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No complementarity no gain – Net diversity effects on tree productivity occur once complementarity emerges during early stand development

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32 **Short running title:** Temporal dynamics of diversity-productivity relationships in trees

33
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35 (<https://doi.org/10.6084/m9.figshare.14885907.v1>)

36
37 **Author contributions:** A.P., P.R., and C.M. designed the IDENT-MTL tree diversity
38 experiment; A.P., and C.M. were in charge of the experiment, W.S.K. contributed to
39 conceptualization, J.U. collected the data during the last 3 years of the experiment. Many grad
40 students, postdocs and interns who worked on the IDENT-MTL experiment collected the data.
41 J.U. performed the analyses, and wrote the first draft of the manuscript. All authors contributed
42 substantially to revisions.

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49
50 **ABSTRACT**

51
52 Although there is compelling evidence that tree diversity has an overall positive effect on forest
53 productivity, there are important divergences among studies on the nature and strength of these
54 diversity effects and their timing during forest stand development. To clarify conflicting results
55 related to stand developmental stage, we explored how diversity effects on productivity change
56 through time in a diversity experiment spanning 11 years. We show that the strength of diversity
57 effects on productivity progressively increases through time, becoming significantly positive
58 after 9 years. Moreover, we demonstrate that the strengthening of diversity effects is driven

59 primarily by gradual increases in complementarity. We also show that mixing species with
60 contrasting resource-acquisition strategies, and the dominance of deciduous, fast-developing
61 species, promote positive diversity effects on productivity. Our results suggest that the canopy
62 closure and the subsequent stem exclusion phase are key for promoting niche complementarity in
63 diverse tree communities.

64

65 **Key words:** IDENT; biodiversity-ecosystem functioning; tree diversity experiment;
66 productivity; long-term diversity effects; functional traits, resource partitioning; life-history
67 strategy; functional diversity; functional identity

68 INTRODUCTION

69

70 Recent decades have seen a large number of studies, both observational and experimental,
71 investigating the diversity-productivity relationship (hereafter DPR) in forest ecosystems. As a
72 result, there is now a general consensus that diverse tree communities, on average, promote
73 higher biomass production than their species-poor counterparts (Liang et al. 2016; Zhang et al.
74 2012; Paquette & Messier 2011). However, within this body of research there are important
75 divergences in the magnitude of diversity effects, with some studies reporting negligible or only
76 marginal effects (e.g. Tobner et al. 2016; Li et al. 2014). While recent studies have demonstrated
77 how complex interactions between abiotic factors and stand structure explain some of these
78 divergences across different forest types (Jucker et al. 2016; Forrester 2014; Hulvey et al. 2013),
79 much less is known about the mechanisms driving the temporal dynamics of the strength of DPR
80 over time during forest development (Jucker et al. 2020; Taylor et al. 2020; Grossman et al.
81 2018; Huang et al. 2018). In particular, diversity effects are thought to be especially important
82 during the early phases of forest development (i.e. stand establishment, canopy closure, and stem
83 exclusion), when competition for limited resources is the major driver determining the future
84 forest structure and functioning (Fichtner et al. 2018).

85

86 Two main mechanisms have been proposed to explain positive diversity effects on productivity.
87 The first is complementarity effects, which include niche partitioning and interspecific
88 facilitation; and the second is selection effects, which are caused by the dominance of one or few
89 species driving community's productivity (Roscher et al. 2012; Loreau & Hector 2001). These

90 depend, in turn, on species-specific functional traits. Functional traits define species' life-history
91 strategies, thus determining their capacity to grow, survive, and use resources in competitive
92 environments (Violle et al. 2007). Two different approaches to measuring functional aspects of
93 the community can provide mechanistic insights into DPRs as well as the underlying
94 mechanisms at play. The first is functional identity (FI; selection effects) which allows the
95 evaluation of the effect of dominant traits on productivity, whereas the second is functional
96 diversity (FD; complementarity effects) which quantifies the effect of the variability in
97 functional trait values on productivity (Roscher et al. 2012; Morin et al. 2011; Shipley et al.
98 2006; Grime 1998). Long-term studies in grassland biodiversity experiments have already shown
99 that the strength of diversity effects and the relative importance of complementarity over
100 selection tend to increase over time (Reich et al. 2012). This observation explains the ability of
101 functionally diverse communities to progressively optimize the use of limiting resources over
102 time and to enhance soil fertility and nutrient availability (Reich et al. 2012).

103
104 A similar observation of the increasing importance of complementarity effects over time is
105 expected in forest ecosystems (Huang et al., 2018). However, as community dynamics in forests
106 are relatively slow compared to those in grassland ecosystems, complementarity effects driving
107 mixtures' overyielding (i.e. when mixtures' productivity is higher than their components'
108 respective monocultures) might take many years (e.g. a decade or more) to manifest following
109 tree establishment (Jucker et al. 2020; Huang et al., 2018). This is because essential resources
110 such as light and nutrients are normally abundant (relative to demand) in the early years
111 following stand establishment, fulfilling trees' requirements to grow and survive. Consequently,
112 competition among trees for resources are minimal during these early years. This reduces the
113 likelihood of complementarity effects and increases the probability of sampling a dominant, high
114 productive species with a specific set of functional traits driving community productivity (i.e.
115 selection effects) as found by Tobner et al. (2016). However, as stands develop, trees
116 progressively expand their crowns (i.e. canopy closure), gradually intensifying competition for
117 light and growing space. This, in turn, might increase the importance of complementarity effects
118 driving DPR, as is expected under harsher conditions (Searle & Chen 2020; Paquette & Messier
119 2011; Callaway et al. 2002; but see Belluau et al. 2021). For example, mixing species with
120 contrasting life strategies promotes a better use of canopy space (Jucker et al. 2015). This, in

121 turn, reduces competition for light and allows diverse communities to intercept a greater
122 proportion of incoming light and grow faster compared to their respective monocultures (Kunz et
123 al. 2019; Jucker et al. 2015; Pretzsch 2014; Sapijanskas et al. 2014). This helps explain why, in
124 contrast to studies carried out in the early years of tree diversity experiments where negligible or
125 only marginal positive DPRs were found (Tobner et al. 2016; Verheyen et al. 2015; Li et al.
126 2014; Healy et al. 2008), recent studies conducted many years after stand establishment
127 highlighted strong positive diversity effects on productivity (Schnabel et al. 2019; Huang et al.
128 2018; Van de Peer et al. 2017).

129
130 Few studies have analyzed the temporal dynamics of diversity effects on productivity during
131 stand development (e.g. Jucker et al. 2020; Taylor et al. 2020; Huang et al., 2018). Furthermore,
132 much less is known about how underlying mechanisms (Complementarity and Selection) drive
133 this relationship through succession (Huang et al. 2018). Testing these relationships is
134 challenging, as it requires long-term, repeated growth data from a tree diversity experiment that
135 allows separating net diversity effects into complementarity and selection. Only few experiments
136 to date allow conducting such a study as most of them are still in the stand establishment phase
137 where competition for resources is minimal. One of these experiments is IDENT-MTL in
138 Montreal, Canada, which was planted in spring 2009 (Tobner et al. 2014). This experiment is
139 ideally suited to test the temporal dynamics of diversity effects because its high-density design
140 favors development of competition and therefore expression of complementarity.

