

Assessing Functional Diversity-Productivity Relationships in Temperate Forests in Northern Mexico

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1 Assessing functional diversity-productivity relationships in temperate forests in northern Mexico

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41 **Abstract**

42 **Background:** Studies on the relationships between biodiversity and ecosystem productivity have
43 suggested that species richness and functional diversity are the main drivers of ecosystem
44 processes. There is no general pattern regarding the relationship found in various studies, and
45 positive, unimodal, negative, and neutral relationships keep the issue controversial. In this study,
46 taxonomic diversity vs functional diversity as drivers of above-ground biomass were compared,
47 and the mechanisms that influence biomass production were investigated by testing the
48 complementarity and the mass-ratio hypotheses.

49 **Methods:** Using data from 414 permanent sampling plots, covering 23% of temperate forests in
50 the Sierra Madre Occidental (Mexico), we estimated the above-ground biomass (AGB) for trees
51 ≥ 7.5 cm d.b.h. in managed and unmanaged stands. We evaluated AGB-diversity relationships
52 (species richness, Shannon-Wiener and Simpson indices), AGB-weighted mean community
53 values (CWM) of tree species functional traits (maximum height, leaf size, and wood density)
54 and five measures of functional diversity (functional dispersion, functional richness, functional
55 uniformity, functional diversity, and RaoQ index).

56 **Results:** We reveal a consistent hump-shaped relationship between aboveground biomass and
57 species richness in managed and unmanaged forest. CWM_Hmax was the most important
58 predictor of AGB in both managed and unmanaged stands, which suggests that the mechanism
59 that explains the above-ground biomass in these ecosystems is dominated by certain highly
60 productive species in accordance of the mass-ratio hypothesis. There were no significant
61 relationships between taxonomic diversity metrics (Shannon-Wiener and Simpson indices) or
62 measures of functional diversity with AGB. The results support the mass-ratio hypothesis to
63 explain the AGB variations.

64 **Conclusions:** We concluded that diversity does not influence biomass production in the
65 temperate mixed-species and uneven-aged forests of northern Mexico. These forests showed the
66 classic hump-shaped productivity-species richness relationship, with biomass accumulation
67 increasing at low to intermediate levels of species plant diversity and decreasing at high species
68 richness. Functional diversity explains better forest productivity than classical diversity metrics.

69

70 **Keywords:** Taxonomic diversity, functional diversity, complementary hypothesis, mass-ratio
71 hypothesis

72

73 **Background**

74 One of the most important topics in community ecology has been understanding the mechanisms
75 that underlie ecosystem processes. Particularly, the species diversity-ecosystem productivity
76 relationship has been extensively studied in different ecosystems, but the relationship between
77 plant species richness and forest productivity and their underlying mechanisms are still debated
78 (Kirby and Potvin, 2007; Schumacher and Roscher, 2009; Schuldt et al., 2014; Isbell et al., 2015;
79 Zhang and Chen, 2015; Cheng et al., 2018). Most of the studies on this topic have been carried
80 out in relatively simple ecosystems, such as grasslands and monocultures; however, no records
81 were found in "natural" forest ecosystems with a long history of forest management. It has been
82 suggested that species richness is positively correlated with forest productivity (Liang et al. 2016;
83 Niklaus et al. 2017; Li et al., 2018), as a result of niche complementarity (Tilman et al. 1997).
84 That is, as species diversity increases, species resource partitioning increases which favors
85 increases in biomass (Loreau & Hector, 2001). Cardinale et al. (2006) pointed out that variations
86 in ecosystem productivity may be determined by the overabundance of highly productive species,

87 that is, the sampling selection effect or mass-ratio hypothesis (Grime, 1998; Loreau et al., 2001),
88 and not by the variety and complementarity of species. Accordingly, under this scenario it is
89 possible to find that species-poor forest ecosystems are more productive than species-rich forests.
90 Inclusive, other authors have shown that productivity is a poor indicator of plant species richness
91 (Adler et al., 2011). Consequently, there is a lack of clarity about how biodiversity could affect
92 biomass production in natural systems (Zavaleta and Hulvey, 2007).

93 One of the main approaches to understanding the relationship between species diversity and
94 ecosystem productivity has been through taxonomic diversity (Díaz y Cabido 2001). Although,
95 taxonomic diversity might provide a reasonable measure, many of the processes that regulate the
96 functioning of ecosystems are difficult to assign to each species, and it is not possible to
97 determine their relative contributions to ecosystem function and productivity. Accordingly,
98 taxonomic diversity is that assumes that all species are equivalent and does not consider
99 functional differences among species (i.e. functional diversity, FD), which are key determinants
100 of ecosystem function (Tilman, 2001).

101 The importance of functional trait diversity in explaining aboveground biomass production has
102 recently been recognized and debated (Becknell and Powers, 2014; Conti and Díaz, 2013). The
103 concept of functional diversity (FD) is a component of biodiversity that encompasses the
104 characteristics of species and predict more accurately the functioning of the ecosystem (Hooper
105 et al., 2005; Petchey and Gaston, 2002; Cianciaruso et al., 2009). Functional diversity may link
106 morphological, physiological and phenological variation at the individual level with ecosystem
107 processes and patterns (Petchey et al., 2009). Functional diversity metrics are based on traits,
108 which are correlated with function or environmental filters, such as lifestyle, position of the
109 outbreak, and resource use. In relation to the functioning of organisms, the traits modulate their

110 suitability, allow understanding the interactions between organisms and the components of their
111 environment, and link the different levels of organization of ecological systems (McGill et al.,
112 2006; Violle et al., 2007).

113 Some authors have proposed that functional diversity and functional traits may be a more reliable
114 predictor of ecosystem productivity than species richness, as plant functional traits are often used
115 as proxies to determine whether species have different ecological strategies for resource capture
116 (Vitousek et al, 1993; Lawton & Brown, 1994; Cornelissen et al., 2003; McGill et al., 2006).

117 However, despite efforts to link functional diversity of plant communities and productivity, the
118 relationships are still not entirely clear.

119 Forest management is considered an anthropogenic disturbance type that influences ecosystem
120 functions, such as carbon and nutrient cycle. Likewise, forest management impacts the ecological
121 mechanisms that maintain plant communities, e.g. competition and facilitation (Agrawal et al.
122 2013, Haddad et al. 2015). In even-aged forests, diversity is one of the axes most affected by
123 silvicultural practices, due that during regeneration processes the establishment of the
124 commercially most valuable species is prioritized, altering spatial heterogeneity, with effects on
125 functional diversity, because the environmental and biotic heterogeneity of the associated
126 ecological niches decreases or disappears (Greenberg et al., 2011). Conversely, it has been
127 observed that managed uneven-aged forests embedded in a vegetation matrix tend to maintain
128 greater taxonomic and functional diversity as consequence of the variation in the axes of the
129 ecological niche (Greenberg et al., 2011).

130 Two hypotheses have been widely postulated to understand the effects of diversity on ecosystem
131 processes, the complementarity hypothesis proposed by Tilman (1997) and the mass-ratio
132 hypothesis proposed by Grime (1998). Complementarity hypothesis proposes that taxonomic and

133 functional diversity, as well as the difference in functional traits between species maximizes the
134 diversity of resource use strategies, and less overlap of niches along the resource axes increases
135 the functioning of the ecosystem through the partition of the niche. In natural ecosystems, has
136 been suggested that at very low levels of productivity, species richness is limited, and only a few
137 species are adapted to survive under nutrient-poor conditions. Conversely, at high levels of
138 productivity, competition for light and space leads to competitive exclusion of species and only a
139 few species will be dominant. On the other hand, Grime (1998) postulated that the productivity of
140 a community is determined by the relative abundance of the functional traits values of the
141 dominant contributors to the plant biomass. According to this hypothesis, ecosystem properties
142 such as biomass should be predictable from the weighted mean community values (CWM) of
143 traits with links to the capture, use, and release of resources at the individual and ecosystem level
144 (Díaz et al. 2007). Likewise, the assumptions of the hypothesis by Grime (1998) consider that
145 functional aspects of the dominant species have a greater influence on ecosystem processes
146 because few highly competitive species increase interspecific competition and, eventually,
147 decrease complementary processes and, in consequence, decrease functional diversity.

148 Functional diversity, like taxonomic diversity, is a multifaceted entity that hardly represents the
149 complexity of the ecosystem in a single index. However, efforts have been made to separate it
150 into three components that represent and quantify independent facets of functional diversity,
151 which are: functional wealth (FR), functional equity (FE) and functional divergence (FD) (Mason
152 et al., 2005). FR represents the niche space occupied by all species in the community. FE
153 represents equity in the distribution of occupied niche space, and FD represents the degree to
154 which the distribution of abundances in the space of the occupied niche maximizes the total
155 variation of the community. On the other hand, a widely used metric is the quadratic diversity of

156 Rao (FDQ, Rao 1982), which represents a generalization of the Simpson's index. This metric
157 comprises valuable properties to describe functional diversity and can be based on various
158 measures of dissimilarity between species (Botta-Dukát 2005, Ricotta 2005, Lepš et al. 2006).
159 Research addressing key ecological processes underlying forest productivity is needed across
160 multiple locations and few studies yet exist that address whether the variation in different aspects
161 of functional diversity coincides empirically with large variation in biomass stocks (e.g. Conti
162 and Díaz, 2013; Grigulis et al., 2013; Finegan et al., 2015).

