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Divergent above- and below-ground biodiversity pathways mediate disturbance impacts on temperate forest multifunctionality

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Keywords:	biodiversity, ecosystem functioning, functional traits, disturbance, natural forests, soil microbes
Abstract:	<p>Biodiversity plays a fundamental role in provisioning and regulating forest ecosystem functions and services. Above-ground (plants) and below-ground (soil microbes) biodiversity could have asynchronous change paces to human-driven land-use impacts. Yet we know very little how they affect the provision of multiple forest functions related to carbon accumulation, water retention capacity and nutrient cycling simultaneously (i.e., ecosystem multifunctionality; EMF). We used a dataset of 22,000 temperate forest trees from 260 plots within 11 permanent forest sites in Northeastern China, which are recovering from three post-logging disturbances. We assessed the mediating effects of multiple attributes of plant biodiversity (taxonomic, phylogenetic, functional, and stand structural) and soil biodiversity (bacteria and fungi)</p>

	<p>on EMF under the three disturbance levels. We found the highest EMF to occur in highly disturbed plots. Biodiversity had a tremendous effect on EMF that overpassed those of both climate and disturbance. However, above- and below-ground biodiversity provided divergent pathways to mediate human disturbance impacts on EMF. The mediating effect of above-ground attributes of plant diversity to post-logging disturbances on EMF was inconsistent, and shifted from negative to positive depending on how the forest ecosystems were performing, while soil microbial diversity exhibited a consistent and positive mediating response pattern. Our study sheds light on the need for integrative frameworks simulatenously considering above and below-ground attributes to grasp the global picture of biodiversity effects on ecosystem functioning and services. Suitable management interventions could maintain both plant diversity and soil microbial diversity, and thus guarantee a long-term functioning and provisioning of ecosystem services in an increasing disturbance frequency world.</p>

1 **Divergent above- and below-ground biodiversity pathways mediate**
2 **disturbance impacts on temperate forest multifunctionality**

3

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23 Statement of authorship:

24 ZY, ML and YL conceived the idea; ZY, FD, SL, AS, WZ, JY, FL, SF, ZH and XW
25 conducted the study and collected the data. ZY analysed the data and wrote the first
26 draft with great support from AS and YL, after which all authors contributed
27 substantially to revision.

28 We confirm that, should the manuscript be accepted, the data supporting the results
29 will be archived in an appropriate public repository (e.g. Dryad) and the data DOI will
30 be included at the end of the article.

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45 Abstract

46 Biodiversity plays a fundamental role in provisioning and regulating forest ecosystem
47 functions and services. Above-ground (plants) and below-ground (soil microbes)
48 biodiversity could have asynchronous change paces to human-driven land-use
49 impacts. Yet we know very little how they affect the provision of multiple forest
50 functions related to carbon accumulation, water retention capacity and nutrient
51 cycling simultaneously (i.e., ecosystem multifunctionality; EMF). We used a dataset
52 of 22,000 temperate forest trees from 260 plots within 11 permanent forest sites in
53 Northeastern China, which are recovering from three post-logging disturbances. We
54 assessed the mediating effects of multiple attributes of plant biodiversity (taxonomic,
55 phylogenetic, functional, and stand structural) and soil biodiversity (bacteria and
56 fungi) on EMF under the three disturbance levels. We found the highest EMF to occur
57 in highly disturbed plots. Biodiversity had a tremendous effect on EMF that
58 overpassed those of both climate and disturbance. However, above- and below-ground
59 biodiversity provided divergent pathways to mediate human disturbance impacts on
60 EMF. The mediating effect of above-ground attributes of plant diversity to
61 post-logging disturbances on EMF was inconsistent, and shifted from negative to
62 positive depending on how the forest ecosystems were performing, while soil
63 microbial diversity exhibited a consistent and positive mediating response pattern.
64 Our study sheds light on the need for integrative frameworks simulatenously
65 considering above and below-ground attributes to grasp the global picture of
66 biodiversity effects on ecosystem functioning and services. Suitable management

67 interventions could maintain both plant diversity and soil microbial diversity, and thus
68 guarantee a long-term functioning and provisioning of ecosystem services in an
69 increasing disturbance frequency world.

