.ac.cn>;
- 140 Naili Zhang <zhangnl@ibcas.ac.cn>;
- 141 Hong-Zhang Zhou <zhouhz@ioz.ac.cn>;
- 142 Chao-Dong Zhu <zhu cd@ioz.ac.cn>;
- 143 Li Zhu <julie@ibcas.ac.cn>;
- 144
- 145 **Type of article:** Letter
- 146

147 **Forest ecosystems contribute substantially to global terrestrial primary**
148 **productivity and climate regulation, but, in contrast to grasslands, experimental**
149 **evidence for a positive biodiversity–productivity relationship in highly diverse**
150 **forests is still lacking¹. Here, we provide such evidence from a large forest**
151 **biodiversity experiment with a novel design² in subtropical China. Productivity**
152 **(stand-level tree basal area, aboveground volume and carbon and their annual**
153 **increment) increased linearly with the logarithm of tree species richness.**
154 **Additive partitioning³ showed that increasing positive complementarity effects**
155 **combined with weakening negative selection effects caused a strengthening of the**
156 **relationship over time. In 2-species mixed stands, complementary effects**
157 **increased with functional distance and selection effects with vertical crown**
158 **dissimilarity between species. Understorey shrubs reduced stand-level tree**
159 **productivity, but this effect of competition was attenuated by shrub species**
160 **richness, indicating that a diverse understorey may facilitate overall ecosystem**
161 **functioning. Identical biodiversity–productivity relationships were found in plots**
162 **of different size, suggesting that extrapolation to larger scales is possible. Our**
163 **results highlight the potential of multi-species afforestation strategies to**
164 **simultaneously contribute to mitigation of climate change and biodiversity**
165 **restoration.**

166 Forest ecosystems harbor around two thirds of all terrestrial plant species, but
167 currently lose biodiversity at high rates which may threaten the production of timber,
168 fiber, fuel and other services beneficial to humans⁴. Observational studies suggest that
169 species-rich forests exceed the productivity of less diverse forests^{5,6}, but co-varying
170 factors (e.g. spatial heterogeneity in abiotic environment, species composition and
171 successional stages; interventions by forest management) make assigning causation

172 difficult. Systematic experimental manipulations of plant species composition in
173 grassland communities⁷⁻⁹ have demonstrated that plant diversity promotes community
174 productivity. This effect has been attributed to positive effects of niche partitioning
175 between species, specifically to complementarity in the use of abiotic resources¹⁰ or
176 interactions with enemies¹¹, or to an increasing contribution of highly productive
177 species in more diverse communities¹². These two types of mechanisms have been
178 related to statistical complementarity and selection effects obtained by additive
179 partitioning³. However, these mechanisms may differ in species-rich forests in which
180 neutral processes may be important^{13,14} and where “diffuse” coevolution may result in
181 niche convergence toward generalist strategies¹⁵. Furthermore, trees have large and
182 persistent vertical structures that support the long-term accumulation of biomass.
183 Several forest experiments have recently been initiated^{16,17}, but these are mainly in the
184 temperate zone or implemented in small plots with a limited species richness
185 gradients¹⁸⁻²³. To close these critical gaps in knowledge¹, controlled experiments in
186 which the diversity of tree species is systematically manipulated are needed. The
187 largest such study concerning numbers of treatments and plots has been established in
188 2009/2010 in subtropical south-east China and is referred to as the BEF-China
189 experiment².

190 Here, we report how stand-level productivity in the BEF-China experiment 3–7
191 years after planting was related to species richness and how variation within species-
192 richness levels was related to trait differences among species. Experimental forest
193 communities were constructed systematically from a pool of 40 tree (Extended Data
194 Table 1) and 20 shrub species, and were established in plots at two hilly sites (in 2009
195 at site A and in 2010 at site B). By the time of our later measurements the tree
196 communities were well established with some canopies exceeding 12 m in height in

197 2016. The design of previous biodiversity experiments had been criticised because not
198 all species were found at all diversity levels, and because the compositions of the
199 experimental communities that were realized were not nested as would be expected
200 with sequential extinction²⁴. We adopted a novel design that avoided these caveats²
201 (see Methods, Extended Data Fig. 1, Extended Data Table 2). In brief, we first created
202 three pools of 16 species per site. These were then repeatedly split into halves,
203 resulting in nested, non-overlapping subsets of 8, 4, 2 and 1 species. We used these
204 sets, and in addition also the full sets of 24 species per site, to plant tree communities
205 comprising 1 to 24 species. We further established plots with two sizes: 0.067 ha
206 (equivalent to the Chinese area unit of 1 mu; 400 individual trees) and 0.267 ha (4
207 mu; 1600 individuals). The larger plots were established for one of the three 16-
208 species pools at each site and included a split-plot treatment that consisted of
209 understorey shrubs planted in the centre of the quadrats formed by four neighbouring
210 trees. Shrubs were planted at a species richness of 0 (no shrubs), 2, 4 or 8, in factorial
211 combination with the tree species-richness treatment. We assessed stand-level tree
212 productivity in all 1-mu plots (including all 1-mu subplots of the larger plots) non-
213 destructively by measuring stem basal area and height of the 16 central trees every
214 year from 2013–2016 in September/October. We used these data, together with data
215 from separately harvested trees to obtain conversion factors, to calculate tree volume
216 and aggregated the individual volume data of live trees to the stand level. To
217 characterize annual stand growth, we further derived yearly increments of stand
218 volume from successive inventories. Using the same method, we determined the same
219 metrics at the population-level (stand-level data separated into species).

220 We found significantly positive effects of the logarithm of tree species richness
221 on both stand volume and annual stand volume increment of trees ($F_{1, 89} = 5.26$, $P =$

222 0.024 and $F_{1,94} = 9.34$, $P = 0.003$, respectively; Fig. 1 and Extended Data Fig. 2, Table
223 1). The size of these effects increased over time ($F_{1,95} = 10.83$, $P = 0.001$ and $F_{1,95} =$
224 12.01 , $P < 0.001$, respectively, for interaction species richness \times year). Similar results
225 were obtained for stand basal area and its increment (Extended Data Fig. 3, Table 1).
226 In 2016, at the end of our measuring period, stand basal area increased on average by
227 $1.65 \text{ m}^2 \text{ ha}^{-1}$ and stand volume by $5.09 \text{ m}^3 \text{ ha}^{-1}$ with each doubling of tree species
228 richness. After seven years of growth, the average 16-species mixture stored $22.0 \pm$
229 4.5 Mg C ha^{-1} above ground, which is double the amount found in monocultures (9.4
230 $\pm 1.1 \text{ Mg ha}^{-1}$, Extended Data Fig. 4) and similar to the productivity of monocultures
231 of commercial plantation species *Cunninghamia lanceolata* ($22.4 \pm 10.7 \text{ Mg C ha}^{-1}$)
232 and *Pinus massoniana* ($21.0 \pm 3.0 \text{ Mg C ha}^{-1}$) that we had planted for reference at the
233 same site (Extended Data Fig. 4, Extended Data Table 4). System-level C
234 sequestration likely is higher, given that additional C will have been allocated to
235 belowground tree organs²⁵ and in part transferred to persistent soil pools important for
236 long-term carbon sequestration. These strong positive effects of tree species richness
237 were driven by faster growth of live trees in more diverse stands, and were unrelated
238 to tree survival rate, which was independent of species richness; if anything, there was
239 a trend towards lower survival at higher richness (Extended Data Fig. 5).

240 The net biodiversity effect²⁶ on productivity increased through time for mixtures
241 of all species-richness levels (Fig. 2, $F_{1,48} = 23.61$, $P < 0.001$). The positive effects of
242 tree species richness on productivity were also reflected in a higher frequency of
243 mixtures that overyielded relative to the ones that underyielded and in many cases of
244 transgressive overyielding²⁶ (Extended Data Table 5). Additive partitioning revealed
245 that the increases of net biodiversity effects were primarily driven by increases in
246 complementarity effects (Extended Data Table 6, $F_{1,31} = 9.61$, $P = 0.004$) and

247 weakening negative selection effects (Extended Data Table 6, $F_{1,37} = 4.61$, $P = 0.038$).

248 In the last year of measurements, selection effects were no longer significantly

249 different from zero (Fig. 2, $F_{1,31} = 3.40$, $P = 0.075$).

250 We observed considerable variation in overyielding among communities of the

251 same species-richness level. Some of this variation was explained by functional

252 diversity but phylogenetic diversity had low explanatory power. For the 48 different

253 2-species mixtures, complementarity effects were positively correlated with the

254 functional distance and selection effects with vertical crown dissimilarity, also

255 referred to as crown complementarity between species (Fig. 3, Extended Data Table

256 7). That vertical crown complementarity²² contributed to overyielding via selection

257 rather than complementarity effects indicated that it was due to asymmetric light

258 competition²⁷ and is consistent with the “competition-trait hierarchy hypothesis”²⁸.

259 Species with high monoculture productivity (Fig. 4a) explained large amounts

260 of variation in stand-level productivity (Fig. 4b), but their contribution was not always

261 positive, as demonstrated by several negative species-level selection effects (Fig. 4c).

262 Despite the positive effect of species richness on community productivity, the

263 population-level responses of each species to species richness varied from positive to

264 neutral to negative (Fig. 4d). These responses did not differ between evergreen and

265 deciduous species (Fig. 4d, $F_{1,159} = 0.89$, $P = 0.347$). A similar decoupling between

266 community- and population-level responses has previously been reported from

267 grassland biodiversity experiments⁸ and indicates that a few positive population-level

268 responses can overcompensate a larger number of negative population-level

269 responses. Nevertheless, the number of species with positive responses to community

270 diversity and the magnitude of their responses increased with time (Fig. 4d).