163 The pine-oak forests of Durango have been ranked as the most important forests in Mexico
164 because of their extent and economic value. These forests are of particular interest, not only
165 because they represent a unique ecosystem (with 20 pine and 43 oak species and often species of
166 *Arbutus*, *Fraxinus*, *Cupressus*, *Juniperus* and occasionally *Abies* and *Pseudotsuga* (González-
167 Elizondo et al., 2012)), but also because they are owned and managed by local communities in
168 the form of collective land ownerships known as "Ejidos", or indigenous land holdings known as
169 "Comunidades" (Madrid et al., 2009). Most of the forests in Durango are uneven-aged, and
170 conifer species occur as mixtures with broadleaf species. This irregularity refers to the spatial
171 arrangement of trees (vertical and horizontal irregularity) and the variation in the age structure of
172 trees and stands. The management of these mixed uneven-aged forests is more complex than the
173 management of even-aged forests, and one of the most pressing research problems is the
174 development of ecological models to define sustainable harvests. In that sense, no study has
175 attempted to evaluate the effect of tree species diversity on forest productivity.

176 In this study, we address two topics widely debated in the current literature. On the one hand, we
177 test the predictive power of taxonomic and functional diversity on above-ground biomass
178 prediction in a managed forest landscape. On the other hand, based on the calculation of the

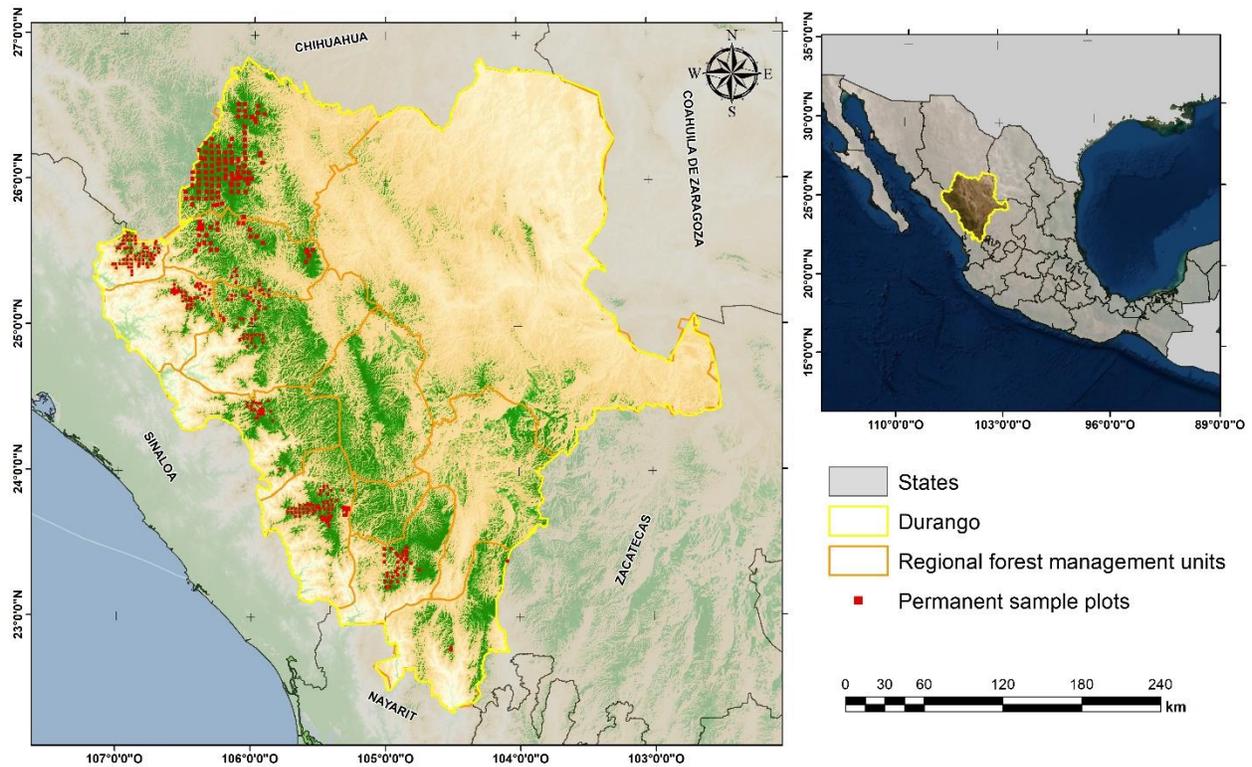
179 taxonomic and functional diversity metrics in managed and unmanaged forests, we evaluate the
180 effect of the complementarity and the mass-ratio hypotheses. In particular, we tested if functional
181 diversity metrics will be a better predictor of forest biomass, and that, since forests are managed
182 under a wood-oriented forestry model, the dominant species will play a predominant role in the
183 diversity-productivity relationship of the ecosystem (hypothesis of the mass-ratio).

184

185 **Materials and methods**

186 Study area and inventory data

187 The study was conducted in the temperate forests of Durango, Mexico (22°20'49" to 26°46'33"
188 N; 103°46'38" to 107°11'36" W), which occupies about 23% of the Sierra Madre Occidental
189 mountain range (Figure 1). The elevation above sea level varies between 1200 and 3200 m
190 (average 2264 m). Precipitation ranges from 443 to 1452 mm, with an annual average of 917 mm,
191 whereas the mean annual temperature varies from 8.2 to 26.2 °C, with an annual average of 13.3
192 °C (Silva-Flores et al., 2014). Dominant vegetation types are pine-oak forests. Some major tree
193 groups occur in these forests, with important tree families including Pinaceae, Fagaceae, and
194 Betulaceae; dominant shrub families include Rosaceae and Ericaceae. These forests are shaped
195 by more than one century of timber oriented forestry, mainly by selective removals for
196 sustainable timber production, but also for the maintenance of biological diversity and uneven-
197 aged stand structures (Padilla et al., 2019).



198
 199 Figure 1. Study area

200
 201 Temperate forests in Mexico are uneven-aged multispecies forests, and occupy 32.3 million
 202 hectares (17 per cent of the land area). These forests are the richest ecosystems in Mexico with
 203 some 7000 plant species (Challenger, 1998), of which ~150 are pine species and 170 oak species;
 204 together represent more than 50% of all known pine and oak species worldwide (CONABIO,
 205 2000). Durango is the most important forestry state in Mexico, with 4.9 million ha of natural
 206 forests (mostly managed) and an average timber production of 1.8 million m³ in the last decade
 207 (29.7% of the national forest production) (SEMARNAT, 2016). These forests are shaped by more
 208 than one century of timber oriented forestry, mainly by selective removals for sustainable timber
 209 production, but also for the maintenance of biological diversity and uneven-aged stand structures
 210 (Padilla et al., 2019).

211 The data were obtained from 414 permanent sample plots (PSP) used to monitor the growth and
212 yield of Durango's forests (Crecente-Campo et al., 2014), of which 365 are placed in managed
213 stands and 49 in unmanaged stands. The plots were mostly measured between 2011 and 2015,
214 and cover the main forest types and the current diameter distributions of commercial forests in
215 Durango. The plots are 50×50 m in size and were distributed by systematic sampling, with a
216 variable grid ranging from 3 to 5 km. The following variables by species were recorded:
217 diameter at breast height (measured in cm at 1.3 m above ground level), total tree height (m),
218 height to the live crown (m), azimuth (°) and radius (m) from the centre of the plot to all trees
219 equal or larger than 7.5 cm on diameter at breast height (DBH). The following stand variables
220 were calculated from the tree data recorded in each plot: stems per hectare (N), stand basal area
221 (G , $m^2 ha^{-1}$), quadratic mean diameter (d_g , cm), and dominant height (H_0 , m). Dominant height
222 was calculated from the proportion of the 100 pine trees with the largest diameter per hectare.
223 The PSP represent two broad conditions based on management history and structural attributes:
224 (1) unmanaged stands (more than 50 years of non-management history); and (2) managed stands,
225 with components of structural heterogeneity in form of multi-layered canopy.

226 Biomass estimates

227 Aboveground biomass (AGB) was considered as measure of stand productivity. AGB of live
228 trees in each plot was estimated using species-specific allometric equations based on DBH and
229 total height (h) developed specifically for all major Durango coniferous and broadleaf tree
230 species (Vargas-Larreta et al., 2018). We used the biomass equations outlined by Rojas-García et
231 al. (2015) for rare species. equations outlines by Vargas-Larreta et al. (2018) were used for those
232 tree species for which no biomass equations have been developed.

