

1 **Stabilizing effects of diversity on aboveground wood production in forest**
2 **ecosystems: linking patterns and processes**

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26 **Abstract**

27 Both theory and evidence suggest that diversity stabilizes productivity in herbaceous plant
28 communities through a combination ofoveryielding, species asynchrony and favourable
29 species interactions. However, whether these same processes also promote stability in forest
30 ecosystems has never been tested. Using tree ring data from permanent forest plots across
31 Europe, we show that aboveground wood production is inherently more stable through time
32 in mixed-species forests. Faster rates of wood production (i.e., overyielding), decreased year-
33 to-year variation in productivity through asynchronous responses of species to climate, and
34 greater temporal stability in the growth rates of individual tree species all contributed
35 strongly to stabilizing productivity in mixed stands. Together, these findings reveal the
36 central role of diversity in stabilizing productivity in forests, and bring us closer to
37 understanding the processes which enable diverse forests to remain productive under a wide
38 range of environmental conditions.

39 **Introduction**

40 There is growing concern that if biodiversity loss continues unabated, ecosystems will
41 inevitably lose much of their ability to function effectively (Cardinale *et al.* 2012). The
42 realization that species losses often lead to ecosystem declines is largely the result of two
43 decades' worth of research exploring the link between diversity and ecosystem functioning
44 (Hooper *et al.* 2012). A key finding that has emerged from this field is that diversity not only
45 promotes ecosystem processes, but also serves to stabilize them through time (Tilman 1999;
46 Isbell *et al.* 2009; Hautier *et al.* 2014). The best example of the stabilizing influence of
47 diversity on ecosystem-level processes comes from grasslands, where numerous studies have
48 shown that interannual fluctuations in primary productivity are consistently lower in diverse
49 herbaceous communities compared to species-poor ones (Hautier *et al.* 2014). Coupled with
50 theoretical work, these observations are often cited as evidence that diversity stabilizes
51 productivity across plant communities (Loreau & de Mazancourt 2013), including in forests
52 (Thompson *et al.* 2009). However, whether diversity actually contributes to stabilizing
53 productivity in forests has never been tested directly.

54 Forest aboveground wood production (AWP) is both an important indicator of ecosystem
55 functioning and a valuable ecosystem service (Gamfeldt *et al.* 2013). Recent work has shown
56 that diverse forests generally have higher rates of AWP than monocultures (Zhang *et al.*
57 2012). Determining whether diversity also contributes to stabilizing AWP through time could
58 help improve current forest management and conservation strategies (Nadrowski *et al.* 2010;
59 Nabuurs *et al.* 2013). In particular, identifying the possible mechanisms behind diversity-
60 stability relationships in forests is crucial, as underlying drivers may vary among ecosystems
61 (Jiang & Pu 2009; Loreau & de Mazancourt 2013; Gross *et al.* 2014). Although forests share

62 certain basic features with model systems such as grasslands, they also differ from them in a
63 number of key ways. One aspect in particular – the fact that species in herbaceous
64 communities change in relative abundance among years, while shifts in community
65 composition occur much more slowly in forests – is likely to be especially relevant in
66 determining which processes drive stability. In grasslands, the stabilizing effects of diversity
67 hinge on the assumption that composition is flexible among years (Gonzalez & Loreau 2009;
68 Allan *et al.* 2011; Mariotte *et al.* 2013). How does the slower dynamism of forests influence
69 the relationship between diversity and stability?

70 Temporal stability of community productivity (hereafter “stability”) is a measure of how
71 much productivity fluctuates around its long-term mean between years (Tilman 1999).
72 Because stability is expressed as the ratio between mean productivity (μ) and its variation in
73 time (σ , indicating the standard deviation of productivity), any process which affects either μ
74 or σ will alter stability (Lehman & Tilman 2000; Isbell *et al.* 2009). Of the mechanisms
75 which have been proposed to explain why diversity stabilizes productivity, three in particular
76 –overyielding, species asynchrony and species interactions – are regarded as general
77 stabilizing forces (Tilman 1999; Hector *et al.* 2010; Hautier *et al.* 2014). These processes
78 ultimately result from a more efficient partitioning of resources in mixed-species
79 communities, and act together to promote stability (Fig. S1 in Supporting Information).

80 *Overyielding*: greater-than-expected productivity of species mixtures, also known as
81overyielding (Tilman 1999), is thought to result primarily from niche partitioning and
82decreased competition among interspecific neighbours (Loreau & Hector 2001). In
83grasslands,overyielding has been shown to promote stability by increasing μ (Hector *et al.*
842010). Given thatoveryielding also seems to be widespread in forests (Paquette & Messier

85 2011; Zhang *et al.* 2012; Gamfeldt *et al.* 2013; Vilà *et al.* 2013), mixed-species stands may
86 well exhibit greater stability as a result of faster rates of AWP. Nonetheless, additional
87 drivers of overyielding, such as asynchrony itself (e.g., Allan *et al.* 2011), are unlikely to
88 operate in forests as they too require community composition to respond rapidly to
89 environmental conditions.

90 *Species asynchrony*: asynchronous responses of species to fluctuating environmental
91 conditions are a consequence of niche differences among species (Loreau & de Mazancourt
92 2008). The fact that species maximise fitness under different environmental conditions has
93 important implications for diversity–stability relationships, as it allows mixtures to remain
94 productive under a wider range of environmental conditions than any given monoculture
95 (e.g., Tilman 1999). Consequently, mixing species with contrasting climatic preferences will
96 tend to stabilize productivity by lowering σ (Loreau & de Mazancourt 2013). Species
97 asynchrony can be thought of as a form of temporal complementarity among species and has
98 been shown to be a key driver of stability in grasslands (Tilman 1999; Hector *et al.* 2010;
99 Hautier *et al.* 2014). However, the inability of forests to adjust their compositions to match
100 interannual variations in climate may partially limit the importance of asynchrony as a
101 promoter of stability in these systems (see “*Species interactions*” below).