141
142 In this study, we analyze how diversity at initial stage affects stand-level development of
143 productivity. Our analysis focuses on basal area because it cumulates annual increments and
144 subsequent mortality, and therefore best indicates the trajectory of stand development. We focus
145 on the early stages of stand development covering the stand establishment, canopy closure and
146 the beginning of the self-thinning stages. We hypothesize that the strength of the DPR increases
147 with stand development, driven primarily by co-varying complementarity effects as competition
148 for resources increases. To complement this analysis, we further explored how the functional
149 composition of tree communities (i.e. functional diversity and identity) contributed to DPR over
150 time. We expect that functional diversity and identity both explain net diversity effects on
151 productivity, with the former being a stronger relative predictor.

152

153

154 MATERIAL AND METHODS

155

156 *Site description*

157

158 The study was conducted in IDENT-MTL tree diversity experiment that was established in Ste-
159 Anne-de-Bellevue (near Montreal, Quebec, Canada, 45°25'30.1"N, Long 73°56'19.9"W, 39
160 m.a.s.l.) in the spring of 2009. Mean annual temperature is 6.2°C and mean annual precipitation
161 totals 963 mm (climate.weatheroffice.gc.ca). The experiment was planted on a former
162 agricultural field that was intensively managed for decades. The soil consists of a 20-70 cm deep
163 sandy layer overtopping clay (Tobner et al. 2016).

164

165 In the spring of 2009, an area of 0.6 ha was planted with 1- or 2-years old tree seedlings (Tobner
166 et al. 2014). The experiment includes 12 North American temperate forest species - five broad-
167 leaf species and seven conifers (Table 1). This experiment is part of the 'International Diversity
168 Experiment Network with Trees' (IDENT) that includes several sites in North America, Europe
169 and Africa (Verheyen et al. 2015).

170

171

172 *Experimental Design*

173

174 Two orthogonal gradients were established: 1) a species richness gradient, and 2) a functional
175 diversity gradient (Table S3). This design allows separating the two different diversity effects.
176 The functional diversity gradient consists of plots with species combinations of equal species
177 richness but increasing functional diversity. The functional diversity levels are repeated using
178 different species combinations and are pooled in groups of similar FD value (Table S3).

179

180 Trees were planted in square plots of 8 x 8 individuals (i.e. 64 trees), with 50 cm spacing among
181 trees and 1.25 m between plots to allow movement and minimise inter plot interactions (Tobner
182 al. 2014). The experiment includes monocultures of all 12 species, 14 combinations of two-

183 species mixtures, 10 combinations of four-species mixtures and one mixture including all 12
184 species (Tobner et al. 2014) for a total of 37 different tree communities (i.e. unique species
185 composition). Each community was replicated four times in a randomised block design for a
186 total of 148 plots and 9,472 trees (note that the site includes more plots addressing other
187 questions that were not used in this experiment) (Tobner et al. 2014). The proportion of species
188 within plots was equal and their distribution randomised with restrictions to prevent
189 monospecific patches (see Tobner et al. 2014 for details). The distribution of trees within the
190 plots remained constant in all the blocks; however, the distribution of plots within blocks was
191 randomised.

192

193 Around the outermost rows of the experiment, three rows of trees at 50 cm distance were planted
194 to minimise edge effects. A fence to protect against herbivory by large vertebrates was
195 constructed around the experiment and all plots were regularly weeded manually during the first
196 years to eliminate herbaceous competition.

197

198

199 *Cumulative productivity as measured by tree basal area*

200

201 We used basal area (G ; m^2/ha) as a proxy for cumulative aboveground productivity at the plot
202 level from 2009 to 2019. Only the inner 6 x 6 trees of each plot were used to minimize edge
203 effects from neighbouring plots. The basal diameter (at 15 cm aboveground) of every live tree
204 was measured at the end of each growing season from 2009 to 2019, hereafter years 1 to 11,
205 from which species G were computed for each year and plot. Note that mortality was, therefore,
206 taken into account when computing species G . We attributed tree mortality solely to competition
207 for resources as any visible damage by biotic (pathogens or insect herbivores) or abiotic factors
208 were negligible over the first 11 years. Total G of a plot was simply the sum of species G . Net
209 diversity effects (NE), complementarity effects (CE) and selection effects (SE) were calculated
210 according to Loreau and Hector (2001, details below) using the estimated G values for each year
211 and plot.

212

213

214 **DATA ANALYSIS**

215

216 *Quantification of the diversity effects and its underlying mechanisms*

217

218 We followed Loreau and Hector's (2001) approach to calculate the net diversity effects (NE) as
219 well as complementarity (CE) and selection (SE). This approach is based on the calculation of a
220 general deviation of yield in mixture (observed yield, Y_O) from that in monoculture (expected
221 yield, Y_E , eqn 1). A $NE = 0$ indicates that the performance of the mixture is equal to the weighted
222 average of respective component monocultures (i.e. no diversity effect; the mixture performs as
223 expected from monocultures). A $NE > 0$ indicates a positive diversity effect and when $NE < 0$, a
224 negative diversity effect. This approach also allows for partitioning the net diversity effects (NE)
225 into complementarity (CE) and selection effects (SE) (Loreau & Hector 2001).

226

$$\begin{aligned} NE &= Y_O - Y_E = CE + SE \\ &= N\overline{\Delta RY}\overline{M} + N\text{cov}(\Delta RY, M) \end{aligned} \quad (1)$$

229

230 Both mechanisms of diversity effects (CE and SE) hinge on the calculation of the relative yield
231 of each species (RY, De Wit 1960), expressed in this equation as ΔRY (eqn 2).

232

$$\Delta RY = \frac{\text{yield}_A(\text{Mixture})}{\text{yield}_A(\text{Monoculture})} - P_A \quad (2)$$

234

235 Where P is the proportion of the species at the initial stage in mixture.

236

237 CE is the mean of the deviation from the expected relative yield of each species in the mixture (
238 $\overline{\Delta RY}$) multiplied by the mean of each species' yields in monoculture (\overline{M}) and by the number of
239 species (N). Therefore, CE averages positive and negative diversity effects of all species in the
240 mixture. On the other hand, SE is the covariance between species' relative (ΔRY) and
241 monoculture yields (M) multiplied by the number of species in the mixture (N). SE is positive
242 when the most productive species in monoculture performs better in the mixture. Alternatively,
243 SE is negative when the less productive species in monoculture overyield in the mixture. In case

244 of both high and low productive species in monocultures overyielding in the mixture, SE can be
245 positive or negative depending on the stronger effect.