233 Traits measurements

234 Three functional traits were selected to quantify plant functional diversity: maximum tree height
235 (Hmax, m), wood density (WD, g cm⁻³), and leaf size (LS, cm). Functional traits Hmax
236 (community-level mean of plot-specific maximum tree height values) and WD are the most
237 important and commonly studied traits, and are accurate predictors of stand biomass (Ruiz-
238 Benito et al., 2014; Wu et al., 2015). Tree height was measured in the field, whereas the data for
239 wood density were extracted from the literature for the major tree species in Mexico (Ordoñez et
240 al., 2015). LS values were compiled from Farjon and Filer (2013) and García and González
241 (2003).

242 Taxonomic diversity and functional diversity

243 Diversity indices such as species richness (number of species per plot; S), and species diversity
244 (Shannon–Weener index; H', and Simpson's index; λ), as well as trait-based functional diversity
245 metrics, were used as diversity and functional diversity metrics, respectively. For each plot, we
246 calculated community-weighted mean trait (CWM), as well as functional richness (FRic),
247 functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and
248 Rao's quadratic entropy index (RaoQ) (Rao, 1982).

249 The CWM of a single trait was calculated as the averaged trait value in the community, weighted
250 by the abundance of the species (Garnier et al., 2004):

251
$$CWM_x = \sum p_i x_i$$

252 where CWM_x is the CWM for the trait x, p_i is the relative abundance of species i in the
253 community and x_i is the trait value for the species i.

254 Rao's index (RaoQ) is one of the most common indices of functional diversity, and estimates the
255 abundance-weighted variance of the dissimilarities between all species pairs (Lepš et al., 2006).

256 RaoQ was calculated as follows:

$$257 \quad RaoQ = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j$$

258 where p_i and p_j are the relative abundances of species i and j , and the d_{ij} values are the
259 dissimilarities between species i and j in the community. As proposed by Mason et al. (2005) and
260 by Villéger et al. (2008) the convex hull volume method was used as a measure of FRic. The
261 FEve was measured using a minimum spanning tree which links all the species in the
262 multidimensional functional space (Villéger et al., 2008). Functional dispersion (FDis) is the
263 weighted distances from a weighted centroid in multitrait space using plot-specific trait values,
264 and functional divergence index (FDiv), defined as the variance in the attribute values of the
265 species present at a site, represents the variation in trait values, weighted by the abundance of
266 each species in the community (Mason et al., 2003). It is calculated as:

$$267 \quad FDiv = \frac{2}{\pi} \arctan(5V)$$

268 where 5 is a scaling factor used to define the index over a range of 0–1 and V is the weighted
269 variance of trait x , expressed as:

$$270 \quad V = \sum p_i (\ln x_i - \ln x)^2$$

271 where x_i is the trait value for the species i and

$$272 \quad p_i = \frac{a_i}{\sum a_i}$$

273 where a_i is the relative abundance of species i in the community. FDiv has no units, and its value
274 ranges between 0 and 1, where 0 = low or no trait diversity, and 1 = high trait diversity.

275 Functional diversity metrics (CWM, FDis, FRic, FEve, FDiv, and RaoQ) were calculated by
276 using the 'dbFD' function of Lalibertè and Legendre (2010) of the FD package in R (R Core
277 Team, 2019). The species diversity indices (Shannon–Wiener index; H' , and Simpson's index; λ)
278 were calculated for each plot with the 'vegan' package in R (R Core Team, 2019).

279 Statistical analyses

280 As the visual inspection of AGB plotted against taxonomic diversity and functional diversity
281 measures clearly indicated a unimodal relationship, we fitted a quadratic model to the data using
282 multiple non linear regression by adding a quadratic polynomial term, which assessed how stand
283 biomass was related to diversity (S , H' , λ), mean trait values (CWM) and functional diversity of
284 the stands. All analyses were performed in R (R Core Team, 2019).

285 **Results**

286 A total of 67,991 trees were recorded, comprising 63 plant species belonging to 14 genera and 9
287 families. The dominant families were Fagaceae (26 species), Pinaceae (15 species), and
288 Cupressaceae (eight species). The most abundant species were *Pinus durangensis* (14,683 stems),
289 *Quercus sideroxyla* (7,891), *P. arizonica* (7,281), *P. cooperi* (5,309), *P. teocote* (4,354), *P.*
290 *strobiformis* (3,082), *P. leiophylla* (2,696), *Q. crassifolia* (2,675), *P. herrerae* (2,215) y *Juniperus*
291 *depeana* (2,001). Tree number per plot ranged from 64 to 466 stems, with an average value of
292 158 stems per plot.

293 Minimum, maximum and mean values of diversity metrics and functional diversity indices, as
294 well as of AGB for the analysed plots are summarized in Table 1. The number of species (S) per
295 plot, for trees ≥ 7.5 cm dbh, ranged from 3 to 14 species, with an average species richness of 7

296 species per plot. Aboveground biomass was highly variable across all plots, ranged from 12.24 to
 297 378.25 Mg ha⁻¹, with an estimated average value of 135.51 Mg ha⁻¹ (± 70.2 Mg ha⁻¹) (Table 1).
 298 Shannon–Wiener index and Simpson’s index ranged from 0.09 to 2.21 and from 0.03 to 0.88,
 299 respectively. The CWM of Hmax (CWM_Hmax) ranged between 16.67 and 46.1; the CWM of
 300 leaf size (CWM_LS) was 1.49 to 25.22, whereas the CWM range for wood density (CWM_WD)
 301 was from 0.37 to 0.63.

302 Table 1. Minimum, maximum and mean values of diversity metrics and functional diversity
 303 measures, as well as of AGB for the analysed plots.

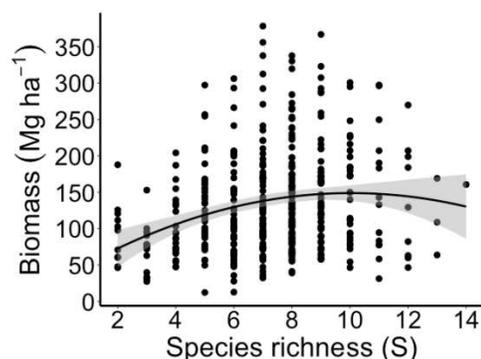
Measure	All plots (414)			Managed stands (365)			Unmanaged stands (49)		
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
Species richness (S)	2	14	7.0 \pm 2.1	3	14	7.5 \pm 2.1	2	12	6.78 \pm 2.34
Shannon (H')	0.02	2.21	1.39 \pm 0.4	0.1	2.19	1.4 \pm 0.41	0.22	2.21	1.32 \pm 0.46
Simpson (λ)	0.03	0.88	0.66 \pm 0.2	0.03	0.87	0.66 \pm 0.17	0.09	0.88	0.63 \pm 0.19
CWM_Hmax	16.67	46.1	36.98 \pm 4.4	16.7	46.1	37.1 \pm 4.29	12.24	38.28	28.45 \pm 5.87
CWM_LS	1.49	25.22	12.84 \pm 4.1	3.9	24.5	13.1 \pm 3.93	1.49	25.22	10.73 \pm 4.84
CWM_WD	0.37	0.63	0.47 \pm 0.05	0.37	0.63	0.47 \pm 0.05	0.38	0.61	0.46 \pm 0.06
FRic	0.04	8.16	3.52 \pm 1.57	0.04	8.11	3.54 \pm 1.48	0.54	8.16	3.47 \pm 2.05
FEve	0.01	0.85	0.54 \pm 0.16	0.01	0.85	0.54 \pm 0.16	0.06	0.83	0.54 \pm 0.18
FDiv	0.31	1.00	0.80 \pm 0.12	0.31	1.00	0.81 \pm 0.11	0.40	0.99	0.78 \pm 0.13
FDIs	0.06	1.82	1.12 \pm 0.36	0.06	1.82	1.13 \pm 0.36	0.09	1.78	1.05 \pm 0.41
RaoQ	0.05	3.44	1.60 \pm 0.69	0.05	3.44	1.62 \pm 0.67	0.07	3.27	1.48 \pm 0.79
AGB (Mg ha ⁻¹)	12.24	378.25	135.5 \pm 70.2	30.38	378.25	137.8 \pm 69.6	12.24	337.75	114.42 \pm 73.26

304
 305 Species richness was greater in managed stands than in unmanaged ones (average 7.5 and 6.78,
 306 respectively); as well as the mean values of Shannon–Wiener (H') and Simpson (λ) indices (Table

307 1). Meanwhile, the CWM mean values of Hmax, LS and WD were higher in managed stands
308 than in unmanaged stands; the same case was for all functional diversity measures (Table 1).
309 Unmanaged stands accumulated 16.9% less AGB than managed stands (Table 1); the minimum
310 AGB value (12.24 Mg ha⁻¹) was found in the unmanaged stands, whereas the maximum AGB
311 value (378.25 Mg ha⁻¹) was recorded in managed stands; on average, managed stands had more
312 biomass than unmanaged stands (average 137.8 and 114.42 Mg ha⁻¹, respectively).