271 Competition by understorey shrubs planted in the gaps between the trees
272 reduced stand-level tree volume (Extended Data Table 8, $F_{1,234} = 4.80$, $P = 0.029$), but
273 this effect decreased with shrub species richness (Extended Data Table 8, $F_{1,199} =$
274 5.40 , $P = 0.022$) and was negligible when mixtures of 8 shrub species were planted
275 (Extended Data Fig. 6), indicating reduced competition between shrubs and trees at
276 higher shrub diversity levels. The diversity–productivity relationships we found were
277 scale-independent, i.e. they did not differ between 1- and 4-mu plots (Extended Data
278 Table 8, $F_{1,114} = 0.20$, $P = 0.694$ for interaction species richness \times plot size).

279 Our results provide strong evidence for a positive effect of tree species richness
280 on tree productivity at stand-level in establishing subtropical forest ecosystems, and
281 support the idea that highly diverse subtropical forest ecosystems are niche-
282 structured^{22,27}. Seven-year old mixed-species stands can produce an estimated
283 additional aboveground wood volume of $25 \text{ m}^3 \text{ ha}^{-1}$ relative to the average
284 monoculture, which translates to the sequestration of approximately an extra 10 Mg C
285 ha^{-1} (Fig. 1, Extended Data Fig.4). We expect this effect to grow further, given that we
286 did not observed any signs of a deceleration over the present measurement period.
287 The size of the biodiversity effects we found for these forests is similar to biodiversity
288 effects reported from grassland studies^{8,9}. Given that plant biomass is higher in
289 forests, and that the largest fraction of tree carbon is bound in relatively persistent
290 woody biomass, these effects translate into significant diversity-mediated rates of
291 carbon sequestration. Substantial forest areas are managed world-wide, with large
292 afforestation programs underway in many countries. In China, huge economic efforts
293 are made for afforestation, with a net growth of total forested area by $1.5 \times 10^6 \text{ ha yr}^{-1}$
294 achieved from 2010 to 2015²⁹. However, the overwhelming fraction of newly
295 established forests are monoculture plantations of species with highest productivity in

296 the short term³⁰. Our analysis suggests that a similar productivity could be achieved
297 with mixed plantations of native species, which would result in co-benefits in the
298 form of biodiversity management and a likely higher level and stability of ecosystem
299 services in the longer term.

300

301 **Online content** Methods, along with additional Extended Data display items and
302 Source Data, are available in the online version of the paper; references unique to
303 these sections appear only in the online paper.

304

- 305 1 Clarke, D. A., York, P. H., Rasheed, M. A. & Northfield, T. D. Does
306 biodiversity–ecosystem function literature neglect tropical ecosystems?
307 *Trends Ecol Evol* **32**, 320-323 (2017).
- 308 2 Bruelheide, H. *et al.* Designing forest biodiversity experiments: general
309 considerations illustrated by a new large experiment in subtropical China.
310 *Methods in Ecology and Evolution* **5**, 74-89 (2014).
- 311 3 Loreau, M. & Hector, A. Partitioning selection and complementarity in
312 biodiversity experiments. *Nature* **412**, 72-76 (2001).
- 313 4 FAO. *Global Forest Resources Assessment*. (Food and Agriculture
314 Organization of the United Nations, Rome, Italy, 2010).
- 315 5 Baruffol, M. *et al.* Biodiversity promotes tree growth during succession in
316 subtropical forest. *PLoS One* **8**, e81246 (2013).
- 317 6 Liang, J. *et al.* Positive biodiversity–productivity relationship predominant in
318 global forests. *Science* **354**, 196 (2016).
- 319 7 Harpole, W. S. & Tilman, D. Grassland species loss resulting from reduced
320 niche dimension. *Nature* **446**, 791-793 (2007).
- 321 8 Hector, A. *et al.* Plant diversity and productivity experiments in European
322 grasslands. *Science* **286**, 1123-1127 (1999).
- 323 9 Reich, P. B. *et al.* Impacts of biodiversity loss escalate through time as
324 redundancy fades. *Science* **336**, 589-592 (2012).
- 325 10 Tilman, D., Lehman, C. L. & Thomson, K. T. Plant diversity and
326 ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. USA*
327 **94**, 1857-1861 (1997).
- 328 11 Schnitzer, S. A. *et al.* Soil microbes drive the classic plant diversity–
329 productivity pattern. *Ecology* **92**, 296-303 (2011).

- 330 12 Huston, M. A. Hidden treatments in ecological experiments: re-evaluating the
331 ecosystem function of biodiversity. *Oecologia* **110**, 449-460 (1997).
- 332 13 Wang, X. *et al.* Stochastic dilution effects weaken deterministic effects of
333 niche-based processes in species rich forests. *Ecology* **97**, 347-360 (2016).
- 334 14 Bruelheide, H. *et al.* Community assembly during secondary forest succession
335 in a Chinese subtropical forest. *Ecol Monogr* **81**, 25-41 (2011).
- 336 15 Hubbell, S. P. Neutral theory and the evolution of ecological equivalence.
337 *Ecology* **87**, 1387-1398 (2006).
- 338 16 Scherer-Lorenzen, M. The functional role of biodiversity in the context of
339 global change. In *Forests and Global Change* (eds David A. Coomes, David
340 F. R. P. Burslem, & William D. Simonson) 195-238 (Cambridge University
341 Press, 2014).
- 342 17 Verheyen, K. *et al.* Contributions of a global network of tree diversity
343 experiments to sustainable forest plantations. *Ambio* **45**, 29-41 (2016).
- 344 18 Grossman, J. J., Cavender-Bares, J., Hobbie, S. E., Reich, P. B. &
345 Montgomery, R. A. Species richness and traits predict overyielding in stem
346 growth in an early-successional tree diversity experiment. *Ecology* **98**, 2601-
347 2614 (2017).
- 348 19 Potvin, C. & Gotelli, N. J. Biodiversity enhances individual performance but
349 does not affect survivorship in tropical trees. *Ecol Lett* **11**, 217-223 (2008).
- 350 20 Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N. & Loreau, M. Tropical
351 tree diversity enhances light capture through crown plasticity and spatial and
352 temporal niche differences. *Ecology* **95**, 2479-2492 (2014).
- 353 21 Tobner, C. M. *et al.* Functional identity is the main driver of diversity effects
354 in young tree communities. *Ecol Lett* **19**, 638-647 (2016).

- 355 22 Williams, L. J., Paquette, A., Cavender-Bares, J., Messier, C. & Reich, P. B.
356 Spatial complementarity in tree crowns explains overyielding in species
357 mixtures. *Nature Ecology & Evolution* **1**, 0063 (2017).
- 358 23 Van de Peer, T., Verheyen, K., Ponette, Q., Setiawan, N. N. & Muys, B.
359 Overyielding in young tree plantations is driven by local complementarity and
360 selection effects related to shade tolerance. *J Ecol* **00**, 1-10 (2017).
- 361 24 Bell, T. *et al.* A Linear Model Method for Biodiversity–Ecosystem
362 Functioning Experiments. *The American Naturalist* **174**, 836-849 (2009).
- 363 25 Sun, Z. *et al.* Positive effects of tree species richness on fine-root production
364 in a subtropical forest in SE-China. *Journal of Plant Ecology* **10**, 146-157
365 (2017).
- 366 26 Schmid, B., Hector, A., Saha, P. & Loreau, M. Biodiversity effects and
367 transgressive overyielding. *Journal of Plant Ecology* **1**, 95-102 (2008).
- 368 27 Niklaus, P. A., Baruffol, M., He, J.-S., Ma, K. & Schmid, B. Can niche
369 plasticity promote biodiversity–productivity relationships through increased
370 complementarity? *Ecology* **98**, 1104-1116 (2017).
- 371 28 Kunstler, G. *et al.* Competitive interactions between forest trees are driven by
372 species' trait hierarchy, not phylogenetic or functional similarity: implications
373 for forest community assembly. *Ecol Lett* **15**, 831-840 (2012).
- 374 29 Keenan, R. J. *et al.* Dynamics of global forest area: results from the FAO
375 Global Forest Resources Assessment 2015. *For Ecol Manage* **352**, 9-20
376 (2015).
- 377 30 Hua, F. *et al.* Opportunities for biodiversity gains under the world's largest
378 reforestation programme. *Nat Commun* **7**, 12717 (2016).
- 379

380 **Extended Data** are available in the online version of the paper.

381

382 **Acknowledgements** We thank the farmers and Chen Lin for help in the field. This
383 study was supported by the German Research Foundation (DFG FOR 891), the
384 National Natural Science Foundation of China (NSFC No. 31270496 and No.
385 31300353), the Swiss National Science Foundation (SNSF No. 130720, 147092) and
386 the European Union (EC 7th Framework Program No. 608422).

387

388 **Author contributions** HB, KM and BS conceived the project with help from all co-
389 authors; YH carried out the measurements; YH, YC, KM, PAN and BS led the data
390 analysis and interpretation. All authors contributed to the writing of the manuscript.

391

392 **Author information** The authors declare no competing financial interests.

393 Correspondence and requests for materials should be addressed to Y.H.

394 (yuanyuan.huang@ieu.uzh.ch), H.B. (helge.bruehlheide@botanik.uni-halle.de), K.M.

395 (kpma@ibcas.ac.cn), P.A.N. (pascal.niklaus@ieu.uzh.ch) or B.S.

396 (bernhard.schmid@ieu.uzh.ch).