102 *Species interactions*: competitive interactions among conspecific neighbours differ from
103 those between individuals belonging to different species (Chesson 2000). These shifts in
104 competitive intensity can strongly affect stability in mixed-species communities (Fig. S1).
105 For instance, greater intra than interspecific competition can enhance individual species
106 growth rates, thereby driving overyielding (Loreau & Hector 2001). In grasslands,
107 competition has also been shown to promote stability by enhancing negative co-variation in

108 productivity (i.e., asynchrony) among species in mixture, a process known as compensatory
109 dynamics (Tilman 1999; van Ruijven & Berendse 2007; Hector *et al.* 2010). However,
110 because competitive interactions among trees unfold over multiple growing seasons,
111 compensatory-type processes are unlikely to occur in forests (Nadrowski *et al.* 2010).
112 Instead, recent work suggests that by alleviating competition and/or promoting facilitation
113 among neighbouring trees, species mixing can reduce interannual variation in species growth
114 rates (Cavard *et al.* 2011; Del Río *et al.* 2013; Forrester 2014).

115 Here we use tree ring data from a network of permanent forest plots distributed across Europe
116 to provide the first comprehensive test of whether diversity stabilizes AWP in forests. We
117 expect stability to increase in diverse forests, but hypothesize that the mechanisms promoting
118 stability will differ, to some extent, from those traditionally associated with model grassland
119 systems. Specifically, we predict that (i) diversity contributes to stabilizing AWP by
120 promoting overyielding; (ii) species asynchrony stabilizes AWP, although this effect may be
121 weakened by the inability of forests to rapidly adjust their composition; (iii) decreased
122 competition and/or facilitative interactions stabilize individual species growth rates in mixed-
123 species plots.

124 **Materials and Methods**

125 STUDY DESIGN

126 The study was conducted across a network of permanent forest plots in Europe which was
127 recently established through FunDivEUROPE, a project aiming to assess the functional
128 significance of forest biodiversity in Europe (<http://www.fundiveurope.eu/>). The plot network
129 was designed specifically to test the effects of diversity on ecosystem functioning in mature
130 European forests, and encompasses six sites which span much of the continent's bioclimatic
131 gradient. Field sites were chosen to be representative of major European forest types, and
132 include boreal forests in Finland, hemiboreal forests in Poland, beech forests in Germany,
133 mountainous beech forests in Romania, thermophilous deciduous forests in Italy and
134 Mediterranean mixed forests in Spain. Here we outline the main features of project design
135 and explain the criteria used to select plots. Further details can be found in Baeten *et al.*
136 (2013) and in Appendix S1.

137 At each site, 30 x 30 m permanent plots with different combinations of locally dominant tree
138 species were established in 2011. Plots range in species richness from 1-3 in Finland, 1-4 in
139 Romania, Germany and Spain, and 1-5 in Italy and Poland. Each target species is represented
140 in all species richness levels, and whenever possible each species combination was replicated
141 at least twice (59 of 91 combinations; see Table S1). In total, the network comprises 209 plots
142 and 16 target species, several of which feature at more than one site (e.g., *Picea abies*, *Pinus*
143 *sylvestris* and *Fagus sylvatica*). The species pool includes conifers, deciduous broadleaves
144 and evergreen broadleaves (for a full species' list see Table S2). All plots were established in
145 mature forest stands (i.e., at least in the mid-to-late stages of stem exclusion) which have

146 received only minimal management interventions in recent years. Care was also taken to
147 select mixtures in which species share similar relative abundances (i.e., high evenness) and
148 the presence of non-target species is minimal (preferably <5% of the total basal area). Finally,
149 in order to allow meaningful comparisons among species richness levels, variation in
150 environmental conditions among plots within a site was kept as low as possible.
151 Consequently, while sites differ strongly from one another in terms of climate, plots within a
152 site share similar elevation, topography and soil quality.

153 ALLOMETRIC DATA

154 Across all 209 plots, stems ≥ 7.5 cm in diameter were identified to species and permanently
155 marked (12939 stems in total). For each stem we recorded diameter (to the nearest 0.1 cm,
156 using diameter tape) and tree height (to the nearest 0.1 m, using a vertex hypsometer, Haglöf
157 AB, Sweden). In addition, we used the crown illumination index (*CI*) to characterize the
158 crown dominance of each tree (Clark & Clark 1992), scoring stems from 1 (suppressed crown
159 receiving no direct light) to 5 (fully exposed dominant crown). *CI* scores effectively capture
160 the degree to which tree crowns are exposed to light (Jucker *et al.* 2014), and were used to
161 model the effects of competition for light on tree growth (see Box 1).

162 Diameter and height measurements were used to estimate the aboveground biomass (*AGB*, in
163 kg C) of each tree based on published biomass functions (Table S2). All selected equations
164 were species-specific, and whenever possible we chose functions developed for trees growing
165 in similar forest types to those found at our sites. *AGB* was expressed in units of carbon by
166 applying the standard conversion of 0.5 g C per gram of biomass. Stems <7.5 cm in diameter
167 were not included in these calculations as their contribution to AWP is negligible compared
168 to that of larger trees (Fig. S4; Stephenson *et al.* 2014).

169 WOOD CORES AND TREE GROWTH ESTIMATION

170 Tree ring data were used to reconstruct past trends in productivity for both species and plots.
171 Between March and October of 2012, we collected bark-to-pith increment cores (5.15 mm
172 diameter increment borer, Haglöf AB, Sweden) for a subset of trees in each plot following a
173 size-stratified random sampling approach (Jucker *et al.* 2014). We cored 12 trees per plot in
174 monocultures and 6 trees per species in mixtures (except in Poland, where only 5 cores per
175 species were taken in all plots due to restrictions imposed by park authorities; Table S3), for a
176 total of 3138 cored trees. Short of coring all trees within a plot, the size-stratified approach
177 has been shown to provide the most reliable estimates of plot-level productivity when using
178 tree ring data, as it ensured that the size distribution of each plot is adequately represented by
179 the subsample (Table S2; Nehrbass-Ahles *et al.* 2014). Wood cores were stored in
180 polycarbonate sheeting and allowed to air dry before being mounted on wooden boards and
181 sanded with progressively finer grit sizes. A high resolution flatbed scanner (2400 dpi optical
182 resolution) was then used to image the cores. From the scanned images we measured annual
183 growth increments for all cored trees, and used these to develop a time series of AWP for
184 each plot covering the 20 year period between 1992 and 2011. The analytical steps involved
185 in estimating AWP from tree ring data are outlined in Box 1.