246

247

248 *Trait data collection and calculation of functional composition*

249

250 We computed functional diversity and identity at the initial stage of the experiment. We
251 considered seven above- and belowground traits that are linked to plant resource-use strategies
252 and competition capacities. They include specific leaf area (SLA), leaf nitrogen content by mass
253 (LNmass), leaf nitrogen content by area (LNarea), net maximum photosynthesis by unit leaf
254 mass (A_{mass}), wood density (WD), specific root length (SRL) and seed mass (seedmass). All
255 trait data were collected from the literature (Belluau 2020; Table S1). We included seed mass
256 because it is a trait associated with differing functional strategies that might influence
257 productivity, rather than due to any direct link between seed size and production. Then, we
258 performed a Principal Component Analysis (PCA) of the trait values at the species level in order
259 to avoid collinearity among traits and identify species main axes of life-history strategies (Fig.
260 1). Seed mass values were log-transformed prior to analysis.

261

262 The first two principal components explained 80% of the variance in traits. The first principal
263 component (PC1) was correlated to wood density (WD), leaf nitrogen content by unit mass
264 (LNmass), specific leaf area (SLA) and specific root length (SRL), clearly separating
265 gymnosperms from angiosperms (Table S2). These functional traits are involved in the
266 acquisition, processing and conservation of resources and, hence, define species' life history
267 strategy largely by influencing growth vs survival trade-offs (Reich 2014). It is worth noting that
268 WD is a highly phylogenetically conserved trait (i.e. less variable within phylogenetic groups
269 than expected by chance) with angiosperms typically having significantly denser wood than
270 gymnosperms (Zhang et al. 2021), as evidenced in our PCA, with that factor overwhelming the
271 typical within-group association of high WD with slow growth (Swenson & Enquist 2007). As a
272 result of this strong phylogenetic conservatism, high WD -a 'slow' trait - is positively correlated
273 with high values of 'fast' leaf traits among the studied species, which is different than the general
274 pattern observed in nature (Reich 2014). The second principal component (PC2) was related only

275 to seed mass (Table S2). Seed mass is considered as an indicator of the trade-off between
276 colonization (early vs late successional species) and competitive capacity (Turnbull et al. 2004).
277 For example, small-seeded species are typically better colonizers but less shade tolerant and thus,
278 lesser competitors. Using the species scores over these two life-history axes (i.e. principal
279 components), we calculated the communities' FD and FI using functional dispersion (Fdis,
280 Laliberté & Legendre 2010) and community weighted means (CWMs, Lavorel et al. 2008)
281 respectively (i.e. $Fdis_{PC1}$, $Fdis_{PC2}$, CWM_{PC1} and CWM_{PC2}). Functional dispersion is the mean
282 distance in a multidimensional trait space of each species to the center of mass of all species,
283 weighted by their relative abundances (Laliberté & Legendre 2010). We calculated the Fdis for
284 all possible species combinations of two, four and twelve species. CWM values were computed
285 for the two principal components collecting the variance of functional traits following Lavorel et
286 al. (2008). CWMs are, thus, the mean value of each principal component of all species present in
287 a community weighted by their relative abundance. We used the R package FD to calculate
288 CWM and Fdis (Laliberté & Legendre 2010).

289
290

291 *Statistical Analysis*

292

293 We performed a Generalized Additive Model (GAM) with REML estimation to test the effects
294 of time (Year), functional diversity (Fdis) and functional identity (CWM) on net diversity effects
295 (NE). Block and plot (i.e. the different tree communities) were set as random factors (noted R),
296 yielding the following model:

297

$$298 \quad NE = Year + Fdis_{PC1} + Fdis_{PC2} + CWM_{PC1} + CWM_{PC2} + \quad (3)$$

299

$$Year \times Fdis_{PC1} + Year \times Fdis_{PC2} +$$

300

$$Year \times CWM_{PC1} + Year \times CWM_{PC2} +$$

301

$$Plot (R) + Block (R) + \varepsilon$$

302

303 where 'Fdis' is functional dispersion, and 'CWM' community weighed means. The subscripts
304 'PC1' and 'PC2' refer to the principal components obtained from the PCA previously done on
305 the functional trait values that represent two axes of life-history strategies. The best model was

306 selected based on AIC. We ran a variance-based sensitivity analysis from the best model to
307 estimate the deviance explained by each predictor of the model.

308

309 We subsequently explored the effects of FD and FI on NE over time. We performed
310 independent cluster analyses for each of the diversity parameters of the best model (i.e. F_{disPC1} ,
311 CWM_{PC1} and CWM_{PC2}). The cluster analysis classifies the different mixtures of the experiment
312 into similarity groups (i.e. clusters) according to a defined distance measure based on their F_{dis}
313 and CWM values. The cluster analyses performed on the diversity components grouped the
314 different mixtures of the experiment into 1) plots with high (no. of plots 16) and low (9)
315 functional diversity on the resource-use strategy axis (i.e. F_{disPC1}); 2) plots with high (5),
316 medium (16) and low (4) mean values on the resource-use strategy axis (i.e. CWM_{PC1}); and 3)
317 plots with high (9), medium (12) and low (4) mean values on the colonization strategy axis (i.e.
318 CWM_{PC2}). We then extracted the fitted NE values from the model (eqn 3) and plotted them 1)
319 against the measured CE and SE over time to observe the temporal dynamics of the forces
320 driving the NE, and 2) against the different F_{dis} and CWM groups generated by the cluster
321 analyses.

322

323 Finally, we tested whether mixtures performed better than expected compared to their respective
324 monocultures over the duration of the experiment (after 11 years). We applied two-tailed t-tests
325 ($n = 4$ blocks) to determine when net diversity effects were significantly different from zero. We
326 then applied one-tailed t-tests to determine whether some mixtures performed significantly better
327 than even the best monoculture (i.e. transgressive overyielding).

328

329

330 RESULTS

331

332 Our results show a non-linear increase in net diversity effects (NE) over time (Fig. 2). Net
333 diversity effects were negative from year 3 to 6 after the establishment of the experiment,
334 became positive after year 8, and then significantly so from year 9 onward (Fig. 2). This
335 strengthening of the net diversity effect was primarily driven by gradual increases in
336 complementarity effects as stands developed (notably > year 5), while during the first years,

337 negative selection effects (which peaked in year 6) were more common in driving the net
338 diversity effects (Fig. 2). In the last year of the experiment (year 11), net diversity effects had
339 accumulated enough through time to be easily detected looking at plot total G, with six mixtures
340 overyielding their component monocultures, and four even showing transgressive overyielding
341 (Fig. S5).