397

398 METHODS

399 **Study site and experimental design**

400 The BEF-China experimental platform was established in Jiangxi Province, China
401 (29°08'–29°11'N, 117°90'–117°93'E). Climate at the site is subtropical, with mean
402 annual temperature and precipitation of 16.7°C and 1800 mm, respectively (averaged
403 from 1971–2000)³¹. A large-scale tree biodiversity experiment was established in
404 2009–2010 on two sites (A and B) of approximately 20 ha each, with a total of
405 226'400 individual trees planted. Here, we use all plots in which random species-loss
406 scenarios were simulated. The species pool contains 40 tree species (Extended Data
407 Table 1), 24 for each site (of which eight are shared between sites). The 24 species at
408 each site were divided into three 8-species sets. By combing these 8-species sets in all
409 possible ways, three pools of 16 species were created. The species in each 16-species
410 pool were put in random sequence and then repeatedly divided in halves until
411 monocultures were obtained. This procedure resulted in 70 unique species
412 compositions per site (Extended Data Table 2) and ensured that each tree species
413 occurred in equal overall proportion at each diversity level. We further included
414 monoculture plots with two commercially important tree species, *Pinus massoniana*
415 and *Cunninghamia lanceolata*, as reference, with 5 replicate plots per species and site.
416 Each plot was 25.8 × 25.8 m in size and planted with 400 tree individuals arranged on
417 a rectangular 20 × 20 grid with 1.29 m spacing between rows and columns. To
418 minimize edge effects, plots were established adjacent to each other, with trees thus
419 forming a continuous cover across the entire site. Site A was planted in 2009, site B in
420 2010.

421 Plots of one species pool per site (pools A1 and B1 at sites A and B,
422 respectively, Extended Table 2) were additionally replicated in plots that were four

423 times larger and thus contained 1600 trees. These large plots were subdivided into
424 four quadrants in which a factorial understorey shrub-diversity treatment was
425 established. These four subplots either had no shrub understorey (0 species), or shrubs
426 planted in all the centers between 4 adjacent trees, at a diversity of 2, 4 or 8 shrub
427 species (Fig. 1a).

428 The design we use here consisted of 140 small plots (1 mu) and 64 large plots
429 (4 mu). Out of this total of 396 1-mu sized (sub)plots, nine had to be excluded
430 because these were not established due to a lack of sapling material or high initial
431 mortality. All plots were weeded annually to remove emerging herbs and woody
432 species that were not part of the planting design.

433

434 **Tree measurements**

435 We assessed stand-level and population-level tree growth by measuring the height of
436 trees and maximum and minimum stem diameter at 5 cm above ground to calculate
437 basal area. We focused on the central $4 \times 4 = 16$ trees of each 1-mu (sub)plot to avoid
438 edge effects. These measurements were repeated annually in September/October from
439 2013 to 2016. We aggregated these tree-level data at the species (i.e. population) and
440 stand level.

441 We further calculated a cylindrical tree volume as the product of basal area and
442 height. The true volume was then obtained by multiplying this proxy with a form
443 factor determined by a complete harvest of 154 trees in natural forest near the
444 experimental sites. The total volume of each harvested trees was calculated as ratio of
445 total aboveground dry biomass and average wood density. Similarly, tree biomass was
446 determined by multiplying the cylindrical volume of each experimental tree with a

447 biomass conversion factor determined based on the harvested trees (Extended Data).

448 Biomass was converted to carbon content³² by multiplying with 0.474 g C g⁻¹.

449

450 **Complementarity effect and selection effect**

451 We used the additive partitioning method of Loreau & Hector³ to decompose net
452 biodiversity effects (NEs) of productivity measures into complementarity (CEs) and
453 selection effects (SEs), separately for each year and diversity level. CEs and SEs
454 depend on relative yields of species, which we calculated using monoculture biomass
455 as denominator. If a species failed to establish in monoculture (which was the case for
456 *Meliosma flexuosa*, *Castanopsis eyrei* and *Machilus grijsii*), or had a mortality
457 exceeding 80% (*Quercus phillyreoides*, *Phoebe bournei*), it was excluded from the set
458 of target species in the corresponding mixtures³³. Formally, CEs and SEs are related
459 to (co)variances and therefore were square-root transformed with sign reconstruction
460 $(\text{sign}(y)\sqrt{|y|})$ prior to analysis, which improved the normality of residuals³.

461

462 **Overyielding and underyielding**

463 Overyielding describes the case where the productivity of a mixture exceeds the
464 average productivity of monocultures of component trees²⁶. Conversely,
465 underyielding identifies a lower yield of the mixture relative to monocultures.

466 Transgressive overyielding indicates that the productivity of a mixture exceeds the
467 productivity of the monoculture of the most productive component species.

468 Transgressive underyielding is defined similarly. We determined overyielding and
469 underyielding of all mixtures relative to monocultures. Capitalizing on the nested
470 nature of our design, we further determined the same metrics using the two mixtures
471 with half the set of species as reference, instead of monocultures, i.e. we tested

472 whether combining communities with two sets of species resulted in a community
473 that produced more or less biomass than expected on the assumption of no
474 interactions among the sets (overyielding) or that community productivity would be
475 determined by the more productive set of species alone (transgressive overyielding).
476

477 **Vertical crown complementarity**

478 We quantified the interspecific complementarity in vertical crown extent of trees in
479 2016. The crown extent was determined as interval between the lowest side-branch
480 and the top of a tree in monocultures. These data were averaged across all surviving
481 trees of the 16 central individuals planted in a plot. We then calculated vertical crown
482 complementarity in 2-species mixtures as proportional dissimilarity of the crown
483 extents between the two species:

$$484 \quad PDS_{A,B} = \frac{x_{A \setminus B} + x_{B \setminus A}}{x_{A \cup B}}$$

485 where $x_{A \setminus B}$ indicates the vertical extent (in meters) that is occupied by A but not by B
486 (vice versa for $x_{B \setminus A}$), and $x_{A \cup B}$ indicates the extent occupied by at least one of the
487 species. This index is equivalent to one minus the proportional similarity index
488 proposed by Colwell and Futuyma³⁴.

489

490 **Statistical analysis**

491 We used analysis of variance based on type-I sum of squares linear mixed-effects
492 models to assess the effects of tree species richness (and additional design variables)
493 on productivity³⁵. All analyses were done in R 3.3.2 and ASReml-R³⁶. The models
494 included the fixed effects site, tree species richness (\log_2 -transformed), year
495 (continuous variable, centered over our observation period), the interaction \log_2 (tree
496 species richness) \times year, and the interaction site \times year. Random effects were species

497 composition (with a separate variance component for each site), plot (with a separate
498 variance component for each site), subplot, and the interactions of all these random
499 terms with year. Model residuals were checked for normality and homogeneity of
500 variances.

501 For the analyses of shrub diversity effects, the model contained the additional
502 fixed effects shrub presence (a two-level factor: 0 vs. 2, 4 or 8 shrub species), plot
503 size (a two-level factor: 1 vs. 4 mu), log₂ of shrub species richness (for shrub-species
504 richness >0), and the interactions of all these terms with log₂(tree species richness)
505 and with year. Random effects were species composition (with a separate variance
506 component for each site), plot (with a separate variance component for each site),
507 subplot, and the interactions of all these random terms with year (Extended Data
508 Table 6). The interaction of year and site and the site-specific variance terms
509 estimated for some random terms accounted for the fact that site B was established
510 one year after site A and that trees at site B were therefore smaller.

511

512 31 Yang, X. *et al.* Establishment success in a forest biodiversity and ecosystem
513 functioning experiment in subtropical China (BEF-China). *European Journal*
514 *of Forest Research* **132**, 593-606 (2013).

515 32 Martin, A. R. & Thomas, S. C. A reassessment of carbon content in tropical
516 trees. *PLoS One* **6**, e23533 (2011).

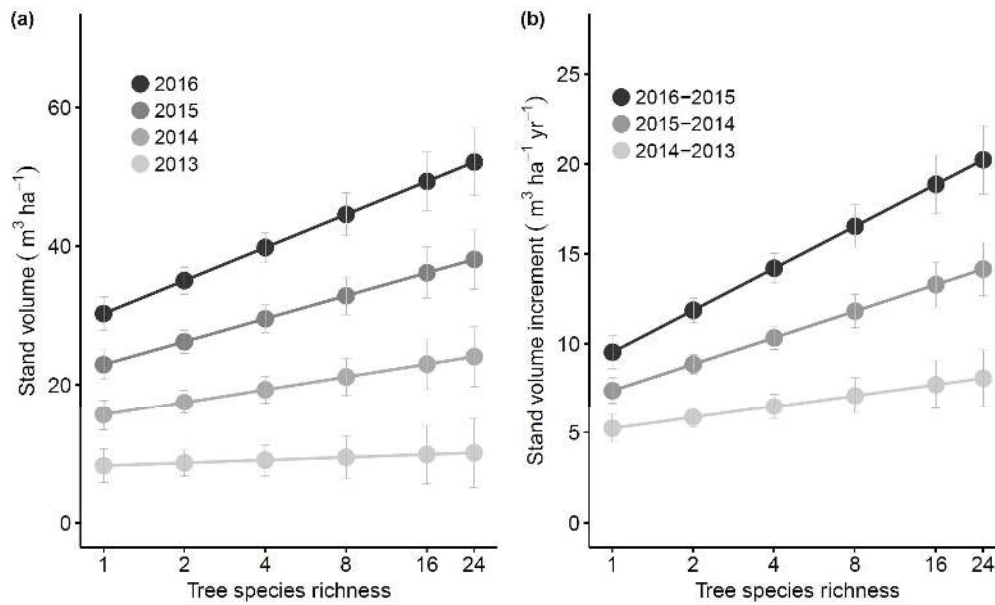
517 33 Marquard, E. *et al.* Plant species richness and functional composition drive
518 overyielding in a six-year grassland experiment. *Ecology* **90**, 3290-3302
519 (2009).