186 STABILITY OF PLOT-LEVEL AWP

187 For each plot, temporal stability of AWP was calculated as AWP_{μ}/AWP_{σ} , where AWP_{μ} is a
188 plot's temporal mean AWP and AWP_{σ} is the standard deviation in AWP between 1992 and
189 2011 (Lehman & Tilman 2000; Hautier *et al.* 2014). Linear regression models were used to
190 test whether stability of AWP increases with species richness across the plot network. To
191 determine whether diversity-stability relationships vary among forest types, the model also

192 included a covariate for site (factor with six levels) as well as an interaction term between
193 species richness and site (equivalent to fitting separate slopes and intercepts for each study
194 site). Both stability of AWP and species richness were log-transformed to normalize
195 residuals. Support for the fitted model was assessed by comparing its AIC score with that of a
196 model which accounted exclusively for variation in the response among sites. This modelling
197 approach was chosen after careful comparison with alternative multivariate models
198 (Appendix S5), and was adopted in all subsequent analyses. In addition to this, we conducted
199 a sensitivity analysis to determine whether our choice to model stability of AWP over 20
200 years – as opposed to a shorter time period – impacted our results (e.g., as a result of the
201 effects of tree mortality on AWP). This revealed that diversity–stability effects have not
202 changed over time (Appendix S4).

203 OVERYIELDING

204 We tested for overyielding by regressing AWP_{μ} against species richness, again allowing the
205 modelled relationship to vary among sites. To complement this, we then used an approach
206 recently developed by Gross *et al.* (2014) to determine whether stabilizing effects are the
207 result of increased μ (i.e., overyielding), decreased σ , or both. This consists in first regressing
208 $\log(AWP_{\mu})$ and $\log(AWP_{\sigma})$ against $\log(\text{species richness})$ for each site separately, and then
209 plotting the slopes of the regressions (β_{μ} and β_{σ}) against each other to ascertain whether they
210 diverge from the expected 1:1 line. The method takes advantage of the fact that the slope of
211 the log-log regression between stability of AWP and species richness is equivalent to $\beta_{\mu} - \beta_{\sigma}$
212 (Appendix S6). Simply knowing where points fall within the β_{μ} vs β_{σ} plot can therefore be
213 used to infer whether stabilizing effects are the result of changes in the mean or variance of
214 AWP (Gross *et al.* 2014).

215 SPECIES ASYNCHRONY

216 Until recently, little consensus existed on how to quantify asynchrony in species responses to
217 fluctuating environmental conditions for communities with more than two species. Loreau &
218 de Mazancourt (2008) provided a solution by developing a community-level measure of
219 species synchrony (φ) which effectively captures how the growth of multiple species
220 differentially fluctuates in time. We define species asynchrony as $1 - \varphi$, and for each plot
221 calculated:

222
$$\text{Species asynchrony} = 1 - \frac{AWP_{\sigma}^2}{(\sum_{i=1}^S G_{\sigma i})^2}$$

223 where $G_{\sigma i}$ is the standard deviation in biomass growth of species i in a plot with S species
224 (Hautier *et al.* 2014). A ranges between 0 (complete synchrony) and 1 (perfect asynchrony),
225 and tends to increase as either S and/or $G_{\sigma i}$ become larger. An appealing feature of Loreau &
226 de Mazancourt's (2008) approach is that φ increases as the average pairwise temporal
227 correlation among species becomes stronger (Fig. S9). Species asynchrony was only
228 quantified for plots with two species or more, as monocultures are by definition synchronous
229 on account of the fact that community-level variance in AWP (AWP_{σ}^2) is determined entirely
230 by the variance in biomass growth (G_{σ}^2) of the single constituent species.

231 We used linear regression to determine whether species asynchrony stabilizes AWP, and
232 tested whether increased stability in more asynchronous communities is the result of
233 decreased AWP_{σ} . In addition, asynchrony was regressed against species richness to
234 understand how the two relate in forests. Prior to model fitting asynchrony was logit-
235 transformed to account for its values being bounded between 0 and 1.

237 Following the same approach used to quantify stability of AWP, we define temporal stability
238 of biomass growth as G_{μ}/G_{σ} , where G_{μ} is a species' temporal mean biomass growth (between
239 1992 and 2011) and G_{σ} is the standard deviation in biomass growth over the same time period
240 (Tilman 1999). To quantify stability of biomass growth, we first used the individual growth
241 models described in Box 1 to estimate the biomass growth of a tree of mean diameter
242 growing in both monoculture and mixture for each year between 1992 and 2011. From these
243 growth predictions we then quantified G_{μ} and G_{σ} of trees in both monoculture and mixture,
244 giving us a set of paired estimates of stability for each species (i.e., for each species, stability
245 of trees of the same size growing either in monoculture or mixture). To ensure unbiased
246 comparisons, species with insufficient data to robustly estimate growth in monoculture were
247 excluded from further analyses, giving us estimates of biomass growth stability for a total of
248 16 species. The approach described here for quantifying stability of biomass growth was
249 compared against a number of alternative methods, all of which yielded quantitatively similar
250 results (Appendix S6).

251 Assuming that trees are more likely to interact negatively with neighbours of their same
252 species (e.g., intraspecific > interspecific competition), we expect species mixing to stabilize
253 biomass growth rates through increased growth performance of species in mixture (i.e.,
254 higher μ and/or lower σ). To test whether stability of biomass growth increases with diversity
255 we used a paired *t*-test to compare each species' stability in monoculture against that in
256 mixture. Then, to determine whether stabilizing effects are the result of increased G_{μ} or
257 decreased G_{σ} , we again used Gross *et al.*'s (2014) approach to graphically partition stability
258 into μ and σ components.