313 Aboveground biomass – diversity relationship

314 Aboveground biomass values varied considerably with species richness (S), and a significant
315 relationship between AGB and number of species was found for all plots together (Table 2). It
316 was observed a slight trend for the entire data set, through a smooth unimodal curve of AGB
317 respect to species richness (Figure 2). The relationship was quadratic (2nd order polynomial
318 regression: $R^2=0.07$, $p<0.001$; Table 2), showing the well-known hump-shaped relationship
319 between biomass and diversity; i. e., AGB was highest at medium species richness values and
320 then decreased with the stand number of species. Average AGB among species richness values
321 ranged from 69.6 to 160.6 Mg ha⁻¹ (Figure 2), with the highest AGB mean values associated with
322 values from 7 to 9 species per plot.



323 Figure 2. Aboveground biomass - species richness relationship. Solid line indicates the fit of a
 324 second degree polynomial model ($R^2=0.07$, $p<0.001$). Shaded areas represent the 95% confidence
 325 interval.

326 Aboveground biomass was unrelated to Shannon (H') and Simpson's (λ) indices (Figures not
 327 shown); in fact, stand biomass was not affected by any of these two diversity indices when all
 328 plots were pooled together. AGB variability increased with the Shannon's index value and were
 329 higher at medium H' values (1.3 – 1.7). Highest AGB value ($378.25 \text{ Mg ha}^{-1}$) was found
 330 associated with a Simpson's value of 0.75.

331 Aboveground biomass – functional diversity relationships

332 A second order polynomial regression was performed to evaluate whether AGB were linked to a
 333 nonlinear relationship with trait functional diversity. The results showed that functional diversity
 334 measures outperform traditional diversity metrics (S , H' , λ), as well as functional traits (LS ,
 335 WD), to explain the variation of AGB. The only relationship we found between AGB and a
 336 CWM measure was between AGB and the trait H_{max} ; i. e., AGB was significant quadratic
 337 related to CWM_H_{max} ($R^2=0.12$; $p<0.001$; Table 2); no significantly quadratic relationship
 338 between AGB and CWM_LS or CWM_WD was observed.

339 Table 2. Goodness of fit statistics for the second degree quadratic model on different groups of
 340 predictor variables (diversity metrics, community-weighted means of trait values (CWM) and
 341 functional trait diversity (FD)) for aboveground biomass for all permanent plots pooled together.

	Diversity metrics			CWM			Functional diversity (FD)				
	S	H'	λ	H_{max}	LS	WD	FD _{is}	FD _{iv}	FE _{ve}	FR _{ic}	RaoQ
All plots											
R^2	0.07	0.02	0.01	0.12	0.01	0.01	0.05	0.02	0.03	0.06	0.06
$F_{1,411}$	14.33	3.757	1.656	27.54	0.432	1.786	10.23	2.526	5.351	12.74	12.72
p	<0.001	0.024	0.192	<0.001	0.649	0.169	<0.001	0.081	0.005	<0.001	<0.001

342

343 On the other hand, AGB was significantly correlated with four of the five functional diversity
 344 measures (FDis, FEve, FRic, and RaoQ) when all plots were pooled together (Table 2).
 345 Significance was weaker for the AGB-FEve relationship (explained variance = 3%) compared
 346 with those observed for FDis (5%), FRic (6%) and RaoQ (6%). The overall relationship between
 347 AGB and functional diversity (except FDiv) was quadratic; i. e., biomass increased with
 348 functional diversity values and then decreased afterwards. In all cases AGB was highest at
 349 medium FD values.

350 AGB in relation to diversity measures in managed and unmanaged forest stands
 351 Table 3 presents a summary of the 2nd order polynomial regression models fitted to AGB-diversity
 352 metrics and functional diversity relationships, in both managed and unmanaged stands. Among
 353 the diversity metrics, only species richness (S) in managed stands was a significant predictor of
 354 AGB (Table 3); whereas the AGB-CWM_Hmax relationship was highly significant in both
 355 managed and unmanaged stands, with a variance explained of 12% and 42%, respectively; CWM
 356 of leaf size (CWM_LS) was significant predictor only in unmanaged stands. Relationships
 357 between AGB and the five functional diversity measures were significant only for three of them
 358 (FDis, Fric and RaQ) in managed stands, whereas only FDis was significant in unmanaged
 359 stands; the variance explained by FDis was higher in unmanaged stands (12%) than in managed
 360 stands (5%) (Table 3).

361 Table 3. Goodness of fit statistics for the second degree quadratic model on different groups of
 362 predictor variables (diversity metrics, community-weighted means of trait values (CWM) and
 363 functional trait diversity (FD)) for aboveground biomass for managed and unmanaged stands.

Diversity metrics			CWM			Functional diversity				
S	H'	λ	Hmax	LS	WD	FDis	FDiv	FEve	FRic	RaoQ
Managed stands										

R^2 (%)	0.05	0.02	0.01	0.12	0.01	0.02	0.05	0.01	0.01	0.05	0.07
$F_{1,362}$	9.626	2.181	0.923	24.3	1.365	1.454	9.151	2.096	2.355	8.722	12.17
p	<0.001	0.114	0.398	<0.001	0.235	0.234	<0.001	0.124	0.096	<0.001	<0.001
Unmanaged stands											
R^2	0.10	0.06	0.05	0.42	0.43	0.08	0.12	0.01	0.05	0.04	0.09
$F_{1,46}$	2.598	1.492	1.332	15.39	15.77	1.883	12.822	0.978	1.058	0.833	1.956
p	0.085	0.235	0.274	<0.001	<0.001	0.165	<0.001	0.022	0.356	0.442	0.154

364

365 Figures 3, 4 and 5 present the relationships between AGB and diversity metrics, community

366 weighted mean (CWM) trait values, and functional diversity measures calculated for managed

367 and unmanaged stands. As the visual inspection of species richness, as well as Shannon-Wiener

368 and Simpson indices, plotted against AGB clearly indicated a unimodal relationship in both

369 managed and unmanaged stands (Figure 3). The highest AGB values were related to species

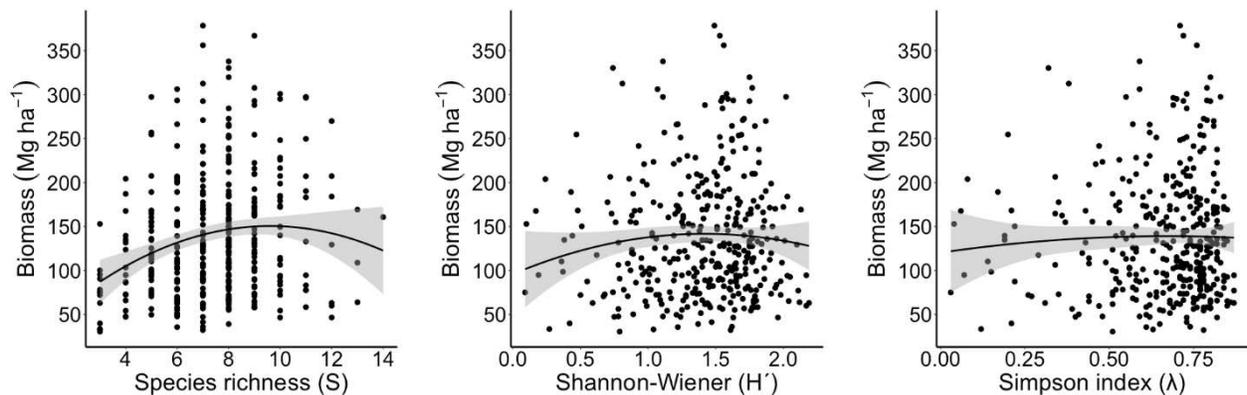
370 richness values between 7 and 9 in both cases; the same behavior of AGB respect to Shannon-

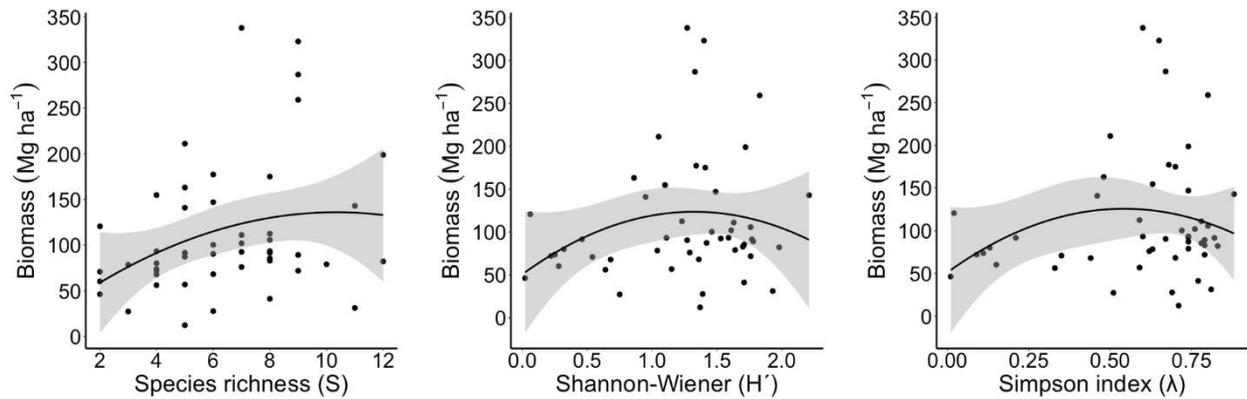
371 Wiener and Simpson indices was observed in both type of stands, with the maximum AGB