520 34 Colwell, R. K. & Futuyma, D. J. On the measurement of niche breadth and
521 overlap. *Ecology* **52**, 567-576 (1971).

522 35 Schmid, B., Baruffol, M., Wang, Z. & Niklaus, P. A. A guide to analyzing
523 biodiversity experiments. *Journal of Plant Ecology* **10**, 91-110 (2017).
524 36 Butler, D., Cullis, B., Gilmour, A. & Gogel, B. Analysis of Mixed Models for
525 S language Environments: ASReml–R Reference Manual. *Queensland DPI*,
526 *Brisbane, Australia*. URL
527 <https://http://www.vsni.co.uk/downloads/asreml/release2/doc/asreml-R.pdf>
528 (2007).
529

530 **Data availability statement**

531 The data supporting the findings of this study will be deposited in Pangaea with the
532 accession code <https://doi.pangaea.de/xxxxxxxxxxxxxx>.
533



534

535

536

Figure 1 | Stand-level tree volume (a), and its annual increment (b) as a function

537

of tree species richness from 2013–2016. The figure shows predicted means and

538

standard errors based on fitted mixed models (Table 1). Effects of species richness

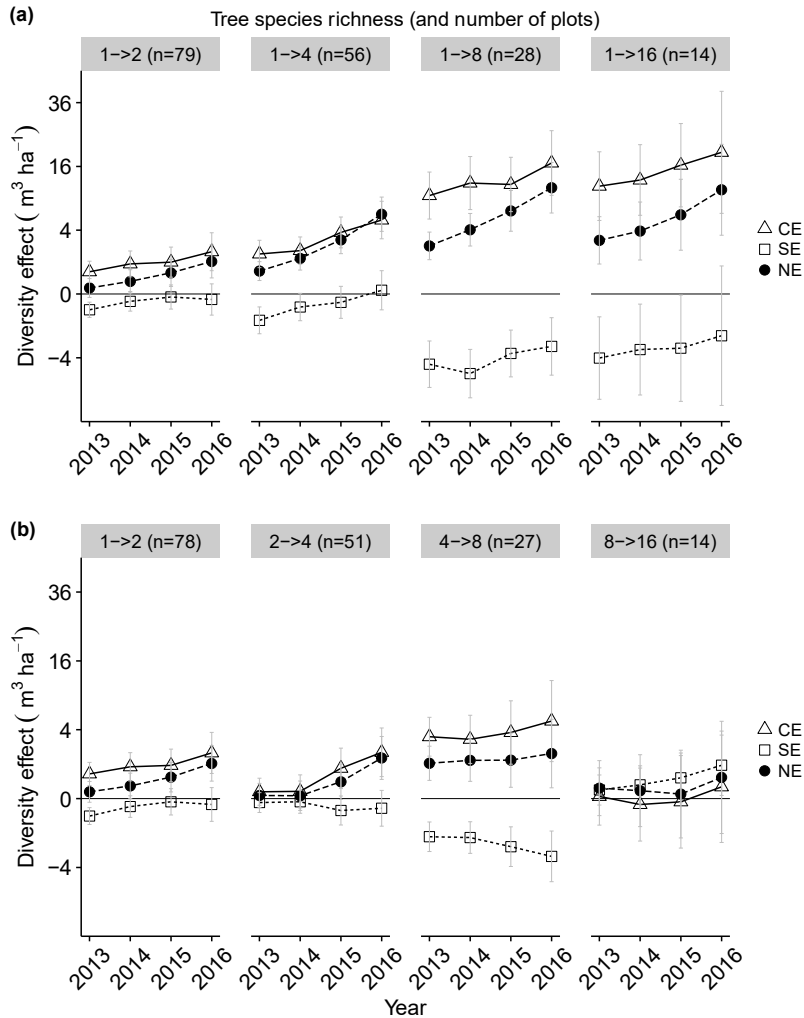
539

were significantly positive and increased significantly throughout the observation

540

period.

541



542

543 **Figure 2 | Changes over time in the net biodiversity effect (NE) and its additive**

544 **components, complementarity effect (CE) and selection effect (SE), on stand-**

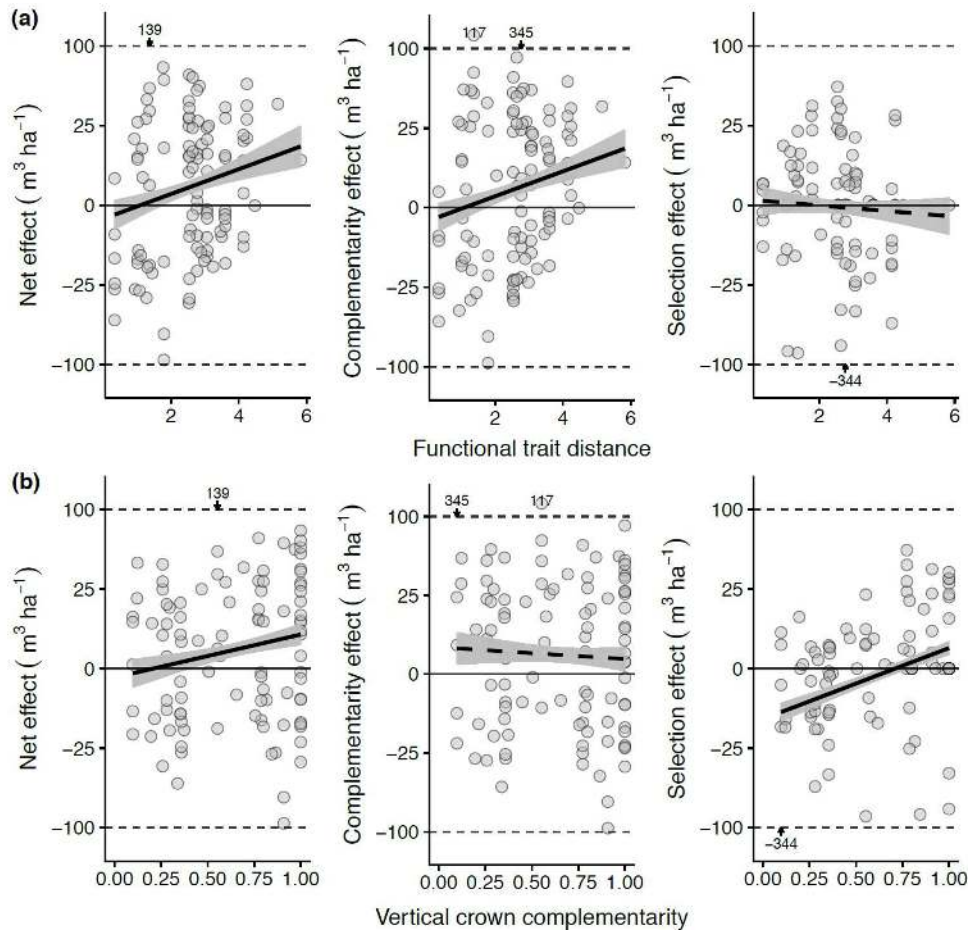
545 **level tree volume.** The figure shows means and standard errors. In (a), diversity

546 effects were calculated with monocultures as reference (Extended Data Table 6), in

547 (b) with component mixtures of half the number of species as reference. The y-axes

548 are square root-scaled to reflect the quadratic nature of biodiversity effects.