342

343 Further analysis of the effect of tree communities' functional trait-based composition on
344 productivity shows that net diversity effects vary substantially among mixtures during the early
345 stages of stand development. We observed that mixtures characterized by species with
346 contrasting resource-use strategies (i.e. high F_{dis_PC1}) performed similarly to their constituent
347 monocultures during the first years of the experiment. However, starting in year 6, these tree
348 communities progressively increased their productivity compared to their respective
349 monocultures, increasingly overyielding from year 9 onwards (Fig. 3). Mixtures characterized by
350 species with similar resource-use strategies (i.e. low F_{dis_PC1}) showed similar productivity to
351 their monoculture counterparts during the whole experiment except for the last year when, in
352 general, they slightly overyielded (Fig. 3).

353

354 In addition, we also observed that the functional identity of tree communities (i.e. CWM_PC1
355 and CWM_PC2) had a substantial effect on mixtures' productivity over time. For instance,
356 mixtures with highly acquisitive resource economic traits (other than WD) (i.e. medium and high
357 CWM_PC1) showed, in general, an increasing trend of diversity effects since year 6 that started
358 to overyield from year 9 onwards (Fig. 4). Conversely, mixtures in the "slow" end (again, other
359 than WD) of the resource economic spectrum (i.e. low CWM_PC1) showed, in general, negative
360 diversity effects from year 8 onwards (i.e. negative NE; Fig. 4). Seed mass CWM had a negative
361 relationship with overyielding. In mixtures with low and medium values of seed mass, diversity
362 effects tended to increase progressively over time, overyielding their constituent monocultures in
363 the last three years (Fig. 5). In contrast, mixtures dominated by late-successional species (i.e.
364 high CWM values of seed mass) showed negligible or even negative diversity effects during the
365 early stages of stand development except for the last year, where, in general, they slightly
366 overyielded (Fig. 5).

367

368

369 DISCUSSION

370

371 Here we present the results of what is, to the best of our knowledge, the first study with trees to
372 test the temporal dynamics of both net diversity effects and its component mechanisms,
373 complementarity and selection, on cumulative productivity during the first decade of stand
374 development. Our results support the widespread evidence from prior studies that mixtures are,
375 on average, more productive than monocultures of their constituent species. Our study brings
376 new insight into the temporal changes of such effects; showing that the strength of net diversity
377 effects on cumulative productivity is non-linear during the first phases of stand development,
378 taking many years to manifest itself (Fig. 2). While an earlier study of the same experiment
379 found, on average, a negligible net diversity effect on cumulative productivity by year 4 (i.e.
380 Tobner et al., 2016), these updated results over a longer temporal scale show i) that the strength
381 of the net diversity effects on cumulative productivity increases throughout stand development
382 (Jucker et al. 2020; Taylor et al. 2020), and that ii) this is driven by gradual increases of
383 complementarity (Huang et al. 2018; Sapijanskas et al. 2014). Previous studies have shown how
384 complex interactions between resource availability, climatic conditions and stand structures can
385 explain some of the variation in the strength of net diversity effects on productivity across
386 different forest ecosystems (Mori 2017; Jucker et al. 2016; Jucker et al. 2014; Forrester 2014).
387 Our results mirror the long-term studies in grasslands (Guerrero-Ramírez et al. 2017; Reich et al.
388 2012) and forest ecosystems (Huang et al. 2018). They show that changes in the relative
389 importance of complementarity and selection effects during the first stages of stand development
390 strongly influence net diversity effects on productivity over time.

391

392 *The emergence of complementarity's larger role under increased competition is the key driver of*
393 *the positive diversity-productivity relationships during stand development*

394

395 During the first years following stand establishment we found that, on average, net diversity
396 effects were driven by opposing forces of complementarity and selection (i.e. negligible net
397 diversity effects; Fig. 2). This is consistent with our expectations that in years immediately
398 following stand establishment, high resource availability eliminates or reduces the opportunity

399 for complementarity to have much of an impact on productivity (Taylor et al. 2020; Forrester
400 2014; Zhang et al. 2012; Paquette & Messier 2011). Instead during this phase, selection effects
401 have more impact on productivity (Tobner et al. 2016).

402
403 Net diversity effects were negligible at first due to negative selection effects being larger than
404 initially weak (but positive) complementarity effects. This means that, overall, the species with
405 relatively high monoculture productivity had lower performances in mixtures. The opposite was
406 true for species with relatively low monoculture productivity. Selection effects have been
407 hypothesized to be more important in more stable and productive environments, whereas in more
408 stressful environments complementarity effects are expected to be more important (the stress
409 gradient hypothesis, Bertness & Callaway 1994; but see Belluau et al. 2021). In this study, the
410 intense agricultural activity at the study site prior to the experiment establishment, and the
411 complete removal of herbaceous competition during the first years, resulted in resource-abundant
412 conditions for trees, possibly favoring selection effects initially (Tobner et al. 2016). However,
413 as stands underwent canopy closure and entered the stem exclusion phase, resource competition
414 among trees intensified (c. year 5 or 6; Fig. S4). In diverse stands, the impact of competition may
415 have been reduced since the likelihood of two individuals competing for the same niche
416 decreases; this then allows for the emergence of complementarity, and consequently, positive net
417 diversity effects. These strong positive effects must have been driven by the faster growth of
418 surviving trees within mixtures because tree survival rates remained similar between
419 monocultures and mixtures (Fig. S6). Numerous studies have shown that different mechanisms
420 can explain positive diversity effects on productivity, including reduced pest and pathogen loads,
421 or improved resource uptake belowground (Ammer 2019). However, arguably the most
422 important one is the ability of diverse communities to fill canopy space more efficiently than
423 their species-poor counterparts (Jucker et al. 2015; Pretzsch 2014). This reduces competition for
424 light and allows these communities to grow faster overall, compared to their respective
425 monocultures (Jucker et al. 2015; Sapijanskas et al. 2014). Therefore, the increase of competition
426 associated with the canopy closure and stem exclusion phases seems to be a key factor in
427 allowing conditions for mixtures to overyield through niche partitioning or facilitation (Jucker et
428 al. 2020).

429

430 Although our results show a clear strengthening of complementarity through time that
431 determines the positive net diversity effects on productivity, this experiment covered only the
432 early stages of stand establishment, canopy closure and stem exclusion. How long will positive
433 net diversity effects due to complementarity last is unknown, but we suspect they might continue
434 until a later stage of stand development when some tree species will come to dominate again. For
435 example, late-successional species could progressively increase in relative dominance, allowing
436 selection effects to take over again in determining the net diversity effects on productivity.
437 Future research should focus, therefore, on understanding how DPR and its underlying
438 mechanisms are likely to change in the more advanced stages of stand development.