372 values close to 1.5 and 0.7, respectively. The above indicate that the management of these forests

373 has no clear effect on species diversity and, therefore, diversity does not direct affect the

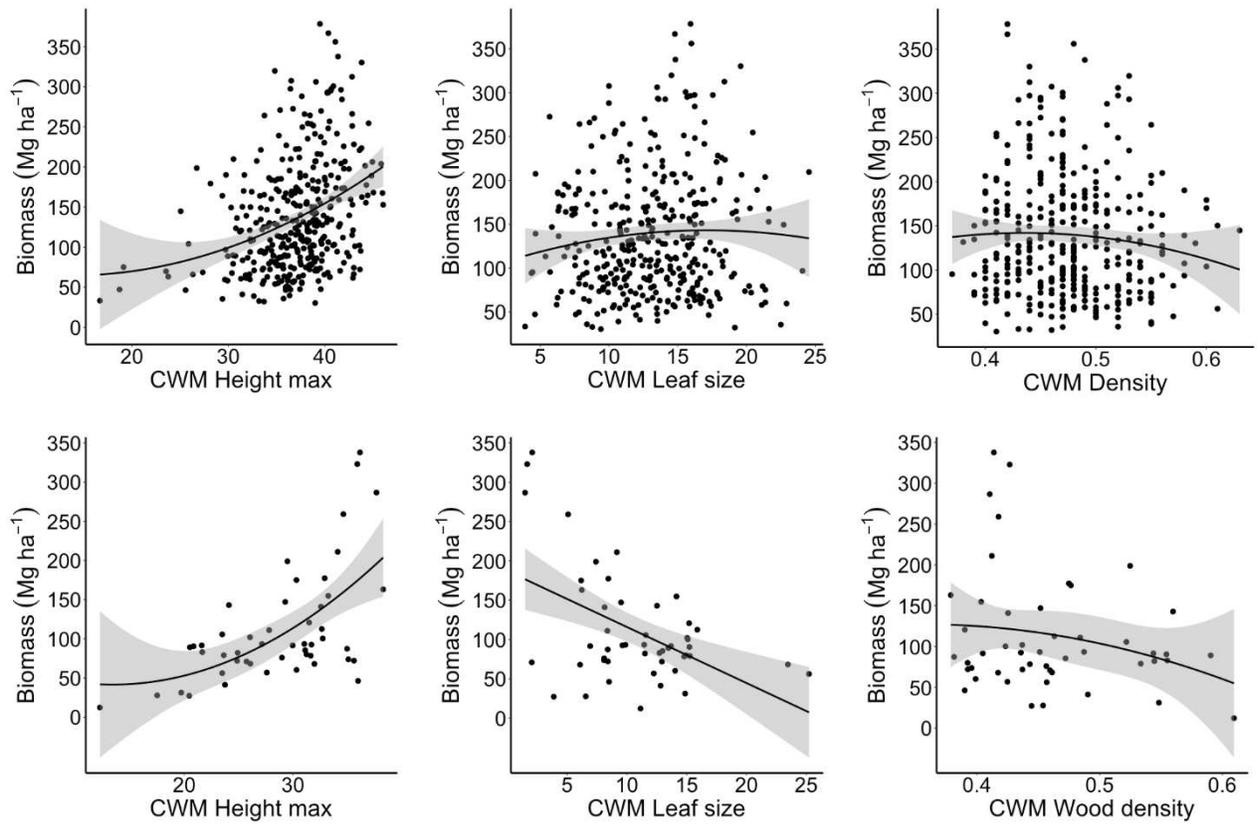
374 diversity-productivity relationship in these forests.



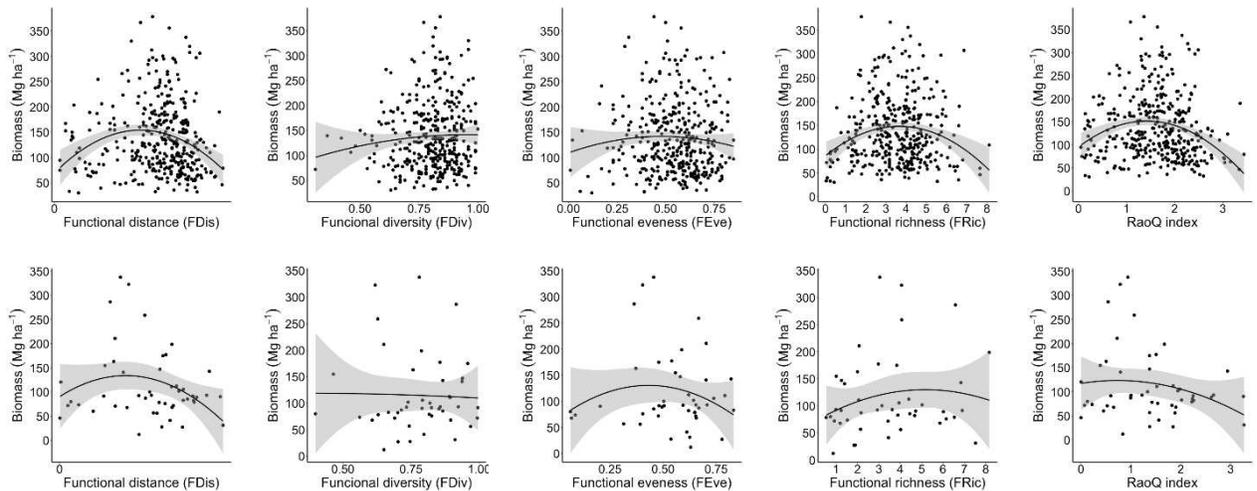


375 Figure 3. Relationships between AGB and diversity metrics calculated for managed (top row) and
 376 unmanaged stands (bottom row). Solid line indicates the fit of a second degree polynomial
 377 model. Shaded areas represent the 95% confidence interval.

378 Aboveground biomass was positively related to CWM of Hmax, showing exactly the same trend
 379 in managed and unmanaged stands (Figure 4). On the other hand, a slight negative relationship
 380 between AGB and wood density trait (CWM_WD) was observed in both type of stands (Figure
 381 4), indicating that stands with harder wood species have lower productivity than stands with
 382 softer wood species. In unmanaged stands, AGB was negatively related to CWM_LS (leaf size
 383 trait), which suggests that higher aboveground biomass in stands without management is associated
 384 with conservative leaf trait values, in this case with small to medium leaf size species (Figure 4).
 385 In managed stands, the AGB-CWM_LS relationship did not show a clear trend, although a
 386 unimodal curve with the highest values of AGB associated to CWM_LS values around 15 was
 387 observed. Finally, no differences between managed and unmanaged stands were observed in the
 388 relationships between AGB and the four indices used to measure functional diversity (Figure 5).



389 Figure 4. Relationships between AGB and community weighted mean (CWM) trait values
 390 calculated for managed (top row) and unmanaged stands (bottom row). Solid line indicates the fit
 391 of a second degree polynomial model. Shaded areas represent the 95% confidence interval.
 392



393

394 Figure 5. Relationships between AGB and functional diversity (FD) measures obtained for
395 managed (top row) and unmanaged stands (bottom row). Solid line indicates the fit of a second
396 degree polynomial model. Shaded areas represent the 95% confidence interval.