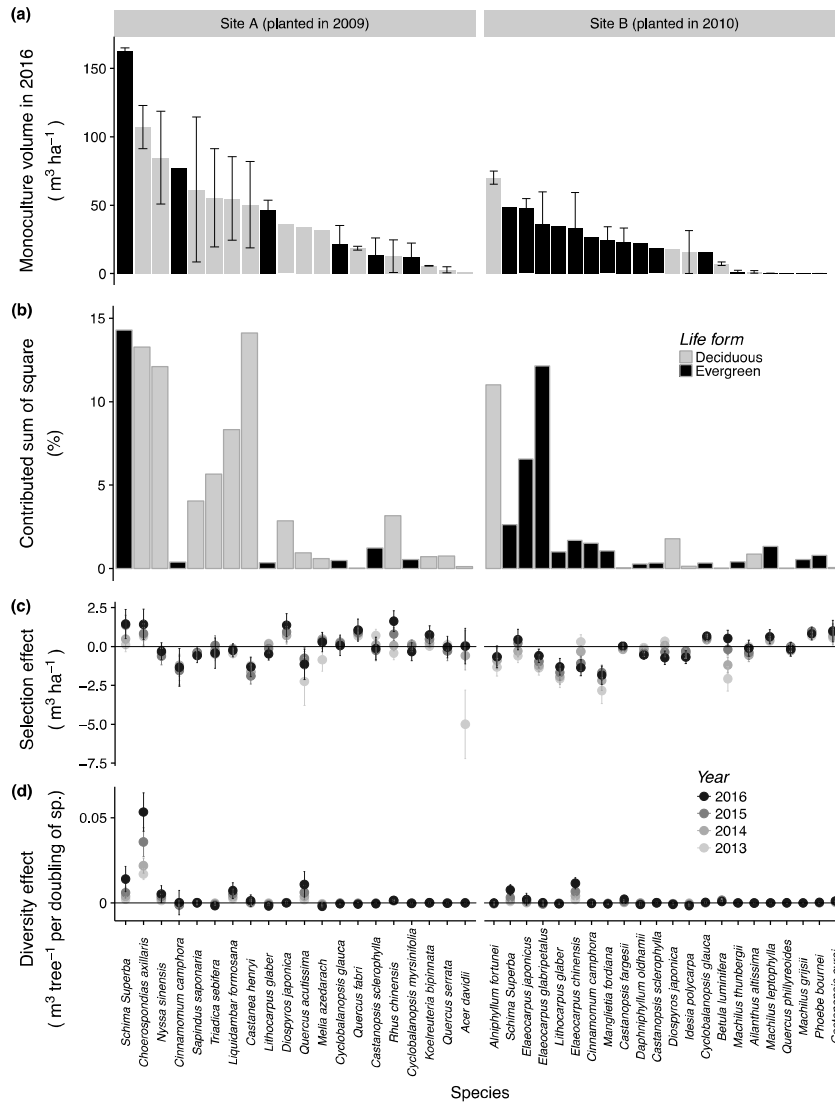
549



550

551 **Figure 3 | Relationships between biodiversity effects and (a) functional trait**
552 **distance and (b) vertical crown complementarity (proportional dissimilarity of**
553 **monoculture vertical crown extent) in 2016 (n = 108). Regression lines and**
554 **confidence bands (indicating \pm standard error of predicted values) are based on**
555 **mixed models (Extended Data Table 7). The y-axes are square root-scaled to reflect**
556 **the quadratic nature of biodiversity effects. Four extreme y-values are moved to the**
557 **plot margin and given as numbers.**

558



559

560 **Figure 4 | Monoculture stand-level tree volume of species in 2016 (a) and the**
 561 **fraction of stand-level tree volume sum of squares explained by the presence of**
 562 **each species in a plot (b), their species-specific selection effects (SEs) on stand-**
 563 **level tree volume (c) and their tree-level volume response to species richness (d).**
 564 Bars indicate standard errors. For (d) the volume of each species, standardized for the
 565 number of originally planted individuals of that particular species, was linearly
 566 regressed against $\log_2(\text{tree species richness})$ with the data from (sub)plots without
 567 shrub species.

568

569 **Table 1 | Mixed-effects models for effects of site, tree species richness (logSR),**
 570 **time (year) and interactions on stand-level tree basal area, stand-level tree**
 571 **volume and their increments.**

Source of variation	Basal area (n = 387)				Volume (n = 387)			
	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
Site	1	120.0	13.80	<0.001	1	100.8	19.21	<0.001
LogSR	1	111.2	6.00	0.016	1	88.7	5.26	0.024
Year	1	125.5	359.90	<0.001	1	103.0	206.30	<0.001
Site × year	1	125.3	5.80	0.018	1	103.7	18.80	<0.001
LogSR × year	1	117.8	16.00	<0.001	1	94.8	10.83	0.001

Source of variation	Basal area increment (n = 387)				Volume increment (n = 387)			
	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
Site	1	123.5	5.10	0.025	1	104.0	14.54	<0.001
LogSR	1	115.7	13.30	<0.001	1	93.9	9.34	0.003
Year	1	111.4	20.90	<0.001	1	104.2	68.85	<0.001
Site × year	1	115.2	4.40	0.037	1	109.2	27.50	<0.001
LogSR × year	1	102.1	10.20	0.002	1	95.1	12.01	<0.001

572

573 Notes:

574 Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table

575 (random terms were community composition, plot, subplot and the interaction of

576 these with year, with site-specific variance components for species composition and

577 plot). Abbreviations: n = numbers of plots in analysis; df = nominator degree of

578 freedom; ddf = denominator degree of freedom; logSR = $\log_2(\text{tree species richness})$. *F*

579 and *P* indicate F-ratios and the P-value of the significance test.

580 EXTENDED DATA

581 Conversion factors for volume, biomass and carbon content

582 We harvested 154 trees in a natural forest in 2010 near the experimental sites to determine
583 conversion factors from cylindrical volume (tree basal area \times height) to true volume and
584 biomass. The trees belonged to eight common species and three life forms (evergreen,
585 deciduous and coniferous) and were chosen to represent a naturally occurring size span of
586 young trees.

587 Trees were separated into large woody parts (stems and large branches with a diameter \geq
588 3 cm), twigs (the apical part of the stem and large branches plus side branches with a
589 diameter $<$ 3 cm), and dead attached material (large dead branches or twigs). Branches were
590 divided into segments of typically about 1 m length. The volume of large woody parts and
591 twigs was determined geometrically, approximating the parts as truncated cone (large woody
592 parts, $V = \frac{1}{3}\pi(r_1^2 + r_1r_2 + r_2^2) \times l$ where l is the length and r_1 and r_2 are the end radius), or cone
593 (twigs, as above but $r_2=0$). The density of these fractions was determined by oven-drying a
594 representative subsample of stem and branch discs or twigs.

595 These geometric and density data were then scaled up to total aboveground tree biomass
596 using a Bayesian framework, modeling twig mass and density in dependence of branch
597 positions within tree crowns³⁷.

598 Conversion factors from cylindrical volume to true volume (and mass) were determined
599 as total tree volume (and tree mass, including leaves) divided by cylindrical volume. We
600 analyzed the variation of these conversion factors with tree size and species life form using
601 mixed effects models with species identity as random term. We found that large trees
602 deviated from the linear relationship of form factor and cylindrical volume, and we therefore
603 removed trees with a cylindrical volume \geq 500 liter from the form factor calibration, leaving
604 a set of 119 trees. Within this set, there was only a small variance among species and no

605 significant effect of life form on the form factor; the form factor decreased linearly with the
606 cylindrical volume of harvested trees (Extended Data Table 3). We therefore used a form
607 factor of $0.5412 \text{ m}^3 \text{ m}^{-3} - 0.1985 \text{ m}^3 \cdot \text{BA} \cdot \text{h}$ (with basal area BA in m^2 and height h in m).
608 The intercept of $0.5412 \text{ m}^3 \text{ m}^{-3}$ is the weighted average form factor of evergreen and
609 deciduous species at size zero (in our study, 19 of 40 species were evergreen and 21
610 deciduous). Biomass factors were determined similarly, yielding a conversion factor of
611 $269.13 \text{ kg m}^{-3} - 141.96 \text{ kg m}^{-3} \cdot \text{BA} \cdot \text{h}$. For the two coniferous species that were planted for
612 comparison in monocultures only, we used separate equations obtained from the harvested
613 trees of the same species *Pinus massoniana* and *Cunninghamia lanceolata*. Here the form
614 factor was $0.5083 \text{ m}^3 \text{ m}^{-3} - 0.1985 \text{ m}^3 \cdot \text{BA} \cdot \text{h}$ and the biomass factor was 216.79 kg m^{-3}
615 $- 141.96 \text{ kg m}^{-3} \cdot \text{BA} \cdot \text{h}$.

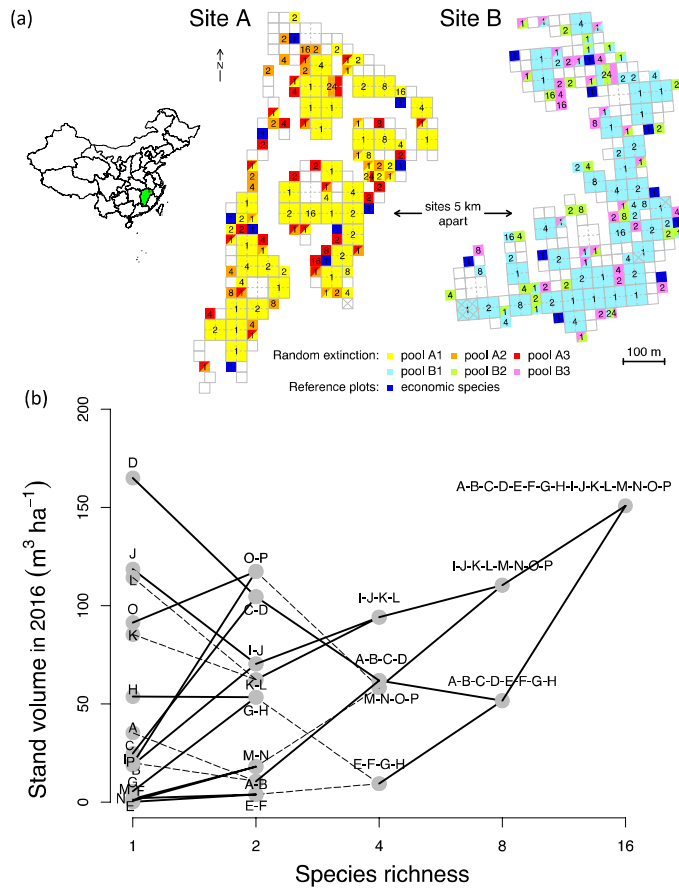
616

617 **Functional trait and phylogenetic distances**

618 We used four functional traits related to the resource-use strategies of tree species: specific
619 leaf area³⁸, branch-wood density³⁸, relative volume growth rate (RGR) and life form
620 (deciduous or evergreen). These traits were determined in plots that were part of the
621 experiment. RGR was calculated as the log-transformed relative difference in stand volume
622 of monocultures between seven (2015 for site A and 2016 for site B) and five years (2013 for
623 site A and 2014 for site B) after planting. We selected the monocultures without shrub
624 treatments. We used site-specific RGR because of the large variation in growth rates between
625 sites A and B. We calculated functional trait distances among species pairs in 2-species
626 communities as Euclidean distances in standardized multivariate trait space (using the four
627 traits as axes).