439

440 *Functional significance of the Net Diversity effects on productivity throughout stand*
441 *development*

442

443 Our analysis of the effects of tree communities' functional composition on productivity shows
444 that mixing fast-growing deciduous species with slow-growing evergreen species (i.e. high
445 Fdis_PC1) progressively increased productivity as competition intensified during stand
446 development (Fig. 3). This seemed to be related to the canopy closure where trees begin to
447 compete for light and where contrasting architectural and physiological traits allow mixtures to
448 benefit from light partitioning (Jucker et al. 2020; Taylor et al. 2020; Williams et al. 2017).
449 Indeed, in a previous study conducted in the same experiment, Williams et al. (2017) observed
450 that in year 4 (coinciding with the emergence of competition; Fig. S4), there was a substantial
451 neighbourhood-driven variation in crown size and shape, indicating that stands had reached the
452 canopy closure and started to compete for light and space, and optimize resource-use to avoid or
453 reduce competition. Increasing diversity effects by mixing species with contrasting life strategies
454 has been related to the vertical canopy stratification and intraspecific crown plasticity throughout
455 stand development (Williams et al. 2020; Jucker et al. 2015; Morin et al. 2011). Through
456 differences in their crown architectures, contrasting species can use different canopy positions
457 (i.e. crown complementarity), reducing competition and allowing for the capture of more light at
458 the community level. Moreover, as competition for light lessens, trees also might invest a greater
459 proportion of fixed carbon towards the development of lateral branches increasing their crown
460 size (i.e. crown plasticity; Williams et al. 2017; Jucker et al. 2015; Forrester 2014). In this

461 regard, vertical stratification and crown plasticity might be the mechanisms driving the net
462 diversity effects observed in this study.

463
464 In addition, we show that, functional identity also plays an important role in driving diversity
465 effects over time. We found that the dominance by slow-developing conifers reduced mixture
466 productivity, compared to more mixed stands and stands dominated by fast-developing
467 deciduous species. Therefore, our study suggests that complementarity effects are also driven by
468 functional identity of specific species (i.e. life-history strategies) that are able to take advantage
469 of diverse conditions, thus leading to overyielding at the community level (Zheng et al. 2021;
470 Grossman et al. 2018). Specifically, our results suggest that effective light acquisition of tree
471 communities dominated by deciduous “fast” developing early-successional species allow these
472 communities to grow faster (Zheng et al. 2021; Hisano & Chen 2020). Fast growth (and
473 consequently better access to light) has been linked to a reduced ability to tolerate competitive
474 pressures such as shading from others (Kunstler et al. 2016). Indeed, all the mixtures that
475 overyielded were mixtures of deciduous and evergreen species (except for one) and all but one
476 contained *B.papyrifera* (Fig. S5). In other words, this light-demanding pioneer species (the most
477 productive monoculture) probably benefited from reduced competition when growing in
478 mixtures, ultimately dominating them and overyielding at the community level. This could
479 promote niche partitioning through the development of multilayered canopies over time, where
480 shade-tolerant species grow under taller, light-demanding pioneers (Jucker et al. 2015; Niinemets
481 2010). Therefore, these results show that both functional diversity and identity of tree
482 communities play important roles in driving positive complementarity effects, thus promoting
483 net diversity effects on productivity in the mid-term (Zheng et al. 2021; Grossman et al. 2018;
484 Van de Peer et al. 2017) – whether complementarity among initially slower growing species
485 would catch up over time is unknown.

486

487

488 CONCLUSION

489

490 Analyzing 11 years of growth records from a tree diversity experiment, we show that diversity
491 effects on productivity strengthen progressively during the early stages of stand development

492 driven by gradual increases of complementarity. While previous studies have shown how abiotic
493 factors and forest structure can explain a considerable amount of variation in the strength of DPR
494 across space, this study highlights that changes in the relative importance of complementarity
495 and selection effects during stand development also play an important role in determining the
496 strength of these relationships over time. This pattern seems to be related to the progression into
497 the canopy closure and stem exclusion phase of stand development, where increasing
498 competition for resources allows positive complementarity effects to develop, and ultimately
499 determines more diverse communities' success in the long-term. Moreover, our study highlights
500 that diversity effects on productivity are affected by both functional diversity and identity. We
501 show that mixing species with contrasting resource-acquisition strategies, and the dominance of
502 deciduous, fast-developing species promote positive diversity effects on productivity during the
503 initial phases of stand development.

504 Our results are important from a management and conservation perspective, as this study shows
505 when and how positive diversity effects should manifest along stand development. Tree diversity
506 experiments are essential to further research on biodiversity and ecosystem functioning in
507 forests. However, existing experiments should be allowed to mature to track the many
508 trajectories that diversity effects could take through more advanced stages of forest succession.

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518 **TABLES**

519 Table 1. Summary of the generalized additive model (REML estimation) of significant diversity
520 indices on net diversity effects (NE; $N = 1100$) over time (fixed effects). Summary includes
521 estimated degrees of freedom (edf), deviance explained (DevExp), and p-values. When edf is
522 close to 1, the effect on NE is linear. And when edf is 2 or greater it is considered non-linear.

523 The model includes Block and Plot as random effects. The "s" and "ti" are GAM-specific terms
 524 that mean smooth term (main effects) and tensor product (interactions) respectively. The
 525 coefficient of determination (R^2) for the whole model was 0.506.

526

527 **FIGURES**

528

529 **Figure 1.** Principal Component Analysis of the functional trait values used to characterize the
 530 species of the experiment. The first Principal Component (i.e. PC1) is explained mostly by Wood
 531 Density (i.e. WD), Specific Leaf Area (i.e., SLA), Specific Root Length (i.e. SRL), and Leaf
 532 Nitrogen Mass (i.e. LNmass). And the second Principal Component (i.e. PC2) is explained

Effect	edf	DevExp	p-value
s(Year)	4.112	0.080	<.001
s(Fdis_PC1)	2.698	0.012	<.001
s(CWM_PC1)	1.111	0.016	<.001
s(CWM_PC2)	1.102	0.019	<.001
ti(Year, Fdis_PC1)	5.461	0.066	<.001
ti(Year, CWM_PC1)	8.510	0.064	<.001
ti(Year, CWM_PC2)	5.291	0.067	<.001

533 primarily by Seed Mass (i.e. Seedmass). Leaf Nitrogen Area (i.e. LNarea) and net maximum
 534 photosynthesis by unit leaf mass (i.e. Amass) were not correlated with any of the two principal
 535 components. Species codes are: Ab, *Abies balsamea*; Ar, *Acer rubrum*; As, *Acer saccharum*; Ba,
 536 *Betula alleghaniensis*; Bp, *Betula papyrifera*; Ll, *Larix laricina*; Pg, *Picea glauca*; Pru, *Picea*
 537 *rubens*; Pre, *Pinus resinosa*; Ps, *Pinus strobus*; Qr, *Quercus rubra*; To, *Thuja occidentalis*.

538 **Figure 2.** Fitted (eqn 3) Net Diversity Effects (NE; Black line \pm confidence interval 95% across
 539 mixtures and blocks; $N = 1100$) on G (m^2/ha) over time driven by complementarity and selection
 540 effects (red and blue bars respectively \pm standard error).