397

398 **Discussion**

399 Numerous studies have documented the relationships between biodiversity and ecosystems
400 productivity, with quite different conclusions including positive, negative, hump-shaped and
401 null relationships (Zhang and Chen, 2015; Barrufol et al., 2013; Adler, 2011; Flynn, 2011).
402 Lehman and Tilman (2000) and Barrufol et al. (2013), for instance, point out that plant diversity
403 increases when the productivity of the community also increases, whereas Kenkel et al. (2000)
404 found that increasing plant diversity does not influence forest productivity. Zhang et al. (2012)
405 performed a meta-analysis of more than 50 studies and found a monotonic increase of forest
406 productivity with plant species diversity. In addition, Vilá et al. (2007) report a positive
407 relationship between species richness and woody productivity across different environmental
408 conditions in Spain. Despite this large number of studies, it has not been possible to establish a
409 definitive pattern that is valid for the pine-oak forests of the Sierra Madre Occidental (Corral-
410 Rivas, et al., 2019). In this study we analyze the effect of species diversity and functional
411 diversity on aboveground biomass by employing 414 permanent plots within uneven-aged
412 temperate forests. The results exhibited a highly variable AGB-species richness relationship, but
413 we identified the hump-shaped (unimodal) relationship between species richness and the
414 accumulation of total biomass (AGB), which has been frequently observed in mature ecosystems
415 (Mittelbach et al., 2001). It is in agreement with the most recent global meta-analyses and
416 empirical findings across different biomes, which reveal a consistent positive concave-down effect

417 of biodiversity on forest productivity across the world (Liang et al., 2016). Our findings reveal
418 that, when species richness is relatively low, AGB is also low, but increases to a certain level of
419 species richness where the biomass is maximum; after this optimal point, AGB trends to be
420 lower. AGB values were highest at medium species richness values (number of species in plots
421 between 7 and 9) and then decreased afterwards. These results are similar to those obtained by
422 Corral-Rivas et al. (2019), who report an optimum level of species richness between 5 and 10
423 species associated with the maximum volume production in temperate forests in northern
424 Mexico. Our findings are also in line with the prevailing conclusions that the AGB-diversity is
425 unimodal, which means that productivity peaks at intermediate levels of diversity (Ding, 2019;
426 Zhang and Chen, 2015; Barrufol et al., 2013; Adler, 2011), but are contrary to Wu et al. (2015),
427 who found that forest biomass in temperate forest in China was positively related ($r^2=0.08$) with
428 species richness; Ammer (2018), who points out that, although it is difficult to generalize a
429 definitive pattern, the shape of the curve relating forest productivity to tree species diversity
430 represents an asymptotic curve, and that it seems to be similar across biomes (Liang et al., 2016).
431 Adler et al. (2011) mentioned that the theoretical basis for a hump-shaped productivity-species
432 richness relationship has been challenged, and that methodological differences confound cross-
433 study comparisons of empirical evidences (Gotelli and Colwell, 2001). We present empirical
434 evidence that the classical hump-shaped species diversity-productivity may be found in the
435 temperate mixed-species and uneven-aged forests of the Sierra Madre Occidental in Mexico.
436 The highest biomass level was found close to 380 Mg ha⁻¹ for the three diversity measures used,
437 and it is related to 7, 0.9 and 2.1 values of species richness (S), Shannon-Wiener (H') and
438 Simpson (λ) indices, respectively (Figure 2). The mechanisms behind these relationships have
439 been discussed in terms of species facilitation and competition. When biomass is relatively low,
440 species richness increase due to interspecific facilitation (Guo, 2007); whereas when biomass

441 accumulates to a certain point, competition leads to lower diversity (Weiner, 2001). This pattern
442 could be consequence of the interspecific interactions at community level, where niche
443 differentiation and facilitative interactions between species improve the utilization of available
444 limiting resources (Wang et al., 2016). In this study, when species richness increased, AGB
445 accumulation had a peak, and then reached a decline. Interestingly, AGB peak corresponded with
446 the average values of species richness, Shanon-Wiener and Simpson indices (Table 1, Figure 2).
447 These results are consistent with Wang et al. (2016), who state that, when species diversity
448 reaches a certain degree, the productivity may also peak at intermediate diversity levels due to
449 saturation in resource utilization.

450 Nevertheless, it is important to point out that this relationship could be influenced by others
451 factors besides diversity, such as environmental factors, whose effect on productivity and
452 species richness change along altitudinal gradients (Wu et al., 2015). In this sense, in additional
453 analysis (not shown) we observed a negative relationship between AGB and altitude ($R^2=0.05$;
454 $F_{2,411}=3.261$; $p<0.039$), and AGB and temperature ($R^2=0.12$; $F_{2,411}=11.885$; $p<0.001$), but a
455 positive trend between AGB and precipitation ($R^2=0.27$; $F_{2,411}=57.443$; $p<0.001$). Due these
456 relationships were not objective of this study, future work should include the impact assess of
457 climatic on AGB variables to confirm these observations.

458 We compare our results with some studies that reported positive or hump-shaped AGB-diversity
459 relationships in terms of correlation degree. We found that the effect of species richness on
460 aboveground biomass production yield up 10% across the temperate pine-oak northern Mexico
461 (Table 3), which is greater than 6% reported by Wu et al. (2015) for boreal and temperate forest
462 across China. For similar forest ecosystems to the one considered in this study, have been
463 reported low R^2 values; for example, Cavanaugh et al. (2014), Potter and Woodall (2014), and
464 Wardle et al. (2006), who reported 0.16, 0.00-0.25, and 0.21, respectively. Wu et al. (2015) states

465 that the R^2 values between diversity and biomass reported are generally less than 0.3, and that
466 more than 70% of variation in forest biomass can not be explained by biodiversity, which
467 coincides with the results obtained in this study.

468 The above discussed confirms that the AGB - species richness relationship is highly complex (Li
469 et al., 2018), and it is because Adler et al. (2011) highlights that productivity is a poor predictor
470 of plant species richness. Such a conclusive statement has led to the use of species-level
471 functional traits or functional-trait based approaches to better link biodiversity with forest
472 productivity.

473 We evaluated the effect of forest management on diversity and AGB production, contrasting
474 managed and unmanaged stands. We were unable to find a clear influence of management on
475 species richness, CWM, or functional diversity, because minimum and maximum values of
476 species richness, as well as all other diversity and functional diversity measures used were similar
477 in both managed and unmanaged stands. These findings extend those of Duguid and Ashton
478 (2013), confirming that there is no clear influence of forest management on understory plant
479 biodiversity when contrasting managed and unmanaged stands. Our results are also in agreement
480 with Paillet et al. (2009), who carried out a study to evaluate biodiversity differences between
481 managed and unmanaged forests in Europe finding that species richness was only marginally
482 higher in unmanaged than in managed forests, which means that the effect of management on
483 biodiversity is not clearly identifiable.

484 We attribute the similar AGB, species richness, as well as all other diversity and functional
485 diversity measures values, in both type of stands, to harvesting regimes. Selective felling is the
486 dominant management type in the Sierra Madre Occidental; it is a management method that
487 prescribes harvest of selected trees within a planning horizon defined by the cutting cycle
488 (ranging up 70 years). A dominant characteristic of this method is the regulation of harvesting

489 regimes to guarantee the natural state and ecological diversity of the forests (Torres-Rojo et al.,
490 2016). This type of management has maintained a diverse structure with small, medium and large
491 trees in a multi-layered canopy, and it has originated uneven-aged multispecies stands. That is
492 compelling evidence that forest management has not changed the AGB-diversity relationships in
493 these forests.

494 In the last two decades, there has been a growing consensus regarding the importance of using
495 functional traits as predictors of productivity measured through biomass (Díaz and Cabido,
496 2001). Furthermore, it has been widely observed that patterns in functional traits can be used to
497 predict relationships in species communities, because they represent the evolutionary processes
498 of species; and the mean values of the traits at the community level are interpreted as results of
499 the niche complementarity or the mass ratio (Cavender-Bares et al., 2009; Götzenberger et al.,
500 2012; HilleRisLambers et al., 2012). In this sense, this study used functional diversity metrics, as
501 well as the community weighted means (CWM) of three functional traits as drivers of the
502 aboveground biomass in managed and unmanaged forest stands. CWM measures explained a
503 larger proportion of variation in aboveground biomass (Table 3) than did diversity metrics or FD
504 measures, in both managed and unmanaged stands, indicating, as Roscher et al. (2012) highlight,
505 that the temperate forests evaluated containing dominant species with different trait combinations
506 reached high productivity. Our analyses showed that AGB was best explained by CWM_Hmax,
507 which indicates that dominant height is the most important trait for high productivity. This has
508 sense, because the dominant height attained by a forest stand at a specified age (known as site
509 index), is the most widely used indicator of potential productivity in forest ecosystems
510 (Hägglund, 1981; Vanclay, 1994).

511 Our results suggest that the mass ratio and environmental filtering hypotheses are not mutually
512 exclusive (Table 3). However, the mass ratio hypothesis explains to a greater extent the

513 relationship between biomass and functional diversity, since it postulates that the production rate
514 of an ecosystem process, e.g. AGB, is mainly determined by a set of dominant species (Grime,
515 1988). Therefore, under the assumptions of the hypothesis, that is, considering that the
516 environment is uniform, the woody species community has the highest biomass production by a
517 set of species with dominant traits (*Pinus cooperi*, *P. durangensis*, *P. arizonica*, *Quercus*
518 *sideroxylla*, and *Cupressus lusitanica* in unmanaged stands; *Pinus durangensis*, *Quercus*
519 *sideroxylla*, *P. arizonica*, *P. herreae*, and *P. cooperi* in manage stands) which, in our study,
520 represent 63 and 65% of the total AGB, respectively.

521 Furthermore, the null relationship between functional equity (FE_{ve}) and aboveground biomass
522 ($R^2=0.05$) confirm the low contribution of environmental filtering and the facilitating processes
523 in biomass production. Studies carried out by Vile et al. (2006), and Sonkoly et al. (2019) in
524 grass ecosystems in France and Hungary, respectively, as well as studies carried out in tropical
525 ecosystems in Brazil (Duarte et al., 2010) and Costa Rica (Finegan et al., 2015) and temperate
526 forests in China (Yuan et al., 2018) found similar patterns regarding the mechanisms that
527 influence biomass.