70

71 **Keywords:** biodiversity; ecosystem functioning; functional traits; disturbance; natural
72 forests; soil microbes

73

For Review Only

74 **Introduction**

75 Forests harbour much of the terrestrial biodiversity, and provide fundamental
76 functions and services, such as biomass production, nutrient cycling and water
77 retention (Gamfeldt et al., 2013; Pan, Birdsey, Phillips, & Jackson, 2013). However,
78 human-driven disturbances, such as habitat destruction and resource overexploitation,
79 can cause drastic terrestrial biodiversity loss and ecosystem changes (Newbold et al.
80 2016, Isbell et al. 2011, Le Provost et al. 2020). For example, selective logging, as a
81 widespread anthropogenic disturbance in natural forest ecosystems, not only exerts
82 critical direct effects on the aboveground biomass stock (Dai et al., 2004), but also on
83 forest biodiversity which includes both above-ground plant diversity and
84 below-ground soil diversity (McGuire et al., 2015), resulting in potentially
85 far-reaching effects on forest multifunctionality (Seidl et al., 2017; Sommerfeld et al.,
86 2018).

87 As the forest recovery proceeds from the post-logging disturbance, subsequent
88 forest biomass recovers when emerging trees grow to occupy the gaps created by the
89 felled trees, and hence, the loss of forest biomass can be compensated if the forests
90 are left to recover, primarily depending on the magnitude of disturbance intensity
91 (Piponiot et al., 2016). Existing theories have mixed predictions for how the whole
92 functions of a community changes during secondary succession. For instance,
93 MacArthur's minimisation principle suggests that more mature and late-stages
94 communities should become more efficient by minimizing energy wastage, thereby
95 maximizing ecosystem functions (MacArthur, 1984). However, a recent study

96 demonstrated that mid-stage communities could be more effective at utilizing
97 resources (Ghedini, Loreau, White, & Marshall, 2018).

98 Meanwhile, most of the current studies investigated a lens of human-driven
99 disturbance impacts to focus on either a single or narrow set of biodiversity attributes
100 and ecosystem functions (Le Provost et al., 2020; Newbold et al., 2016). Ample
101 previous work showed that higher species richness could support multiple forest
102 ecosystem functions simultaneously (multifunctionality hereafter; EMF)(Felipe-Lucia
103 et al., 2018; Gamfeldt et al., 2013). However, the diversity of phenotypes (functional
104 trait diversity) and evolutionary lineages (phylogenetic diversity), rather than the
105 number and abundance of species, could also best predict EMF (Gross et al., 2017; Le
106 Bagousse-Pinguet et al., 2019; Yuan et al., 2020), either because functionally distinct
107 species promote the overall resource use efficiency (i.e. the niche complementarity
108 effect) or by including species that strongly influence ecosystem functioning (i.e. the
109 selection effect) (Loreau & Hector, 2001; Tilman, 1997). Besides, stand structural
110 attributes, such as individual tree size (diameter and/or height) inequality among and
111 within species, could have key implication for the functioning of forest ecosystems
112 (Ali, 2019), by enhancing above-ground light interception and utilization and
113 promoting production efficiency (Gough, Atkins, Fahey, & Hardiman, 2019). In
114 contrast, the functional identity of dominant species, rather than the diversity per se, is
115 often viewed as the main driver of ecosystem functioning (Prado-Junior et al., 2016;
116 Tobner et al., 2016), following the mass ratio hypothesis (Grime, 1998). Ultimately,
117 below-ground organisms, such as soil microbes, represent a large fraction of

118 terrestrial diversity regulating key biogeochemical processes such as nutrient cycling
119 and litter decomposition (Van Der Heijden, Bardgett, & Van Straalen, 2008), and
120 hence, sustaining EMF (Manuel Delgado-Baquerizo et al., 2020; Wagg, Bender,
121 Widmer, & van der Heijden, 2014; Yuan et al., 2020). Yet, we still lack an integrative
122 framework aimed at better understanding how multiple attributes of biodiversity, - the
123 richness and abundance of species (taxonomic diversity), the presence of different
124 evolutionary lineages (phylogenetic diversity), the variety of growth forms and
125 resource-use strategies (functional diversity), and the inclusion of above- and
126 below-ground compartments -, and multiple ecosystem functions (J. E. K. Byrnes et
127 al., 2014) are impacted by human disturbances. This largely hampers our ability to
128 improve the scientific understanding of the relationships between biodiversity and
129 ecosystem functioning to formulate sustainable conservation and management
130 policies in the context of global anthropogenic change (Balvanera et al., 2006;
131 Soliveres et al., 2016).