541 **Figure 3.** Fitted (eqn 3) Net Diversity Effects (NE) on G (m^2/ha) over time for high and low
 542 diversity mixtures grouped by the first principal component (i.e. resource-use strategy, PC1). The
 543 graph shows that plots with high diversity in resource-use strategy (blue line \pm confident interval

544 95%, $N = 704$) overyielded as stands developed. In contrast, plots with low diversity in resource-
545 use strategy (red line \pm confident interval 95%, $N = 396$) showed negligible diversity effects over
546 time, except the last year, where they slightly overyielded.

547 **Figure 4.** Fitted Net Diversity Effects (NE) on G (m^2/ha) over time for mixtures with high,
548 medium, and low CWM values group by the first principal component (i.e. resource-use strategy,
549 PC1). The graph shows that mixtures with high and medium values in the resource-use strategy
550 (blue and green line respectively \pm confidence interval 95%, $N = 220$ and 704 respectively)
551 overyielded over time. Conversely, mixtures with low values (red line \pm confidence interval
552 95%, $N = 176$) showed negative diversity effects over time.

553 **Figure 5.** Fitted Net Diversity Effects (NE) on G (m^2/ha) over time for plots with high, medium,
554 and low CWM values of the second principal component (i.e. colonization strategy, PC2). The
555 graph shows that mixtures with low and medium values in the colonization strategy (red and
556 green lines \pm confidence interval 95%, $N = 176$ and 528 respectively) progressively overyielded
557 as stands developed. However, mixtures with high values (blue line \pm confidence interval 95%,
558 $N = 396$) showed negative diversity effects, except the last year where they also overyielded.