528 On the other hand, our results suggest that forest management is favoring the permanence and
529 abundance of species with commercial importance. The relationship between forest management
530 and the increase in forest biomass as a consequence of the reduction in intra and interspecific
531 competition has been widely documented (Binkley, 2004; Joudvankis et al., 2005). For example,
532 Pretzsch (2005) found that reducing the basal area of beech stands may, to some extent, increase
533 productivity. However, favoring the establishment of a set of high commercial value species may
534 be reducing functional features, functional diversity, and consequently the mechanisms of
535 environmental filtering. Consequently, the null relationship between biomass and functional
536 diversity metrics could be being masked by forest management.

537
538 **Conclusions**
539 Diversity does not influence biomass production in the temperate mixed-species and uneven-aged
540 forests of northern Mexico. These forests showed the classic hump-shaped productivity-species
541 richness relationship, with biomass accumulation increasing at low to intermediate levels of
542 species plant diversity and decreasing at high species richness. Functional diversity explains
543 better forest productivity than classical diversity metrics. Multi-trait functional diversity, but not
544 classical diversity metrics, provides key information to explain forest productivity in these
545 forests, where the single trait maximum tree height seems to be the the better option for
546 understanding the biomass accumulation process in these ecosystems. Although the impact of
547 forest management on biodiversity is still debated, it has not changed the AGB-diversity
548 relationships in the forests of the Sierra Madre Occidental, Mexico.

549

550 **Ethics approval and consent to participate**

551 Not applicable

552 **Consent for publications**

553 Not applicable

554 **Availability of data and material**

555 The dataset used and analysed during current study are available from the corresponding author
556 as reasonable request.

557 **Competing interests**

558 The author(s) declared no potential conflicts of interest with respect to the research, authorship,
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565 **Authors' Contribution**

566 B.V.-L. and J.O.L.-M. conceived the study idea. B.V.-L. and J.J.C.-R, and J.J.H conducted the
567 field data collection. B.V.-L. and J.O.L.-M. performed the analysis and wrote the manuscript. All
568 the authors reviewed the manuscript.

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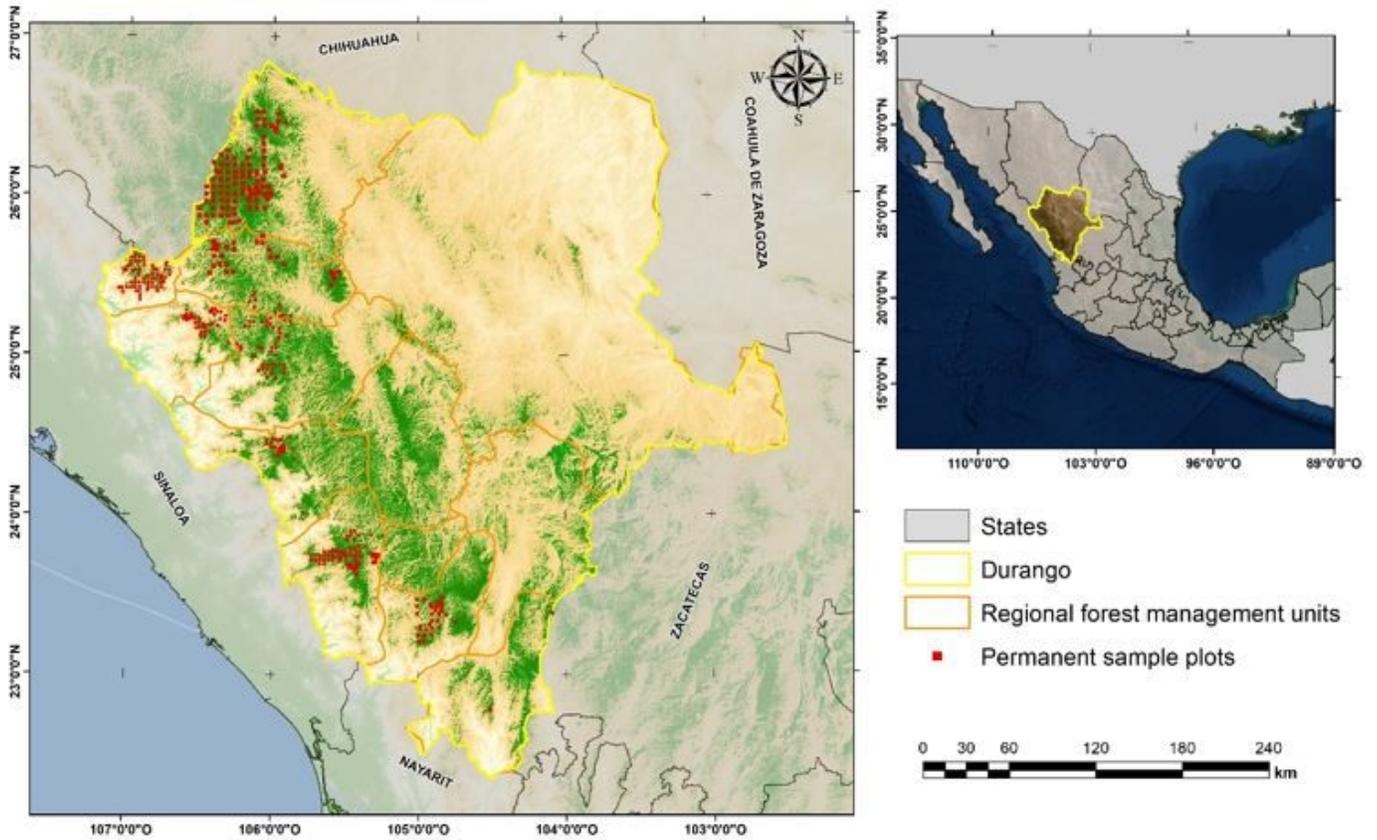
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857

Figures



3

Figure 1

Study area

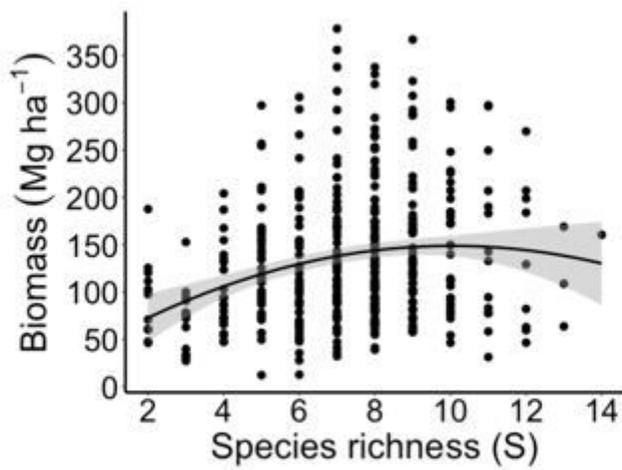


Figure 2

Aboveground biomass - species richness relationship. Solid line indicates the fit of a second degree polynomial model ($R^2=0.07$, $p<0.001$). Shaded areas represent the 95% confidence interval.