132 Here, we used a unique dataset of over 22,000 temperate forest trees belonging
133 to 81 species from 260 plots within 11 permanent plots (i.e. sites) to investigate how
134 multiple attributes of above- (i.e. taxonomic, phylogenetic and functional diversities,
135 and stand structure) and below-ground (i.e. soil bacteria and soil fungi) biodiversity
136 simultaneously influence forest EMF under post-logging disturbances. We also
137 considered multiple climate factors as potential drivers of biodiversity and EMF. We
138 address the following questions: 1) Do nearly undisturbed mature forests exhibit the
139 highest EMF compared with the other disturbed forests, following the MacArthur's

140 (1984) minimisation principle? 2) Do the multiple attributes of biodiversity have
141 differential effects on EMF? and 3) Are the effects of post-logging disturbance on
142 forest EMF equally mediated by above- and below-ground biodiversity pathways?
143

144 **Materials and Methods**

145 *Study sites and field inventories*

146 The study was conducted in temperate forests from the Changbai Mountain (40°54' to
147 44°03'N, 124°47' to 130°09'E), located in Liaoning and Jilin Provinces in
148 Northeastern China (Fig. S1A in Appendix A). The region is characterized by a
149 temperate continental climate with long cold winters and warm summers. Mean
150 annual temperature and precipitation are 2.8 °C and 700 mm, respectively. The
151 dominant vegetation type is a mixed forest dominated by the broad-leaved Korean
152 pine (*Pinus koraiensis*), with high productivity compared to other forests from the
153 same latitude (Stone, 2006). These forests are also hotspots of diversity and home
154 numerous emblematic, but endangered species such as the Siberian tiger (*Panthera
155 tigris longipilis* L.) and ginseng (*Panax ginseng* C.A. May) (Shao, Schall, &
156 Weishampel, 1994). The soils are classified as the Alfisol according to the US soil
157 taxonomy (Yang & Li, 1985). All studied sites have been protected from intensive
158 human disturbance since 1998, as a result of the implementation of a Natural Forest
159 protection. Thus, forests recovering from disturbances include stands with different
160 successional stages in the study area (Chen et al., 2014).

161 Eleven forest permanent plots (> 0.8 ha in size) were established in 2012 and

162 2013 (see Table S1 for details), and have been re-inventoried after five years
163 following a standard field protocol (Yuan et al., 2018). The elevation ranged between
164 653 and 1020 m.a.s.l.. Soil pH ranged between 5.4 and 7.1 (Table S1). Within each
165 plot (Fig. 1B in Appendix A), all individual trees with a DBH \geq 1 cm in contiguous
166 20 \times 20 subplots were tagged, identified, and measured following a standard field
167 protocol (Hao, Zhang, Song, Ye, & Li, 2007). Their geographical coordinates of all
168 individual trees were also recorded. A total of 22,766 individuals belonging to 81
169 species, 46 genera, and 26 families were recorded (Yuan et al., 2018).

170

171 *Quantifying disturbance intensity and climate variables*

172 The disturbance intensity of each plot was evaluated by counting the number of tree
173 stumps that had been removed in the field using a chainsaw in the 1990s (Kahl &
174 Bauhus, 2014). In addition, the official records of the Local Forestry Bureau, Jilin and
175 Liaoning Provinces were examined to collect the relevant selective logging data.
176 Collectively, plots were primarily classified into three disturbance intensity levels,
177 according to the partial harvesting (e.g., thinning, selective harvesting): relatively low
178 (<10%), medium (10-20%), and high (20~30%) disturbance. Plots with a low
179 disturbance level were distributed in the core zone of the Changbai Mountain Nature
180 Reserve (Fig. 1), which was established in 1960 and is part of the World Biosphere
181 Reserve Network under the Man and the Biosphere Project in 1980 (Shao et al., 1994).
182 Plots with medium and high disturbance levels were primarily located around the
183 residential area.

184 We also considered 19 climate variables as potential drivers of EMF, i.e., annual
185 mean temperature, mean diurnal range, isothermality, temperature seasonality,
186 maximum temperature of the warmest month, minimum temperature of the coldest
187 month, temperature annual range, mean temperature of wettest quarter, mean
188 temperature of driest quarter, mean temperature of warmest quarter, mean temperature
189 of coldest quarter, annual precipitation, precipitation of wettest month, precipitation
190 of driest month, precipitation seasonality (coefficient of variation), precipitation of
191 wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and
192 precipitation of coldest quarter. These climate variables were collectively extracted
193 from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), with
194 records from 1970 to 2000 at a 30-arc second spatial resolution (~1 km²).