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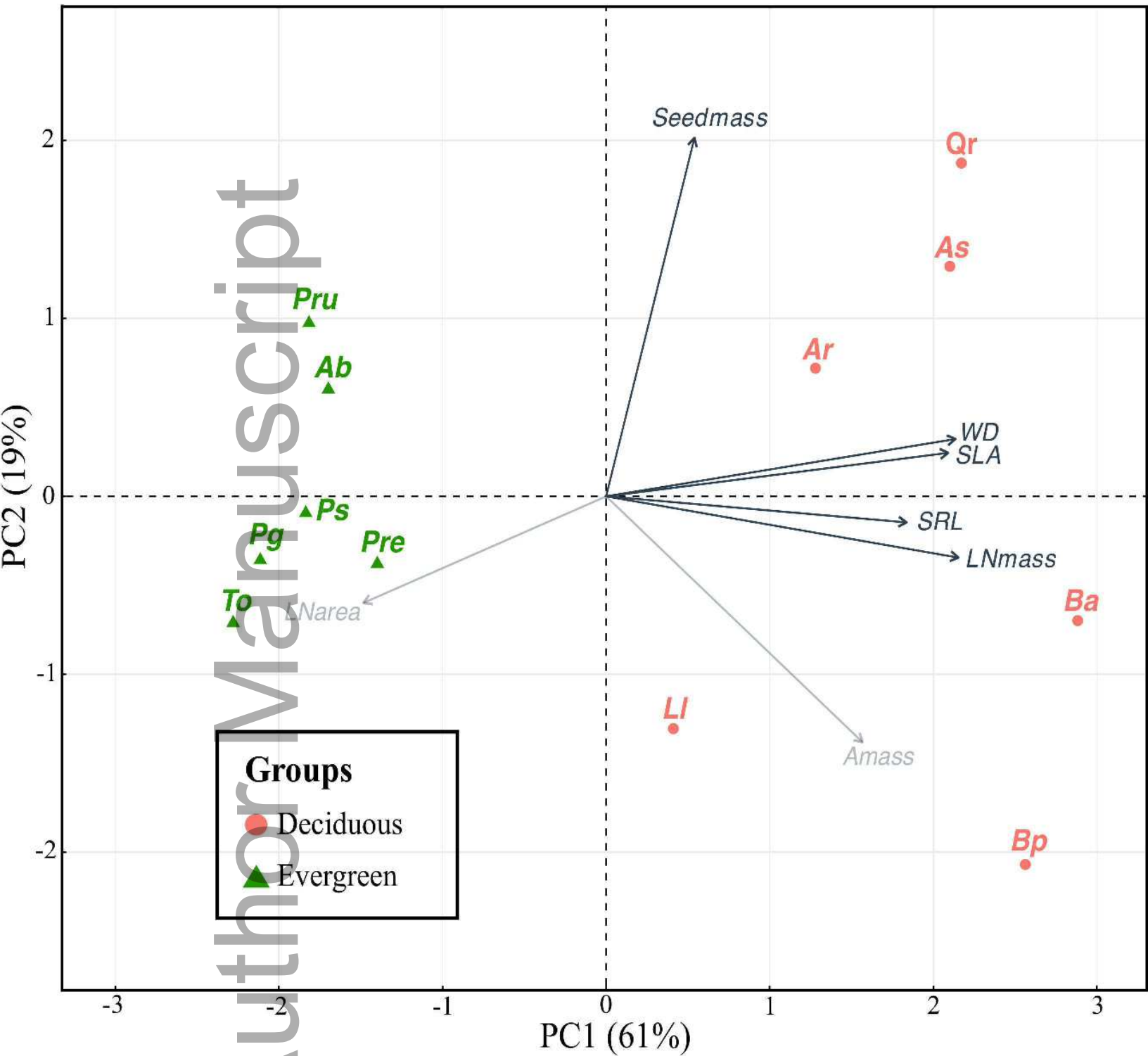
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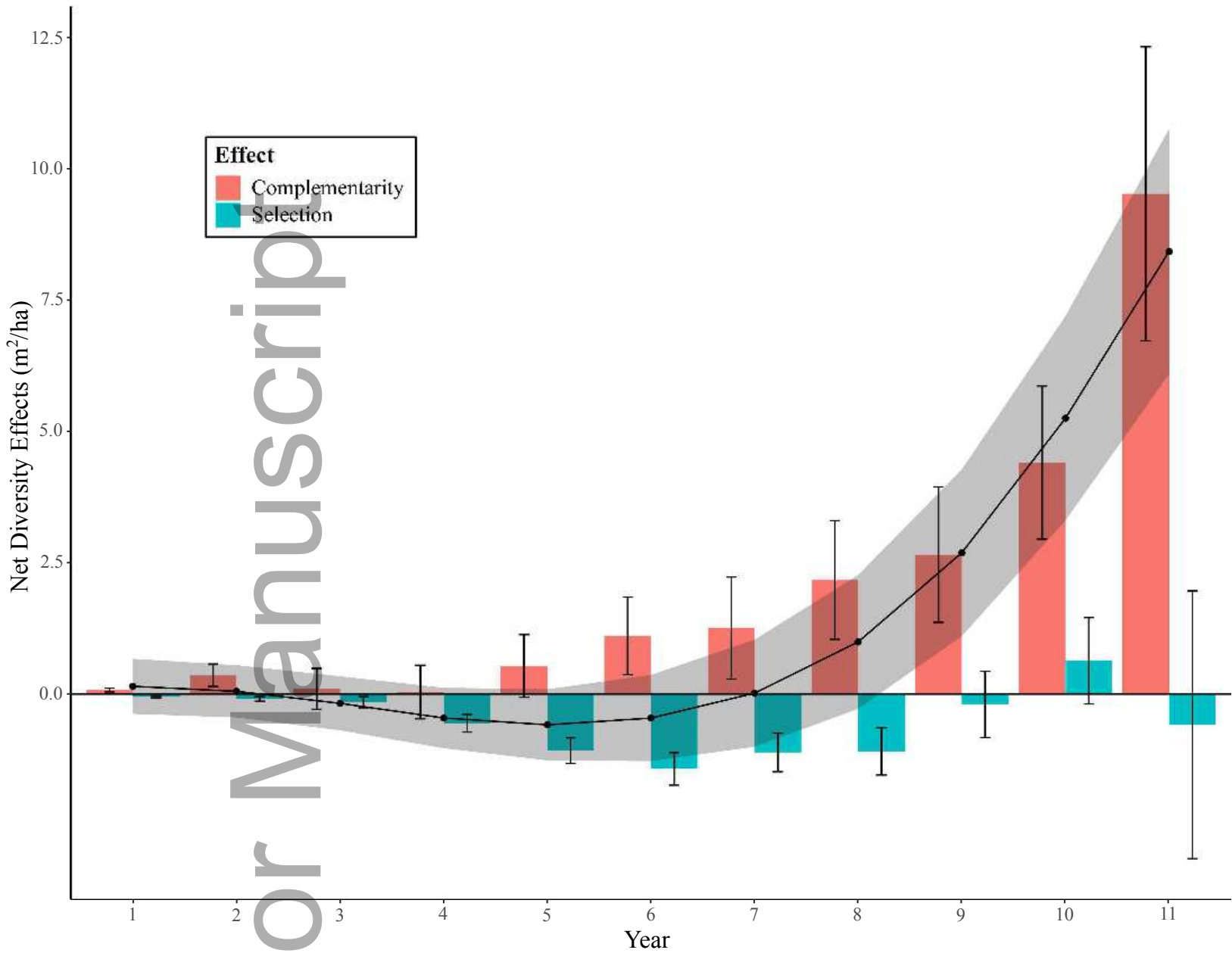
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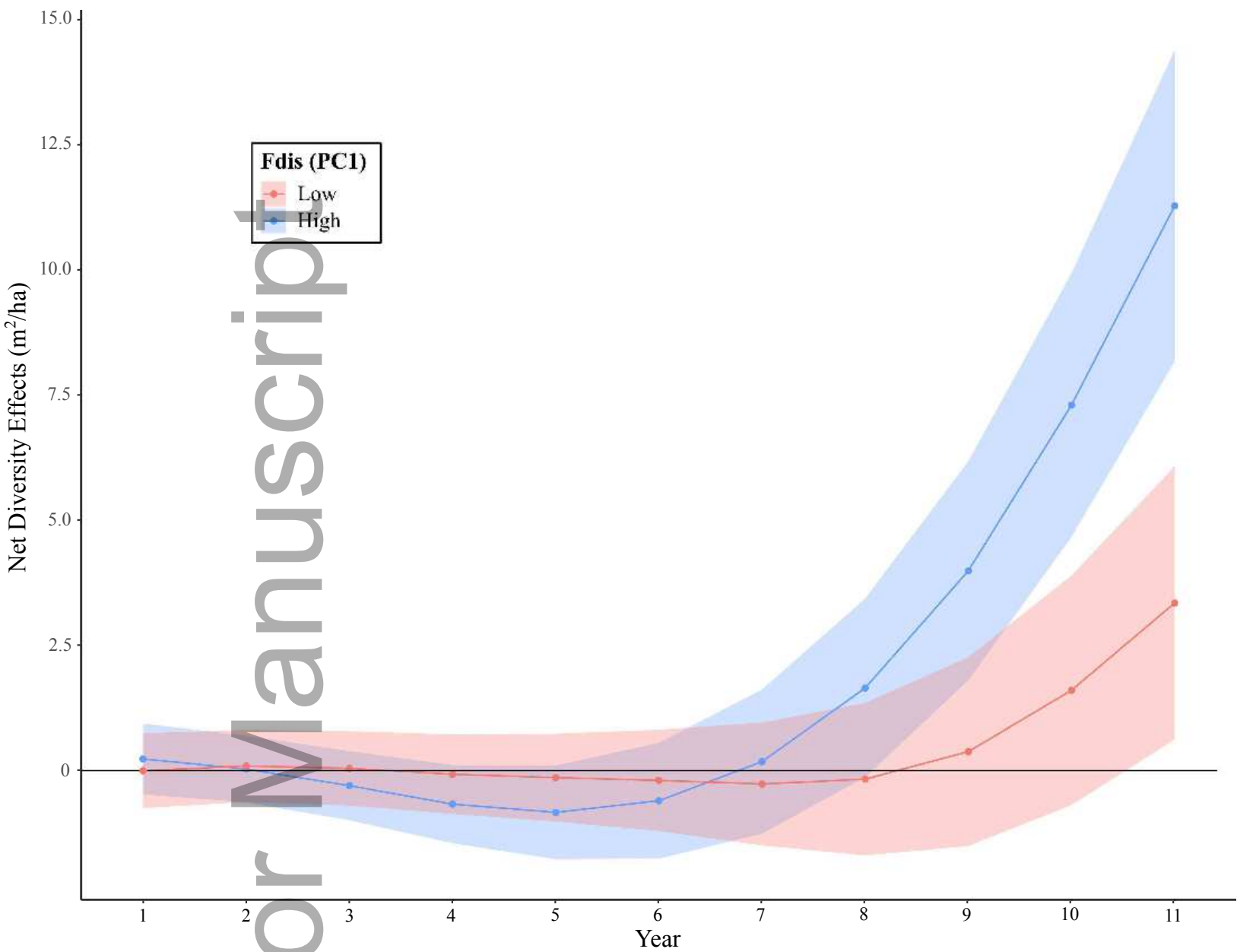