259 **Results**

260 DIVERSITY – STABILITY RELATIONSHIPS IN EUROPEAN FORESTS

261 Diversity contributes strongly to stabilizing AWP over time across the plot network (Table 1;
262 Fig. 1a). The effect of species richness on stability was similar across sites, with the
263 exception of Spain where species mixing was found to destabilize AWP. The stabilizing
264 influence of diversity was the result of both increased AWP_{μ} and decreased AWP_{σ} (Fig. 1b).

265 OVERYIELDING

266 Across the plot network, diverse plots were significantly more productive than monocultures
267 (Table 1). Overyielding (i.e., greater AWP_{μ} in mixtures) occurred at all sites (Fig. 1b),
268 although the effect was noticeably stronger at the southern and northern end of the latitudinal
269 gradient (Spain, Italy and Finland; Fig. S8). In comparison, the relationship between diversity
270 and AWP_{σ} varied much more among sites. Species richness had a strong negative effect on
271 AWP_{σ} in central European countries (Romania, Germany and Poland), but not at higher and
272 lower latitudes (Fig. S8). Spain in particular showed a marked increase in AWP_{σ} in mixed-
273 species plots, to the extent that this effect countered the stabilizing influence of overyielding
274 and resulted in a negative relationship between stability of AWP and diversity at this site
275 (Fig. 1).

276 SPECIES ASYNCHRONY

277 Species asynchrony had a strong positive effect on stability of AWP (Table 1; Fig. 2a). The
278 effect was consistent across sites, albeit slightly weaker in the case of Spain. In general,
279 asynchrony stabilized AWP by causing AWP_{σ} to decrease strongly (Table1; Fig. 2b). As
280 expected, species asynchrony was positively correlated with species richness (Table1).

281 However, the relationship between asynchrony and diversity saturated quickly at all sites
282 (Fig. 3).

283 SPECIES INTERACTIONS AND INDIVIDUAL SPECIES GROWTH RATES OVER TIME

284 Across species, we found that the biomass growth of trees growing in mixture was
285 significantly more stable over time than that of individuals in monoculture (paired $t_{15} = 5.62$,
286 $P < 0.0001$; Fig. 4a). Of the two components of stability only G_{σ} showed evidence of being
287 consistently lower in diverse plots (paired $t_{15} = -2.83$, $P = 0.013$), with variance in biomass
288 growth decreasing for 14 out of 16 species (Fig. 4b). In contrast, although most species also
289 exhibited faster growth in mixture (10 out of 16; Fig. 4b), no systematic increase in G_{μ} was
290 found (paired $t_{15} = -0.25$, $P = 0.81$).

291 When species were grouped by site, stabilizing effects matched those found at the community
292 level. Species from central European sites were primarily stabilized through decreased G_{σ} ,
293 while those from Mediterranean and boreal sites tended to have greater G_{μ} in mixture (Fig.
294 4b). *Pinus sylvestris* and *P. nigra* from Spain typify this response, with faster growth rates in
295 mixture being counterbalanced by equally strong increases in G_{σ} with diversity.

296 **Discussion**

297 We found that diversity generally stabilizes AWP in forests across Europe, suggesting that
298 mixed-species forests are able to maintain consistent rates of productivity across a wider
299 range of environmental conditions compared to monocultures. The stabilizing effect of
300 diversity on forest AWP can be traced back to three key processes:overyielding, species
301 asynchrony and the effect of species interaction on individual species growth rates.

302 **OVERYIELDING**

303 Overyielding occurred across all six study sites, thus contributing to stabilizing AWP over
304 time (Fig. 1b). Our results are consistent with those of previous studies which have found
305 diversity to promote AWP in forests (Paquette & Messier 2011; Zhang *et al.* 2012), including
306 previous work focusing on forests in Europe (Vilà *et al.* 2013). In general, it appears that
307 increased productivity of mixed species plots occurred primarily through niche partitioning
308 processes (e.g., Morin *et al.* 2011; Brassard *et al.* 2013), rather than as a result of increased
309 growth of individual species (Fig. 4b). Recent work has shown that mixing tree species with
310 complementary crown architectures and abilities to tolerate shade can allow diverse forests to
311 exploit canopy space more efficiently (Morin *et al.* 2011; Pretzsch 2014), thereby maximising
312 light interception and growth (Hardiman *et al.* 2011; Jucker *et al.* 2014). An example of this
313 is the development of multi-layered canopies when shade-tolerant species establish below
314 taller, light-demanding trees (Morin *et al.* 2011; Hardiman *et al.* 2013). Similar
315 complementarity effects can also take place belowground (Brassard *et al.* 2013), enabling
316 mixed forests to access a greater portion of available soil nutrients.

317 While overyielding occurred at all sites, the strength of the effect varied considerably among
318 forest types. In particular, a weaker overyielding signal was found in forests at mid-latitudes
319 compared to Mediterranean and boreal sites (Fig. S8), supporting the hypothesis that diversity
320 effects on productivity become stronger in stressful environments (Paquette & Messier 2011).
321 In Germany, Poland and Romania stability was driven primarily by a strong decrease in year-
322 to-year variation of AWP in mixed-species plots, highlighting how diversity–stability
323 patterns are the result of multiple processes affecting both μ and σ . One aspect which could
324 contribute to stability, but which we do not account for in the present study, is the effect of
325 diversity on turnover rates in forests. For instance, if tree species’ mortality rates were to
326 covary with diversity, then determining the net effect of species mixing on stability would
327 require accounting for carbon losses as a result of trees dying. The few studies that have
328 tested diversity-mortality relationships in forests have not found evidence that mortality rates
329 change with diversity in mature forests (Liang *et al.* 2007; Lasky *et al.* 2014). This suggests
330 that the stabilizing effects of diversity on forest carbon dynamics depend primarily on the
331 influence of species mixing on tree growth. However, further work is needed to tease apart
332 the effects of species mixing on rates of forest turnover. Specifically, determining whether
333 stabilizing effects on species growth rates (Fig. 4) also translate into lower risk of mortality
334 for trees in mixture could prove critical.