628 We calculated phylogenetic distances among species pairs as their cophenetic distance in
629 a node age-calibrated phylogenetic tree³⁹.

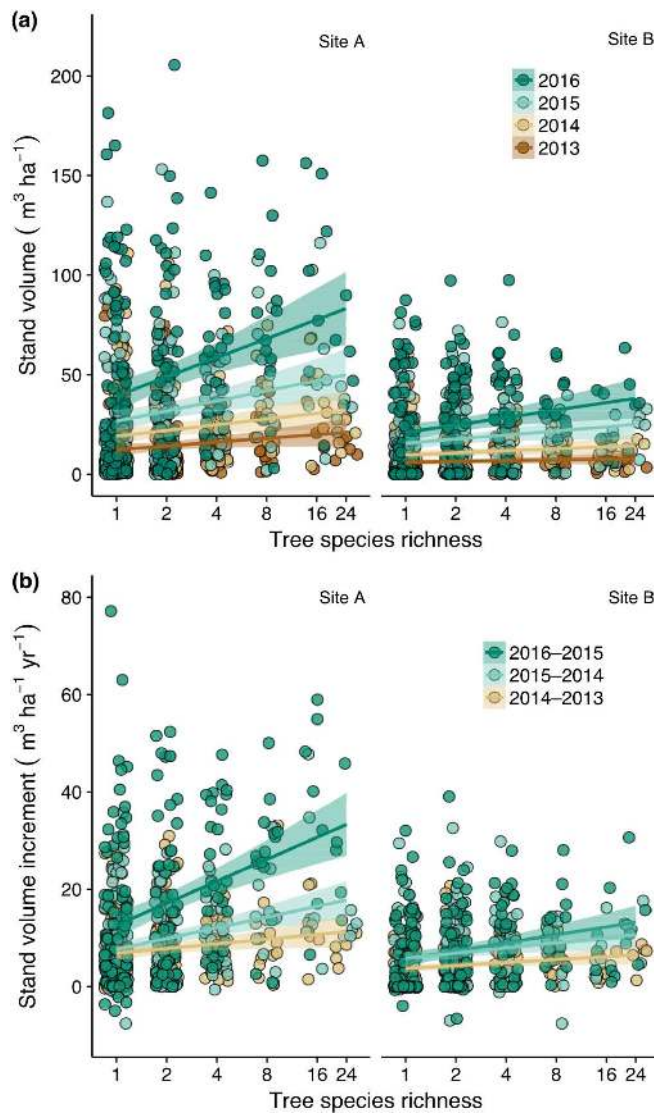
630 We assessed the effects of trait and phylogenetic distances on different components of
631 diversity effects of two-species mixtures with linear mixed-effects models, where we set site
632 and trait/phylogenetic distance as fixed effects, community composition and plot as random
633 effect (with a separate variance component for each site). Measures of diversity effects were
634 square-root transformed with sign reconstruction to improve normality of model residuals.
635



636

637 **Extended Data Figure 1 | Map of BEF-China position and experimental plots of random**
 638 **extinction scenarios and economic trees (a). Results from species pool A1 to illustrate**
 639 **the “broken stick” design (b).** Letters represent different species (A= *Cyclobalanopsis*
 640 *glauca*; B = *Quercus fabri*; C = *Rhus chinensis*; D = *Schima superba*; E = *Castanopsis eyrei*;
 641 F = *Cyclobalanopsis myrsinifolia*; G = *Koelreuteria bipinnata*; H = *Lithocarpus glaber*; I =
 642 *Castanea henryi*; J = *Nyssa sinensis*; K = *Liquidambar formosana*; L = *Sapindus saponaria*;
 643 M = *Castanopsis sclerophylla*; N = *Quercus serrata*; O = *Choerospondias axillaris*; P =
 644 *Triadica sebifera*). Solid lines represent overyielding, while dashed lines represent
 645 underyielding.

646



647

648 **Extended Data Figure 2 | Stand-level tree volume (a) and its increment (b) as a function**

649 **of tree species richness from 2013–2016.** Positive effects of tree species richness increase

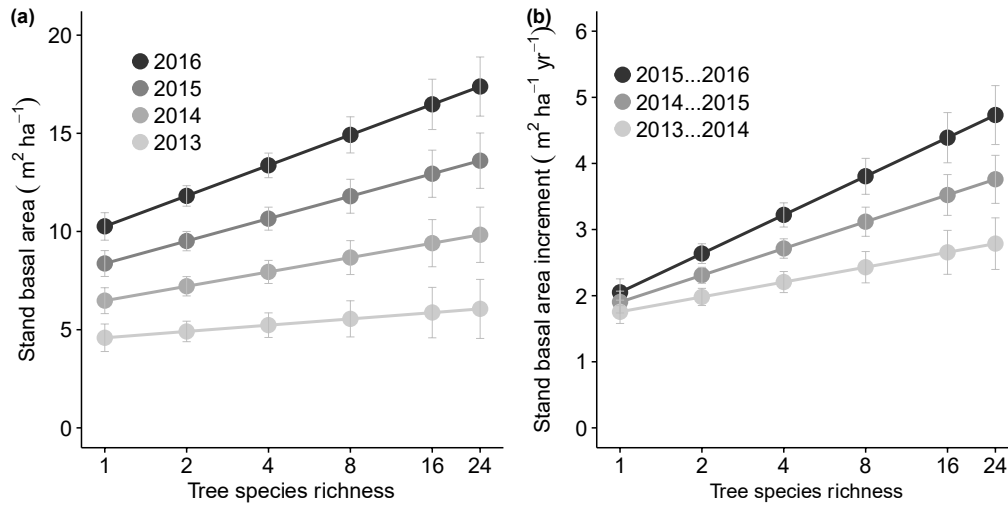
650 with time. Raw data points, regression lines and 95% confidence bands are shown for each

651 year. Note that the extremes of the point cloud necessarily taper off towards higher diversity

652 levels for statistical rather than biological reasons; this is due to the fact that for a given

653 diversity level extreme values are more extreme the larger the sample size is²⁶.

654



655

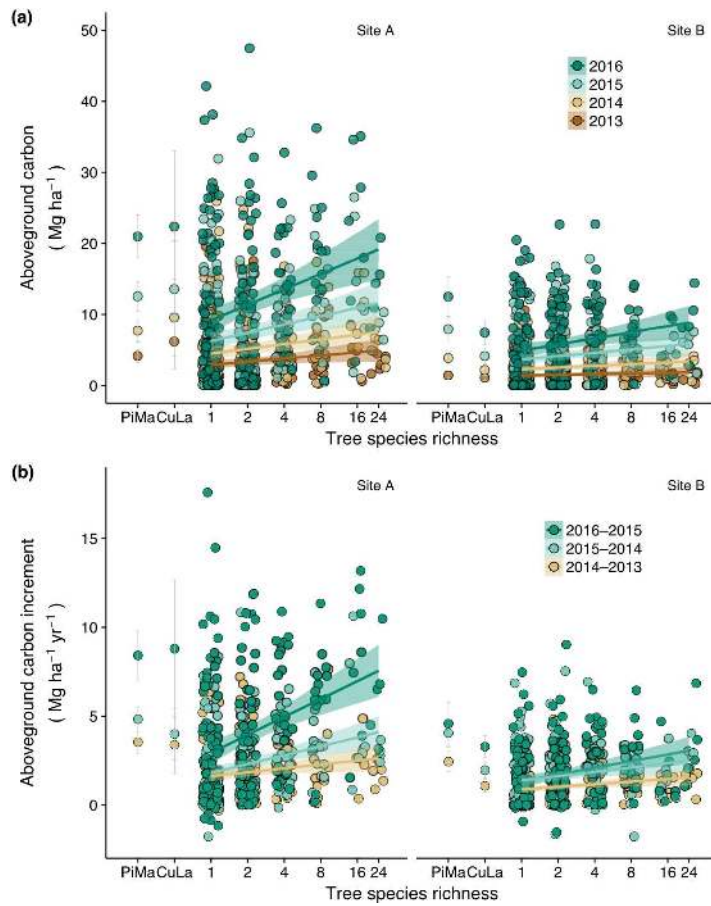
656 **Extended Data Figure 3 | Stand-level tree basal area (a) and its annual increment (b) as**

657 **a function of tree species richness from 2013–2016.** The figure shows predicted means and

658 standard errors based on fitted mixed models (Table 1). Effects of species richness were

659 significantly positive and increased throughout the observation period.