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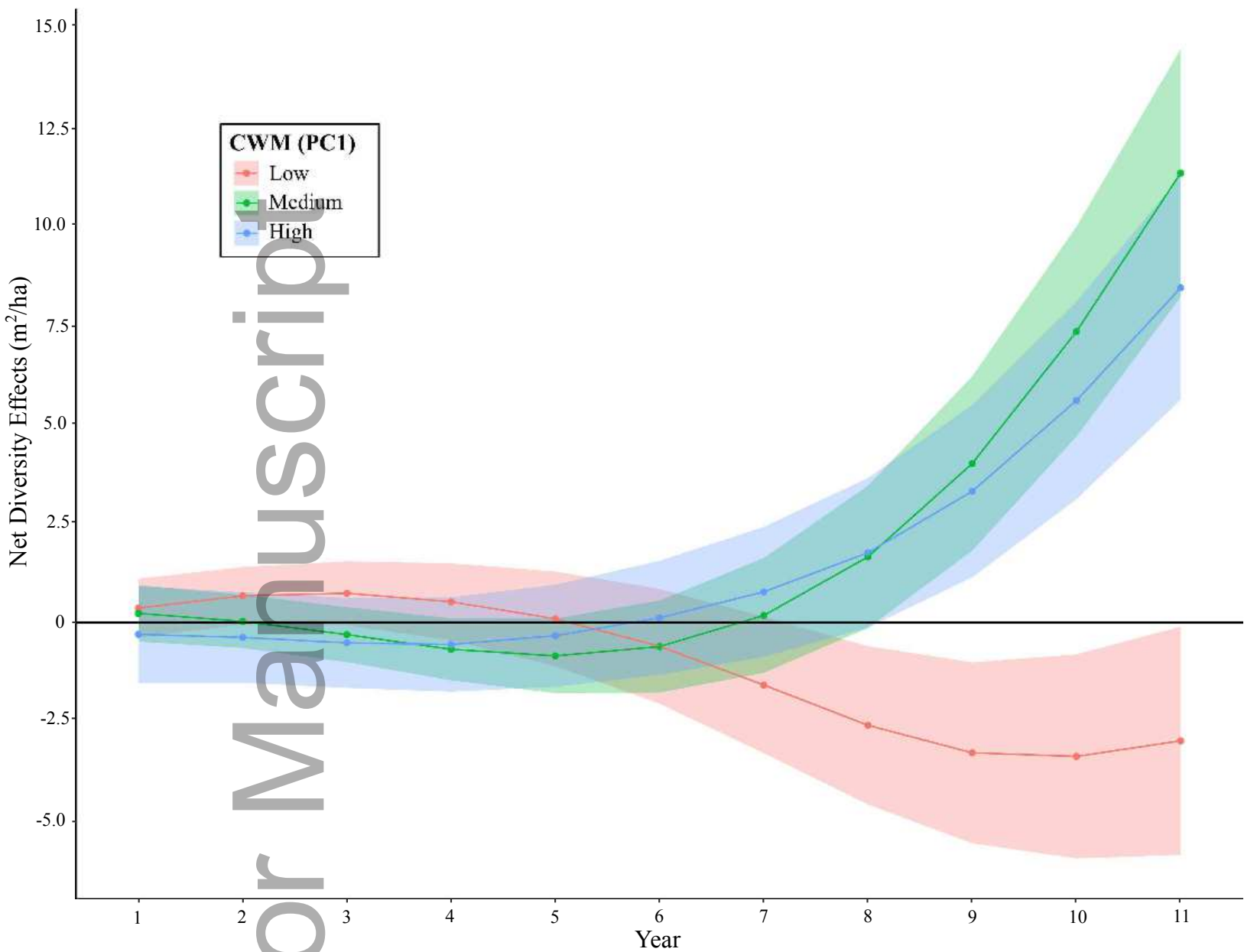
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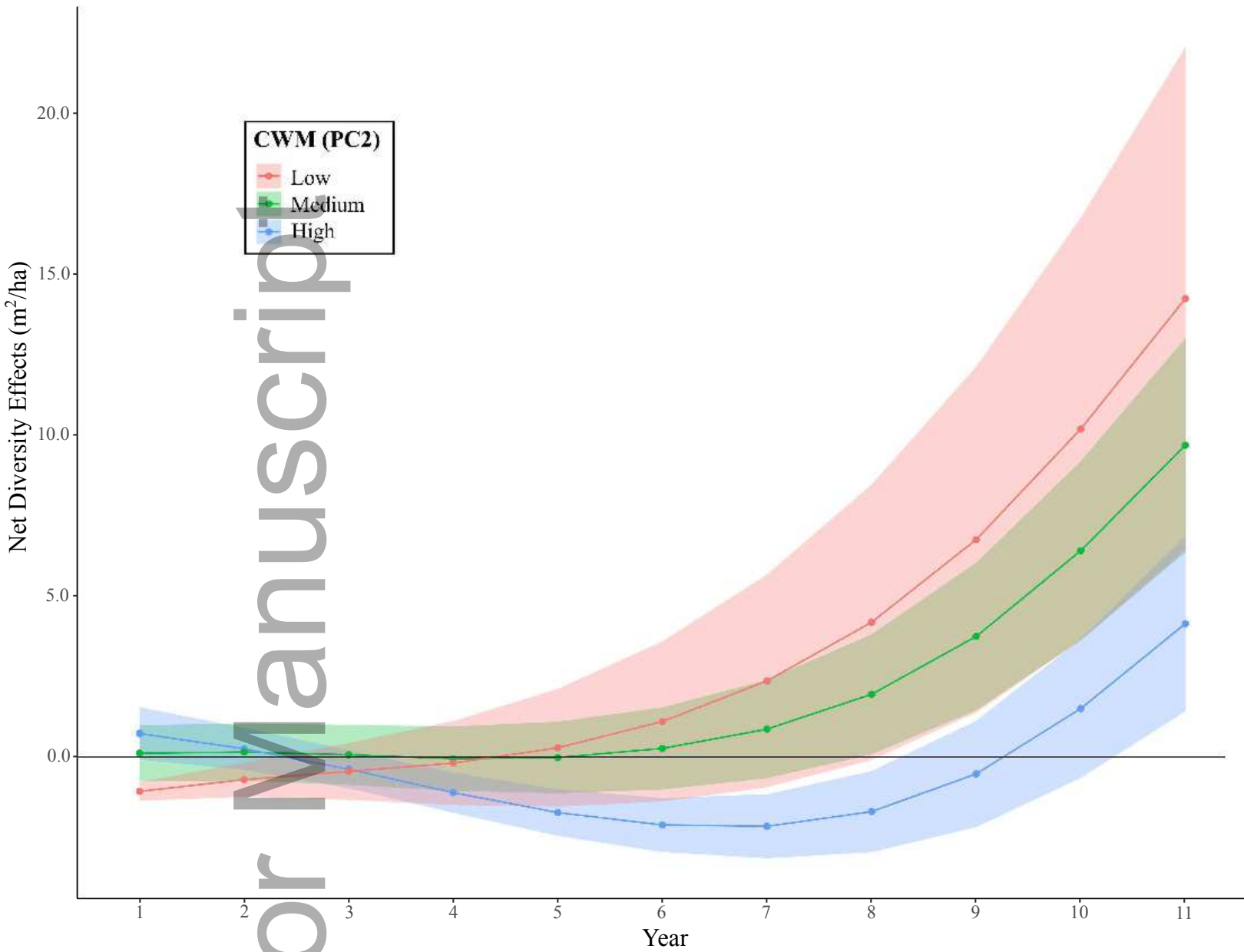
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