335 SPECIES ASYNCHRONY

336 Consistent with theory (Loreau & de Mazancourt 2013), we found species asynchrony to be
337 the single best predictor of stability of AWP in European forests (Table 1). Asynchrony
338 stabilized productivity across forest types, and did so primarily by causing AWP_{σ} to decrease
339 strongly (Fig. 2). A clear link emerged between diversity and species asynchrony, with more

340 diverse plots generally exhibiting greater asynchrony (Fig. 3). Nonetheless, asynchrony
341 saturated quickly as species richness increased, indicating that a high degree of asynchrony
342 can be achieved in mixtures of relatively few tree species. This may be due, in part, to the
343 lack of short-term compensatory dynamics in forests, which have instead been shown to
344 enhance asynchrony in diverse herbaceous communities (Hector *et al.* 2010). In grasslands,
345 each year competition favours those species that are best suited to the climate during the
346 growing season, allowing them to increase in abundance and dominate the community (e.g.,
347 Mariotte *et al.* 2013). As environmental conditions change from one year to the next,
348 competition therefore enhances negative covariation in growth among species in mixture,
349 thereby increasing asynchrony within the community (Gonzalez & Loreau 2009). However,
350 because trees are long-lived and do not regenerate the bulk of their aboveground biomass
351 each year, changes in species composition occur more slowly in forests and are decoupled
352 from interannual variations in climate (Stephenson & Mantgem 2005). As a result,
353 compensatory dynamics are not expected to occur in forests, meaning that the extent to which
354 forests can express asynchrony may be limited compared to systems where species' relative
355 abundances are free to fluctuate between years (e.g., grasslands).

356 Generally, species asynchrony is expected to be less pronounced in communities composed
357 of functionally similar species, as these are expected to show a higher degree of covariation
358 in their response to climate fluctuations (Hector *et al.* 2010; Roscher *et al.* 2011). Similarly,
359 less room for asynchrony is expected in systems where climate exerts a strong control over
360 productivity, as this can also causes species growth rates to covary strongly with one another
361 (Hallett *et al.* 2014). We find evidence of this at either end of our bioclimatic gradient. In
362 both Spain and Finland – where interannual variations in tree growth are strongly determined

363 by rainfall and spring temperatures, respectively – we found that species' growth rates tended
364 to covary more strongly over time compared to other sites (Fig. S9). Strong covariation
365 occurred despite clear functional differences between species at both sites. As a result,
366 asynchrony in Spain and Finland was lower, on average, than at other sites, meaning it could
367 contribute less as a stabilizing driver (Fig. 3 and Fig. S9).

368 SPECIES INTERACTIONS AND INDIVIDUAL SPECIES GROWTH RATES OVER TIME

369 We found that diversity stabilizes species growth rates, thus contributing to the increased
370 stability of AWP in mixed-species plots (Fig. 4). Previous studies of diversity-stability
371 relationships in communities of primary producers have generally reported the opposite
372 pattern, with individual species tending to show greater variation in growth between years
373 when in mixture (van Ruijven & Berendse 2007; Hector *et al.* 2010). This pattern has
374 generally been attributed to the role of compensatory dynamics. However, as we discussed
375 previously, diversity is only likely to destabilize growth rates through compensatory
376 dynamics if species are able to capitalize on short-term competitive advantages by quickly
377 increasing in relative abundance within the community. Consequently, compensatory
378 dynamics are unlikely to be of real importance in communities dominated by species with
379 short life cycles. This may help explain the results of the few studies reporting positive or
380 neutral species-level responses in grasslands (Valone & Hoffman 2003; Houlahan *et al.*
381 2007), as these have tended to focus on natural communities which contain a higher
382 proportion of perennial *vs* annual species compared to experimental studies.

383 As was the case at the community level, increased species stability resulted from both faster
384 and less variable growth rates of trees in mixture (Fig. 4b). However, of the two components
385 of stability, σ was the most affected by species mixing. Although the majority of species

386 showed faster growth in mixture, several did not, indicating that the effects are likely context
387 dependent, varying according to species traits and environmental conditions (Forrester 2014;
388 Jucker *et al.* 2014). In contrast, all but two species exhibited dampened oscillations in growth
389 when in mixture. This suggests that favourable interactions among neighbouring trees in
390 mixture (e.g., reduced competition, facilitation) generally increase the resistance and/or
391 resilience of trees species to perturbations and environmental fluctuations (Pretzsch *et al.*
392 2013). Supporting this, recent work has shown that diversity effects increase in strength
393 under harsh conditions (Paquette & Messier 2011; Jucker & Coomes 2012; Del Río *et al.*
394 2013; Pretzsch *et al.* 2013; Forrester 2014), suggesting that trees in mixture may be able to
395 remain productive even when conditions for growth become suboptimal. There are of course
396 exceptions to this pattern. For instance, it has been suggested that drought can exacerbate
397 competition among neighbouring trees in mixed forests (Grossiord *et al.* 2014). A previous
398 study of the Spanish portion of the dataset analysed here revealed that drought had a greater
399 negative impact on productivity in mixtures compares to monocultures, and found that this
400 was the result of increased competition which negatively impacted the growth of drought-
401 intolerant species (Jucker *et al.* 2014). This explains why forests in Spain exhibited decreased
402 stability in response to diversity and highlights the fact that not all species combinations
403 promote stability. However, our results strongly suggest that Spanish forests represent the
404 exception rather than the rule, and that generally species interactions contribute to stabilizing
405 productivity in forests (Fig. 4).