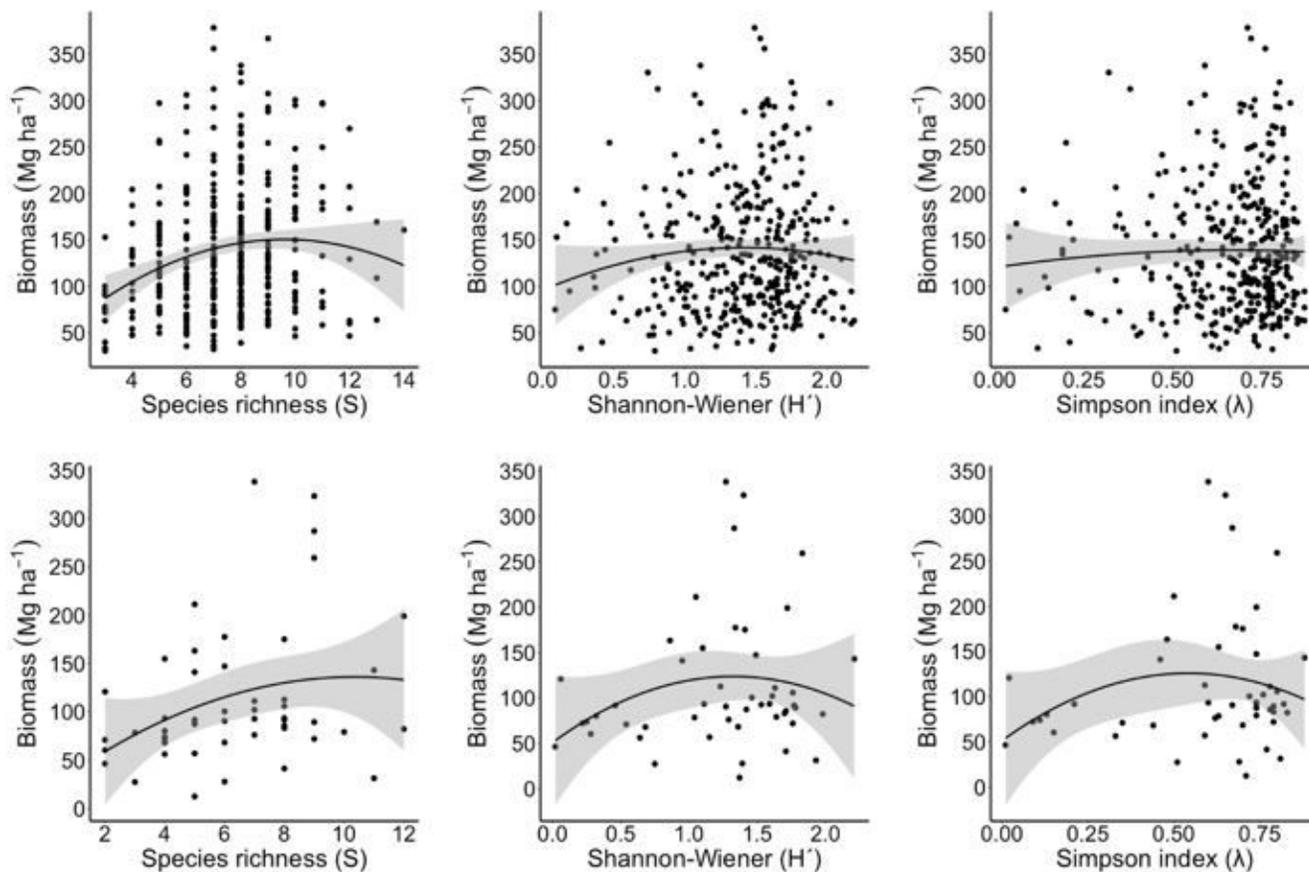


Figure 3

Relationships between AGB and diversity metrics calculated for managed (top row) and unmanaged stands (bottom row). Solid line indicates the fit of a second degree polynomial model. Shaded areas represent the 95% confidence interval.

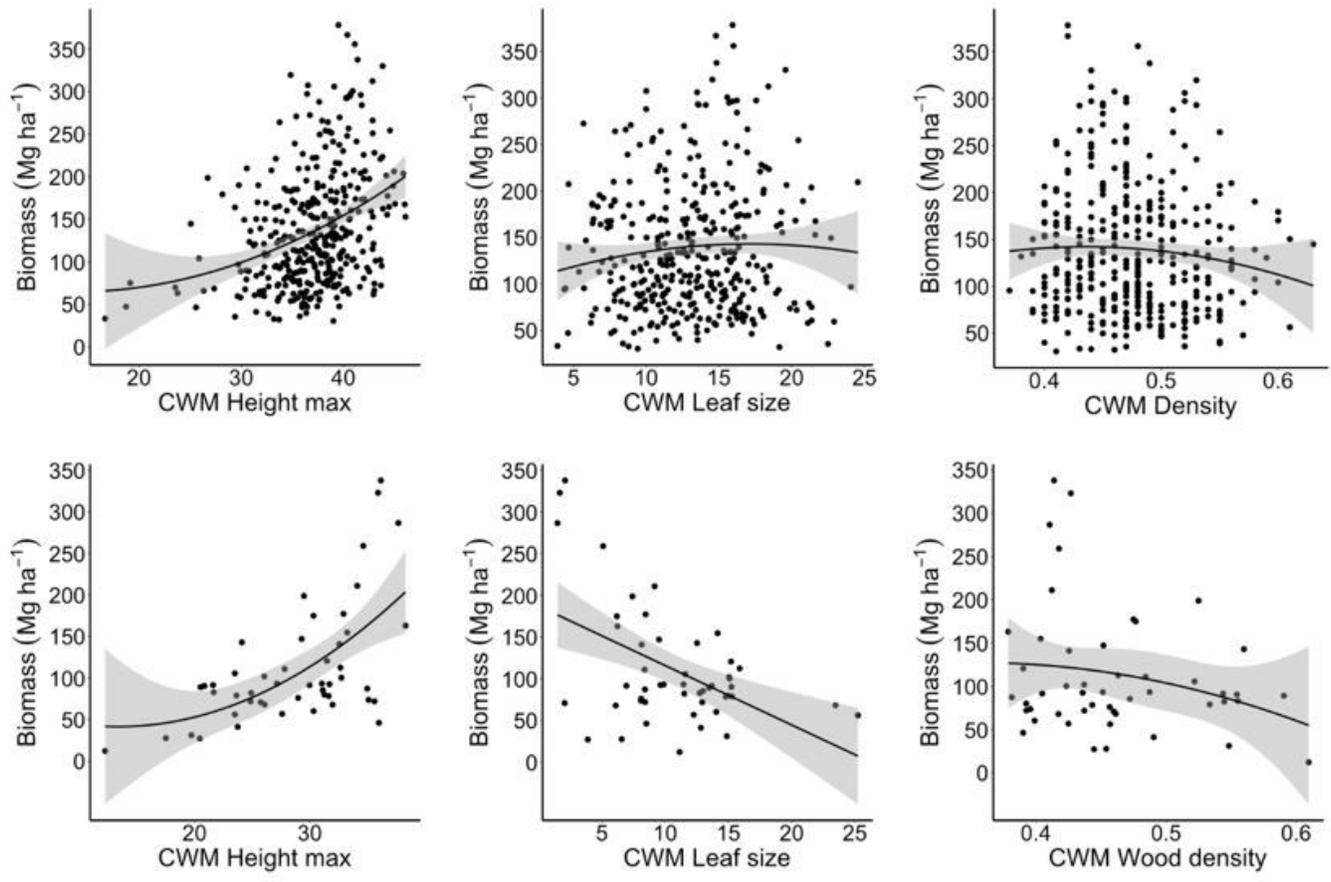


Figure 4

Relationships between AGB and community weighted mean (CWM) trait values calculated for managed (top row) and unmanaged stands (bottom row). Solid line indicates the fit of a second degree polynomial model. Shaded areas represent the 95% confidence interval.

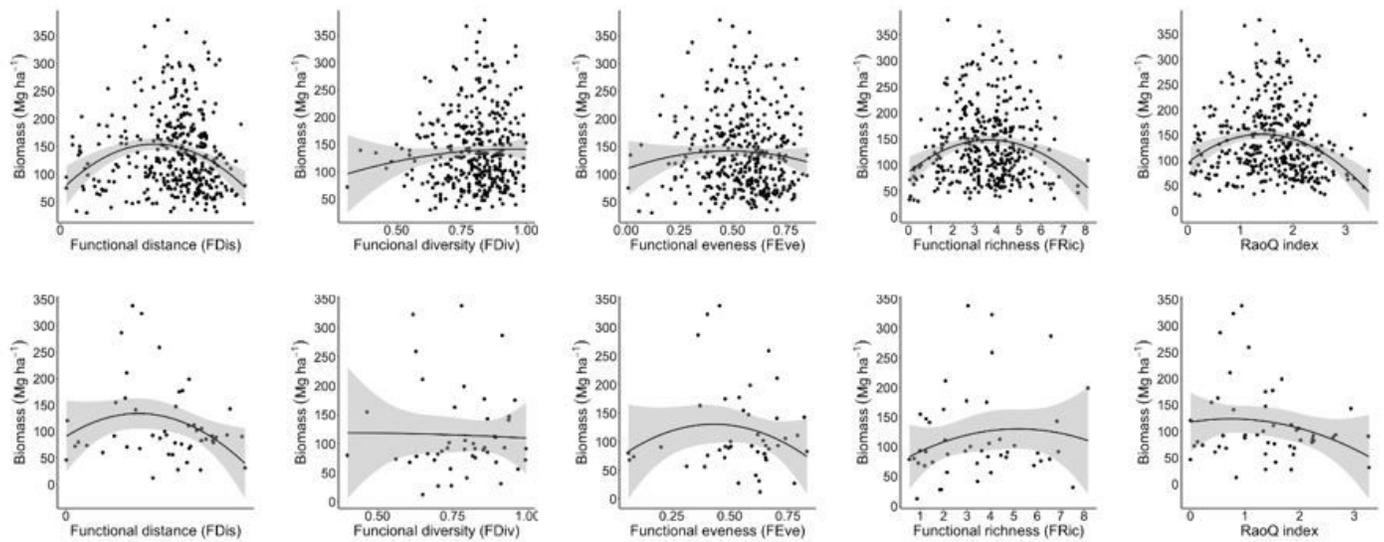


Figure 5

Relationships between AGB and functional diversity (FD) measures obtained for managed (top row) and unmanaged stands (bottom row). Solid line indicates the fit of a second degree polynomial model. Shaded areas represent the 95% confidence interval.