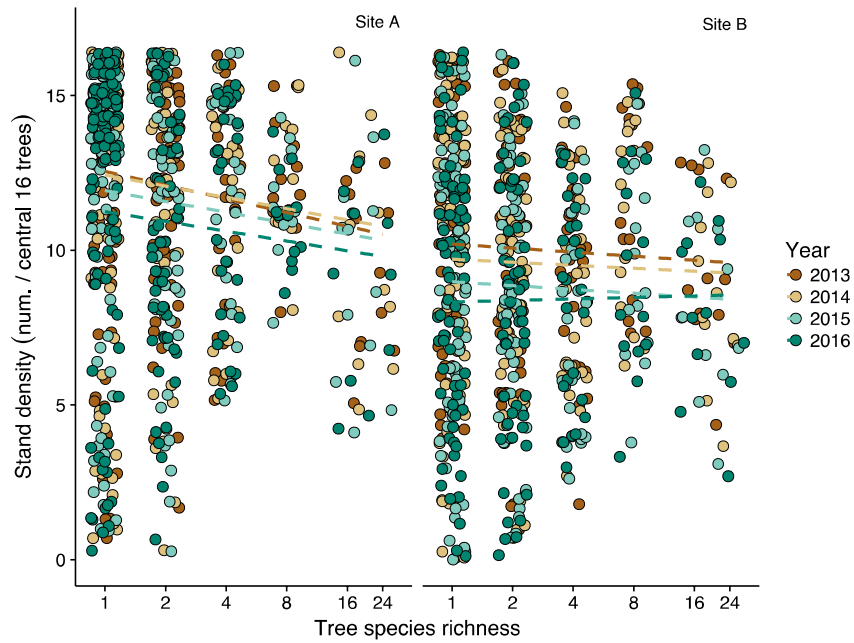
660



661

662 **Extended Data Figure 4 | Aboveground stand-level tree carbon (a) and its annual**
663 **increment (b) as a function of tree species richness from 2013–2016.** Raw data points,
664 regression lines and 95% confidence bands are shown. On the left of each panel means \pm
665 standard errors for the two economic tree species (PiMa = *Pinus massoniana*; CuLa =
666 *Cunninghamia lanceolata*) are inserted. Note that the extremes of the point cloud necessarily
667 taper off towards higher diversity levels for statistical reasons; this is due to the fact that for a
668 given diversity level extreme values are more extreme the larger the sample size is²⁶.

669



670

671

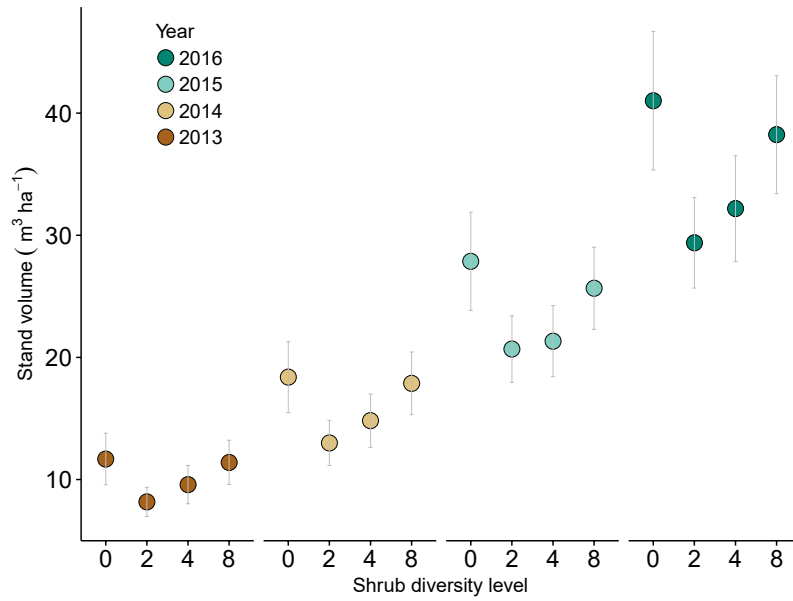
672 **Extended Data Figure 5 | Stand density as a function of tree species richness from 2013–**

673 **2016.** Raw data points together with non-significant regression lines (dashed) are shown.

674 Density indicates the number of surviving trees out of 16 planted in the central area of each

675 plot.

676



677

678 **Extended Data Figure 6 | Effects of shrub diversity on average stand-level tree volume**

679 **in species pools A1 and B1.** Data are from 4mu plots. The figure shows predicted means and

680 standard errors based on a fitted mixed model (Extended Data Table 8).

681

682 **Extended Data Table 1** | List of tree species used in the BEF-China experiment according to
 683 the Flora of China (<http://www.efloras.org> and <http://frps.eflora.cn>).

Species	Abbre-		
	viation	Site	Type
<i>Acer davidii</i> Franchet	AcDa	A	Deciduous
<i>Ailanthus altissima</i> (Miller) Swingle	AiAl	B	Deciduous
<i>Alniphyllum fortunei</i> (Hemsley) Makino	AlFo	B	Deciduous
<i>Betula luminifera</i> H. Winkler in Engler	BeLu	B	Deciduous
<i>Castanea henryi</i> (Skan) Rehd. et Wils.	CaHe	A	Deciduous
<i>Castanopsis carlesii</i> (Hemsley) Hayata	CaCa	A	Evergreen
<i>Castanopsis eyrei</i> (Champion ex Bentham) Tutcher	CaEy	AB	Evergreen
<i>Castanopsis fargesii</i> Franchet	CaFa	B	Evergreen
<i>Castanopsis sclerophylla</i> (Lindley & Paxton) Schottky	CaSc	AB	Evergreen
<i>Celtis biondii</i> Pampanini	CeBi	B	Deciduous
<i>Choerospondias axillaris</i> (Roxb.) Burt et Hill	ChAx	A	Deciduous
<i>Cinnamomum camphora</i> (Linnaeus) J. Presl in Berchtold & J. Presl	CiCa	AB	Evergreen
<i>Cunninghamia lanceolata</i> (Lamb.) Hook.	CuLa	AB	Evergreen
<i>Cyclobalanopsis glauca</i> (Thunberg) Oersted	CyGl	AB	Evergreen
<i>Cyclobalanopsis myrsinifolia</i> (Blume) Oersted	CyMy	A	Evergreen
<i>Daphniphyllum oldhamii</i> (Hemsley) K. Rosenthal in Engler	DaOl	AB	Evergreen
<i>Diospyros japonica</i> Siebold & Zuccarini	DiJa	AB	Deciduous
<i>Elaeocarpus chinensis</i> (Gardner & Champion) J. D. Hooker ex Bentham	EiCh	B	Evergreen
<i>Elaeocarpus glabripetalus</i> Merrill	EiGl	B	Evergreen
<i>Elaeocarpus japonicus</i> Siebold & Zuccarini	EiJa	B	Evergreen
<i>Idesia polycarpa</i> Maximowicz	IdPo	B	Deciduous
<i>Koelreuteria bipinnata</i> Franch.	KoBi	A	Deciduous
<i>Liquidambar formosana</i> Hance	LiFo	A	Deciduous
<i>Lithocarpus glaber</i> (Thunb.) Nakai	LiGl	AB	Evergreen
<i>Machilus grijsii</i> Hance	MaGr	B	Evergreen

<i>Machilus leptophylla</i> Handel-Mazzetti	MaLe	B	Evergreen
<i>Machilus thunbergii</i> Siebold & Zuccarini	MaTh	B	Evergreen
<i>Manglietia fordiana</i> Oliver	MaFo	B	Evergreen
<i>Melia azedarach</i> Linnaeus	MeAz	A	Deciduous
<i>Meliosma flexuosa</i> Pampanini	MeFl	B	Deciduous
<i>Nyssa sinensis</i> Oliver	NySi	A	Deciduous
<i>Phoebe bournei</i> (Hemsley) Yen C. Yang	PhBo	B	Evergreen
<i>Pinus massoniana</i> Lamb.	PiMa	AB	Deciduous
<i>Quercus acutissima</i> Carruthers	QuAc	A	Deciduous
<i>Quercus fabri</i> Hance	QuFa	A	Deciduous
<i>Quercus phillyreoides</i> A. Gray	QuPh	B	Evergreen
<i>Quercus serrata</i> Murray	QuSe	A	Deciduous
<i>Rhus chinensis</i> Mill.	RhCh	A	Deciduous
<i>Sapindus saponaria</i> Linnaeus	SaSa	A	Deciduous
<i>Schima superba</i> Gardn. et Champ.	ScSu	AB	Evergreen
<i>Triadica cochinchinensis</i> Loureiro	TrCo	A	Deciduous
<i>Triadica sebifera</i> (L.) Small	TrSe	A	Deciduous

684

685 Notes:

686 The site column shows the experimental site (A, B) where the species was planted. The type

687 column shows species life form (D = deciduous species; E = evergreen species).

688

689

690 **Extended Data Table 2 | Experimental design**

Site	Pool	Species richness	Plot size	Shrubs	Species composition
A	A1	16	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEy CyMy KoBi LiGl CaHe NySi LiFo SaSa CaSc QuSe ChAx TrSe
		8	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEy CyMy KoBi LiGl CaHe NySi LiFo SaSa CaSc QuSe ChAx TrSe
		4	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEy CyMy KoBi LiGl CaHe NySi LiFo SaSa CaSc QuSe ChAx TrSe
		2	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEy CyMy KoBi LiGl CaHe NySi LiFo SaSa CaSc QuSe ChAx TrSe
		1	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEy CyMy KoBi LiGl CaHe NySi LiFo SaSa CaSc QuSe ChAx TrSe
	A2	16	1mu	no	CaCa LiGl AcDa MeAz CaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
		8	1mu	no	CaCa LiGl AcDa MeAz CaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
		4	1mu	no	CaCa LiGl AcDa MeAz CaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
		2	1mu	no	CaCa LiGl AcDa MeAz CaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
		1	1mu	no	CaCa LiGl AcDa MeAz CaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
	A3	16	1mu	no	AcDa QuAc CaHe RhCh CaSc CiCa LiFo MeAz CaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
		8	1mu	no	AcDa QuAc CaHe RhCh CaSc CiCa LiFo MeAz CaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
		4	1mu	no	AcDa QuAc CaHe RhCh CaSc CiCa LiFo MeAz CaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
		2	1mu	no	AcDa QuAc CaHe RhCh CaSc CiCa LiFo MeAz CaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
		1	1mu	no	AcDa QuAc CaHe RhCh CaSc CiCa LiFo MeAz CaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
B	B1	16	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLu CaFa MaFo QuPh ElCh MaTh AlFo MaLe
		8	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLu CaFa MaFo QuPh ElCh MaTh AlFo MaLe
		4	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLu CaFa MaFo QuPh ElCh MaTh AlFo MaLe
		2	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLu CaFa MaFo QuPh ElCh MaTh AlFo MaLe
		1	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLu CaFa MaFo QuPh ElCh MaTh AlFo MaLe
	B2	16	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
		8	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
		4	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
		2	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
		1	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
	B3	16	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu
		8	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu
		4	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu
		2	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu
		1	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu

691

692 Note:

693 See Extended Data Table 1 for species abbreviations.

694

695 **Extended Data Table 3 | Mixed-effects model for the effects of cylindrical volume and**
 696 **life form on form and biomass factors.**

	Form factor				Biomass factor			
	Df	ddf	<i>F</i>	<i>P</i>	ddf	denDF	<i>F</i>	<i>P</i>
(Intercept)	1	4.4	2418	<0.001	1	4.8	828.9	<0.001
Cylindrical volume	1	105.7	8	0.007	1	114.7	11.2	0.001
Life form	2	4.7	20	0.005	2	4.9	22.1	0.004
Variance components	Component		s.e.	z-ratio	Component		s.e.	z-ratio
Species identity		0.00002	0.00058	0.043		257.90	356.87	0.723
Residual		0.01237	0.00169	7.321		4384.52	590.66	7.423

697

698 Notes:

699 Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table (the

700 random term was species identity). Abbreviations: df= nominator degree of freedom; ddf =

701 denominator degree of freedom; s.e. = standard error; *F* and *P* indicate F-ratios and P-values

702 of the significance tests.

703

704 **Extended Data Table 4 | Mixed-effects models for the effects of site, tree species richness**
 705 **(logSR), time (year) and interactions on aboveground stand-level tree carbon and its**
 706 **increment.**

Source of variation	Aboveground carbon				Aboveground carbon increment			
	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
Site	1	101.30	19.12	<0.001	1	104.70	14.42	<0.001
LogSR	1	89.20	5.16	0.026	1	94.60	9.11	0.003
Year	1	104.20	209.50	<0.001	1	106.20	70.30	<0.001
Site × year	1	104.80	18.47	<0.001	1	110.60	26.78	<0.001
LogSR × year	1	95.90	10.54	0.002	1	97.00	11.63	<0.001

707

708 Notes:

709 Fixed effects were fitted sequentially (type I sum of squares) as indicated in the table
 710 (random terms were community composition, plot, subplot and the interaction of these with
 711 year, with site-specific variance components for species composition and plot).

712 Abbreviations: df= nominator degree of freedom; ddf = denominator degree of freedom;

713 logSR = log₂(tree species richness). *F* and *P* indicate F-ratios and P-values of the significance

714 tests.

715

716 **Extended Data Table 5a | Average number of 1-mu (sub)plots with overyielding (Over)**
 717 **and underyielding (Under) for stand-level tree volume in 2016 across richness levels.**

718

Reference	Target ->	All plots			Transgressive plots		
		Over	Under	<i>P</i> (over>under)	Over	Under	<i>P</i> (over>under)
Component monocultures	2->1	65	47	0.088	43	21	0.005
	4->1	39	17	0.003	14	0	<0.001
	8->1	21	7	0.007	3	0	0.041
	16->1	9	5	0.280	1	0	0.239
	total	134	76	<0.001	62	21	<0.001
Component mixtures with half the number of species	2->1	65	47	0.088	43	22	0.009
	4->2	32	24	0.284	20	9	0.039
	8->4	17	11	0.250	10	6	0.315
	16->8	7	7	1.000	6	5	0.763
	total	121	89	0.027	79	42	<0.001

719

720 **Extended Data Table 5b | Average number of 1-mu (sub)plots with overyielding (Over)**
 721 **and underyielding (Under) for stand-level tree volume in different years.**

Reference	Year	All plots			Transgressive plots		
		Over	Under	<i>P</i> (over>under)	Over	Under	<i>P</i> (over>under)
	2013	126	84	0.004	50	20	<0.001
Component	2014	128	82	0.001	61	21	<0.001
monocultures	2015	133	77	<0.001	60	24	<0.001
	2016	134	76	<0.001	61	21	<0.001
Component	2013	112	98	0.33	69	37	0.002
mixtures with	2014	111	99	0.41	74	40	0.001
half the number	2015	115	95	0.17	73	43	0.005
of species	2016	121	89	0.027	79	42	<0.001

722

723 Notes:

724 *P*-values indicate significance of differences between the numbers of overyielding vs.

725 underyielding plots (χ^2 -test), or between transgressively overyielding vs. transgressively

726 underyielding plots.

727

728 **Extended Data Table 6 | Mixed-effects models for the effects of site, tree species richness**
 729 **(logSR), time (year) and the interaction of the latter two on the biodiversity effects NE,**
 730 **CE and SE.**

	NE				CE				SE			
	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
Intercept	1	60.7	20.43	<0.001	1	50.7	43.54	<0.001	1	52.7	9.29	0.004
Site	1	64.5	0.18	0.675	1	58.9	2.69	0.107	1	59.7	3.74	0.058
LogSR	1	60.5	4.58	0.036	1	50.6	9.79	0.003	1	52.6	5.89	0.019
Year	1	47.7	23.61	<0.001	1	31.3	9.61	0.004	1	37.3	4.61	0.038
LogSR × year	1	47.1	0.81	0.374	1	31.1	0.26	0.617	1	37.0	0.24	0.627

731

732 Notes:

733 Biodiversity effects were square-root transformed with sign reconstruction ($\text{sign}(y)\sqrt{|y|}$).

734 Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table

735 (random terms were community composition, plot, subplot and the interaction of these with
 736 year, with site-specific variance components for species composition and plot).

737 Abbreviations: df= nominator degree of freedom; ddf = denominator degree of freedom. *F*

738 and *P* indicate F-ratios and P-values of the significance tests. The first line “Intercept” shows

739 that the overall mean for all biodiversity effects differs significantly from zero (positively for

740 NE and CE, negatively for SE).

741

742 **Extended Data Table 7 | Mixed-effects models for the effects of functional distance (FD),**
743 **phylogenetic distance (PD) or vertical crown complementarity (PDS) on the biodiversity**
744 **effects NE, CE and SE in 2-species tree stands.**

	NE				CE				SE			
	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
FD	1	34.6	4.34	0.045	1	17.3	5.09	0.037	1	94	0.28	0.600
PD	1	58.4	0.92	0.342	1	76.3	0.07	0.787	1	39.4	0.67	0.420
PDS	1	22.5	3.43	0.077	1	56.5	0.20	0.659	1	8.2	26.43	< 0.001

745

746 Notes:

747 Biodiversity effects were square-root transformed with sign reconstruction ($\text{sign}(y)\sqrt{|y|}$). The
748 effects of FD, PD and PDS were fitted after site (random terms were species composition and
749 plot, considering a separate variance component for each site). Abbreviations: df= nominator
750 degree of freedom; ddf = denominator degree of freedom. *F* and *P* indicate F-ratios and P-
751 values of the significance tests.

752

753 **Extended Data Table 8 | Mixed-effects model for the effects of site, tree species richness**
 754 **(logSR), shrub presence, plot size, shrub species richness (logShrubSR), time (year) and**
 755 **interactions on stand-level tree volume. Data are from species pool A1 and B1, which**
 756 **include a shrub treatment in the planting design.**

Source of variation	df	ddf	<i>F</i>	<i>P</i>
Site	1	46.2	12.20	0.001
LogSR	1	45.0	3.70	0.059
Shrub presence	1	233.5	4.80	0.029
Plot size	1	116.2	0.90	0.353
LogShrubSR	1	198.8	5.40	0.022
Year	1	46.9	86.80	<0.001
LogSR × shrub presence	1	232.2	0.80	0.380
LogSR × plot size	1	114.2	0.20	0.694
LogSR × logShrubSR	1	198.8	0.30	0.606
LogSR × year	1	46.9	7.20	0.010
Shrub presence × year	1	235.1	9.50	0.002
Plot size × year	1	128.7	0.00	0.942
LogShrubSR × year	1	197.1	3.30	0.069

757

758 Notes:

759 Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table
 760 (random terms were community composition, plot, subplot and the interaction of these with
 761 year, with site-specific variance components for species composition and plot).
 762 Abbreviations: df= nominator degree of freedom; ddf = denominator degree of freedom;
 763 logSR = log₂(tree species richness); logShrubSR= log₂(shrub species richness—this term is

764 aliased with shrub presence and plot size and therefore fitted after these to only test for
765 effects of shrub species richness in sub-plots of large plots where shrubs were present). *F* and
766 *P* indicate F-ratios and P-values of the significance tests.

767

768 37 Brezzi, M. Influence of tree species richness on arthropod community patterns and
769 foliar herbivory plus allometric equations to predict tree biomass. *PhD thesis*,
770 *University of Zurich* (2015).

771 38 Kröber, W. *et al.* Early subtropical forest growth is driven by community mean trait
772 values and functional diversity rather than the abiotic environment. *Ecol Evol* **5**,
773 3541-3556 (2015).

774 39 Purschke, O., Michalski, S. G., Bruelheide, H. & Durka, W. Phylogenetic turnover
775 during subtropical forest succession across environmental and phylogenetic scales.
776 *Ecol Evol* (2017) (submitted 26.09.2017, accepted 08.10.2017, ECE-2017-09-01238).