406 IMPLICATIONS FOR FOREST MANAGEMENT AND CONSERVATION

407 During the second half of the twentieth century European forests have functioned as a strong
408 and persistent carbon sink in the northern hemisphere (Ciais *et al.* 2008). However, recent

409 work suggests that this carbon sink may have begun to saturate (Nabuurs *et al.* 2013), as
410 biomass accumulation rates have slowed and disturbance events (e.g., wind damage, forest
411 fires, pest and pathogen outbreaks) have increased in frequency (Seidl *et al.* 2014). More
412 effective management options are therefore needed if forests in Europe are to continue
413 delivering valuable ecosystem services associated with timber production and CO₂
414 sequestration. Traditionally, managing forests with the objective of promoting diversity has
415 been regarded as largely incompatible with the requirements of production forests (Seidl *et*
416 *al.* 2014). Yet growing evidence indicates that this may not be the case, and that maintaining
417 diverse forests has the potential to guarantee both high production yields and deliver a whole
418 range of added co-benefits (Nadrowski *et al.* 2010). This understanding has contributed to the
419 development of new forest management strategies which aim to maximise the resilience and
420 adaptability of forests (Thompson *et al.* 2009; Filotas *et al.* 2014). In this context, our results
421 suggest that maintaining diverse forest landscapes is critical in order to ensure that forests
422 continue to function efficiently in an increasingly uncertain future.

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607 **Supporting information**

608 Additional Supporting Information may be downloaded via the online version of this article
609 at Wiley Online Library (www.ecologyletters.com).

610 **Appendix S1:** FunDivEUROPE field sites and data collection.

611 **Appendix S2:** Estimating height growth from allometric data.

612 **Appendix S3:** Individual tree growth models.

613 **Appendix S4:** Temporal and spatial trends in stability of AWP.

614 **Appendix S5:** Multiple regression analysis of drivers shaping stability of AWP.

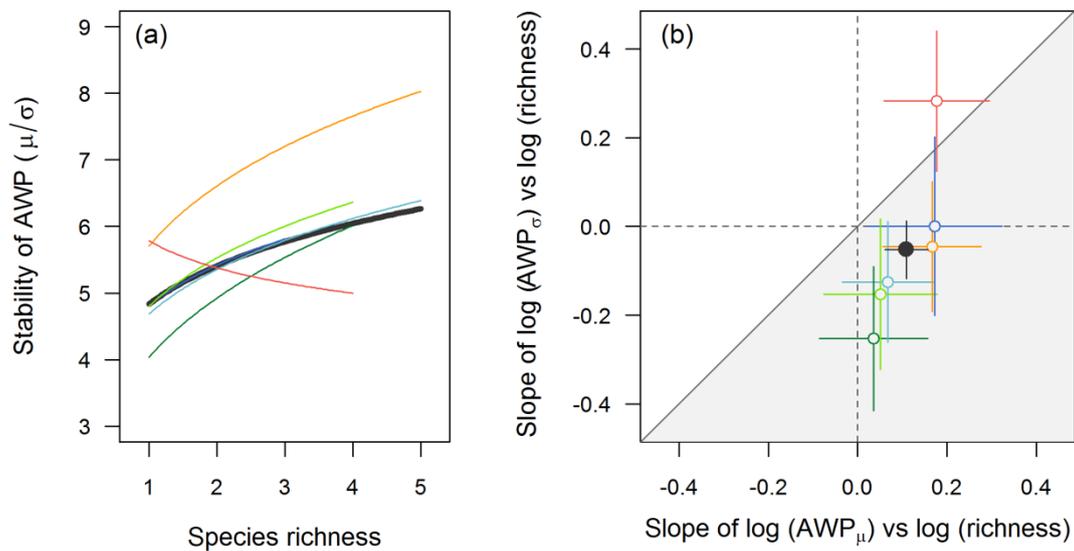
615 **Appendix S6:** Quantifying species-level stability of biomass growth.

616 **Tables**

617 **Table 1:** Model outputs of linear regressions testing hypothesized drivers of stability of
618 AWP. Slopes (\pm standard errors) refer to the effect of model predictors when data is pooled
619 across all sites. Δ AIC column reports the difference in AIC between the fitted model and a
620 model accounting exclusively for variation in the response among sites.

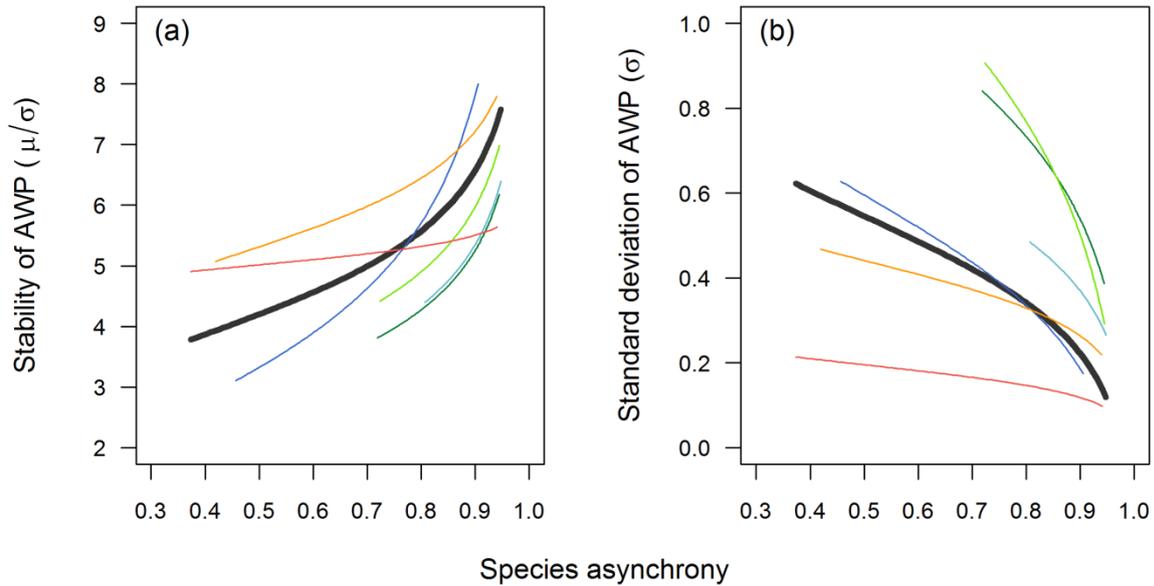
Response	Predictor	<i>P</i>-value	Slope (SE)	R^2	ΔAIC
Stability of AWP	Species richness	<0.0001	0.16 (0.04)	0.23	-15.5
	Asynchrony	<0.0001	0.20 (0.03)	0.41	-73.4
AWP temporal mean	Species richness	0.025	0.11 (0.05)	0.74	-3.2
AWP temporal SD	Species richness	<i>n.s.</i>	-0.05 (0.06)	0.61	1.3
	Asynchrony	<0.0001	-0.41 (0.05)	0.74	-136.9
Asynchrony	Species richness	<0.0001	1.11 (0.15)	0.47	-44.5

621



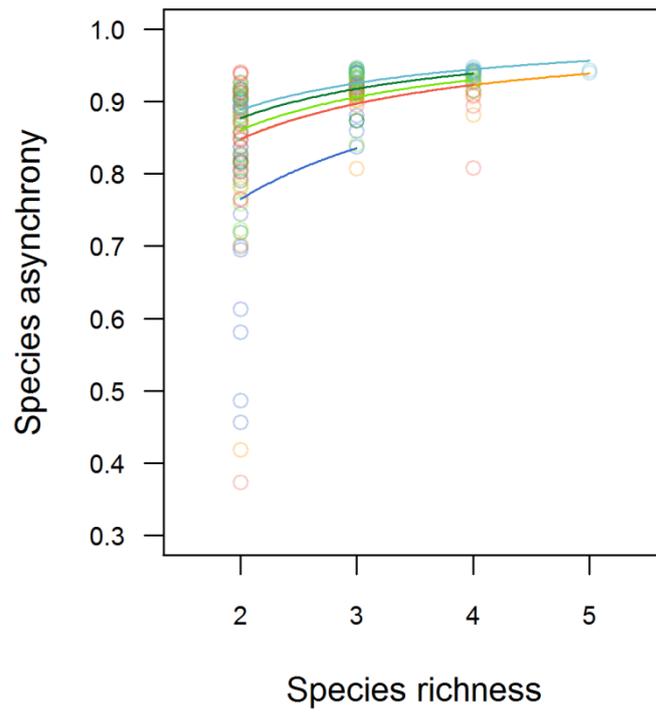
623

624 **Fig. 1:** Community stability as a function of diversity. Panel (a) shows the fitted relationship
 625 between stability of AWP and species richness across the entire plot network (black line) and
 626 for each site separately (coloured lines: Spain = red; Italy = orange; Germany = dark green;
 627 Romania = light green; Poland = light blue; Finland = dark blue). Fitted regression lines were
 628 back-transformed from log-log scale to match original axes. Panel (b) compares the slope of
 629 AWP_{μ} vs species richness (log-log scale) with that of AWP_{σ} vs species richness (log-log
 630 scale) across the entire dataset (filled circle) and for each site separately (open circles). Sites
 631 falling in the grey shaded section of the plot (below the 45° line) exhibit stabilizing effects of
 632 diversity on AWP. Points to the right of the vertical dashed line indicate overyielding, while
 633 points below the horizontal dashed line indicate decreased variation in AWP in mixture. Error
 634 bars denote the standard error of the slope parameters.



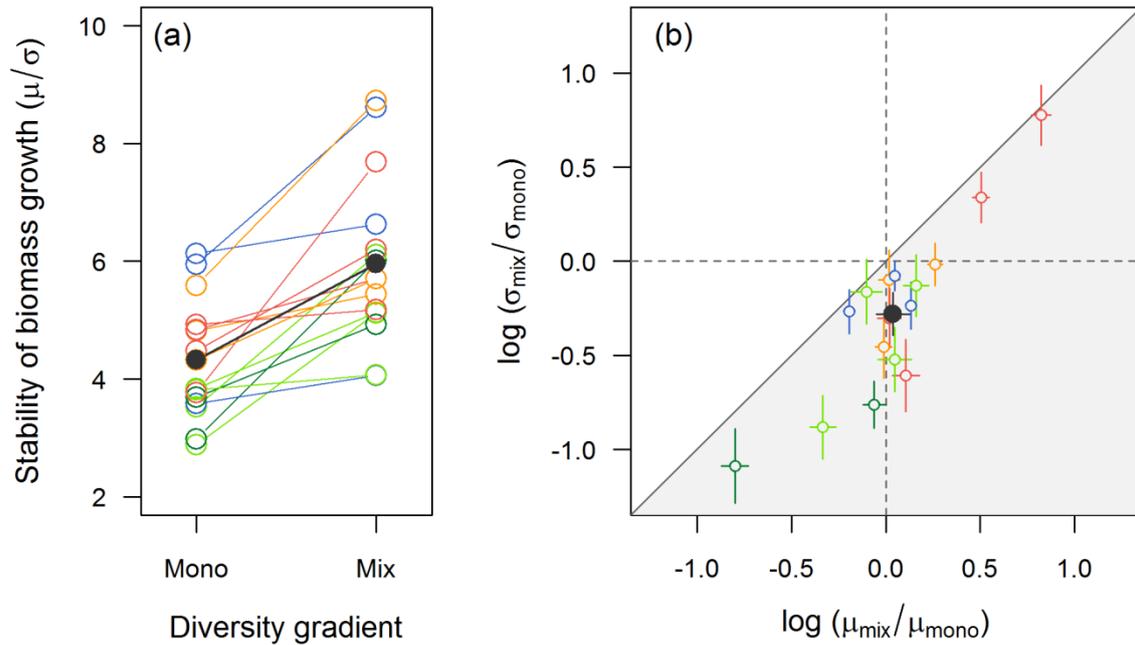
635

636 **Fig. 2:** Modelled relationship between (a) stability of AWP and (b) the standard deviation of
 637 AWP as a function of species asynchrony. Fitted lines show the effects across the entire plot
 638 network (black line) as well as for each site individually (coloured lines: Spain = red; Italy =
 639 orange; Germany = dark green; Romania = light green; Poland = light blue; Finland = dark
 640 blue). Fitted values were back-transformed to match original scales.



641

642 **Fig. 3:** Species asynchrony as a function of species richness for each individual site. Lines
 643 represent back-transformed fitted values from a linear model. Spain = red; Italy = orange;
 644 Germany = dark green; Romania = light green; Poland = light blue; Finland = dark blue.



645

646 **Fig. 4:** Stability of biomass growth as a function of diversity. Panel (a) compares the stability
 647 of biomass growth of individual species growing in monoculture vs mixture. Panel (b)
 648 compares the log of the difference of each species' temporal mean biomass growth in mixture
 649 vs monoculture ($\mu_{\text{mix}}/\mu_{\text{mono}}$), with the log of the difference of the standard deviation in
 650 biomass growth in mixture vs monoculture ($\sigma_{\text{mix}}/\sigma_{\text{mono}}$). The interpretation of the plot is
 651 analogous to that of Fig. 1b. Error bars denote standard errors. In both panels empty circles
 652 correspond to individual species, while average responses across species are represented by
 653 filled circles. Species are grouped by site according to colour: Spain = red; Italy = orange;
 654 Germany = dark green; Romania = light green; Poland = light blue; Finland = dark blue.

655

656 **Text boxes**

657 **Box 1:** Using tree ring data to reconstruct yearly trends in aboveground wood production

658 We followed a four step approach (i–iv) to estimating temporal trends in aboveground wood
659 production (AWP, in Mg C ha⁻¹ yr⁻¹) from tree ring data (Jucker *et al.* 2014). All analyses
660 were performed in R (3.0.1; R Development Core Team 2013).

661 i. **Measuring growth increments from wood cores:** We measured yearly radial
662 growth increments (mm yr⁻¹) for each cored tree from the scanned images. To
663 minimise measurement errors associated with incorrectly placed ring boundaries, we
664 crossdated each sample against a species-level reference curve obtained by averaging
665 all ring-width chronologies belonging to a given species from a given site. In this
666 process, 212 cores which showed poor agreement with reference curves were
667 excluded from further analysis, giving a final total of 2926 tree ring chronologies. At
668 this stage, two plots in Italy were excluded due to lack of data. Both radial growth
669 measurements and crossdating were performed using CDendro (Cybis Elektronik &
670 Data, Saltsjöbaden, Sweden). To capture the range of environmental conditions
671 experienced by trees at each site, our analysis focused on the 20 year period between
672 1992 and 2011. Subsequent testing revealed that the choice of time period did not
673 affect results (Appendix S4).

674 ii. **Converting diameter increments into biomass growth:** We combined radial
675 increments and allometric functions to express the growth rate of individual trees in
676 units of biomass. We focus on biomass growth – as opposed to other measures of tree
677 growth such as diameter or basal area growth – in order to provide a direct measure

678 of aboveground carbon sequestration and storage (Stephenson *et al.* 2014). For each
679 year between 1992 and 2011, we calculated biomass growth (G , kg C yr⁻¹) of cored
680 trees as $G = AGB_{t2} - AGB_{t1}$, where AGB_{t2} is the tree's biomass in the most recent
681 time period (e.g., end of 1992) and AGB_{t1} is its biomass at the previous time step
682 (e.g., end of 1991). For each year, AGB was estimated by replacing current diameter
683 and height measurements used to fit biomass equations with past values. Past
684 diameters were reconstructed directly from wood core samples by progressively
685 subtracting each year's diameter increment. Height growth was estimated by using
686 height-diameter functions to predict the past height of a tree based on its past
687 diameter and plot species composition (Jucker *et al.* 2014; see Appendix S2).

688 iii. **Modelling individual tree biomass growth:** For each year between 1992 and 2011,
689 we fitted separate biomass growth models for each species in which growth is
690 expressed as a function of tree size, competition for light, species richness and a
691 random plot effect:

$$692 \quad \log(G_i) = \alpha_{j[i]} + \beta_1 \times \log(D_i) + \beta_2 \times CI_i + \beta_3 \times SR_j + \varepsilon_i$$

693 where G_i , D_i and CI_i are, respectively, the biomass growth, stem diameter and crown
694 illumination index of tree i growing in plot j ; SR_j is the species richness of plot j ; α_j is
695 a species' intrinsic growth rate for a tree growing in plot j ; β_{1-3} are, respectively, a
696 species' growth response to size, light availability and species richness; and ε_i is the
697 residual error. The structure of the growth model is adapted from Jucker *et al.* (2014)
698 and models were fitted using the *lmer* function in R. Model robustness was assessed
699 both visually, by comparing plots of predicted vs observed growth (Fig. S5), and
700 through a combination of model selection and goodness-of-fit tests (see Appendix

701 S3). Across all species, individual growth models explained much of the variation in
702 growth among trees (Table S4).

703 iv. **Scaling up to plot-level AWP:** To quantify AWP at the plot level, we used the fitted
704 growth models to estimate the biomass growth of all trees that had not been cored.
705 For each plot, we then summed the biomass growth of all standing trees to obtain an
706 estimate of AWP. Growth estimates were generated using the *predict.lmer* function
707 in R. This process was repeated for each year between 1992 and 2011, allowing us to
708 produce a time series of AWP for each plot covering the last 20 years (Fig. S6).
709 Estimates of AWP are based exclusively on the growth of trees present in 2011 and
710 do not account for the growth of trees that died between 1992 and 2011. AWP rates
711 were only weakly correlated among consecutive years, ruling out potential biases
712 associated with temporal autocorrelation in the AWP time series (Appendix S4).