195

196 ***Quantifying above- and below-ground biodiversities***

197 We quantified the taxonomic attributes of aboveground forest diversity using the
198 species richness (S) and Shannon-Wiener diversity indices of tree species (H_S). We
199 built up a supertree for all the trees occurred using online software of Phylomatic
200 (<http://www.phylodiversity.net>) which includes updated time-calibrated branch length
201 of seed plants combining multigene molecular and fossil data (Zanne et al., 2014).
202 Based on the obtained phylogenetic tree, we calculated 1) the Faith's phylogenetic
203 diversity index (PD_F), which quantifies the total length of all branches connecting
204 trees in a given subplot (Faith, 1992), and 2) the phylogenetic species variability (PSV)
205 reflecting how phylogenetic relatedness decreases the variance of a hypothetical

206 neutral trait (Helmus, Bland, Williams, & Ives, 2007). We also investigated the role of
207 functional identity and diversity on EMF by computing the community-weighted
208 mean (CWM) of trait values and the functional dispersion index (FD), respectively.
209 The two indices were weighted by the species' relative basal area within a subplot.
210 Functional traits included maximum tree height, wood density, leaf phosphorus
211 content (LPC), leaf nitrogen content (LNC), specific leaf area (SLA) and leaf area
212 (LA), which are related to life-history and nutrient and water-use efficiencies
213 (Pérez-Harguindeguy et al., 2013) (Appendix B). We also quantified the stand
214 structural diversity (H_D), using the Shannon-Wiener diversity indices of tree size
215 variations (i.e., tree DBHs) using 2 cm DBH as a discrete class (Ali et al., 2016).
216 Meanwhile, individual size inequality (CV_D) was quantified as the coefficient of
217 variation for tree DBH within each subplot, as a proxy for variation in overall tree
218 size. The variability in DBH within natural forests captures the degree of complexity
219 in multilayered stand structure in terms of light capture and use by component species
220 and interacting individuals (reviewed by Ali, 2019).

221 To evaluate the soil fungal and bacterial diversities, we randomly selected two
222 sampling points from the four midpoints between central point and corners in each 20
223 × 20m subplot in August 2018 (Fig. S1C). Five soil cores (3.8 cm diameter, 10 m
224 deep) at each sampling point were collected, pooled and brought to the laboratory for
225 analyses. Each soil sample was further divided into two parts: one for soil microbial
226 diversity measurements (i.e. bacteria and fungi), and the other for soil nutrient
227 analyses after removing roots and stones and air-dried for 24 h. All obtained values

228 were averaged to represent mean soil microbial diversity per subplot. For the
229 calculations of Shannon-Wiener diversity indices of soil fungi and bacteria, samples
230 were rarified to 3,000 sequences for bacteria and 2,200 sequences for fungi per soil
231 sample. Summary of diversity variables is provided in Table S1 in Appendix A. More
232 details about the measurements of plant functional traits and soil microbes are
233 provided in Appendix B.

234

235 ***Quantifying ecosystem multifunctionality (EMF)***

236 We quantified the EMF of the studied forests using nine key functions, i.e., (1) coarse
237 woody productivity (CWP), (2) aboveground biomass of wild edible plants (AGB_w),
238 (3) soil organic carbon density (SOD), (4) litter layer biomass (B_L), (5) water holding
239 capacity of litter layer (WHC_L), (6) water holding capacity of the soil (WHC_s), (7)
240 soil available nitrogen (AN), (8) soil available phosphorus (AP), and (9) soil available
241 potassium (AK) (Table S1 in Appendix A).

242 Coarse woody productivity (Mg ha⁻¹ yr⁻¹) was estimated by summing biomass
243 growth and recruitment rates, which were calculated as the increment of stems alive in
244 the last and first inventories, and the biomass of stems recruited into DBH ≥ 1 cm
245 between the first and last forest inventories, respectively (Yuan et al., 2019). For the
246 quantification of the aboveground biomass of wild edible plants, we first recognized
247 medicinal and edible shrub species according to the Flora Reipublicae Popularis
248 Sinicae (Hong & Blackmore, 2015), and then the mean aboveground biomass stock
249 (Mg ha⁻¹) of wild edible plants was quantified using specific species allometric

250 models (He, Kang, Fan, Gao, & Feng, 2011). Soil organic carbon density (kg m^{-2}) of
251 the 0-10 cm layer was calculated based on the formula $C_d = (1 - \theta_i) \times \rho_i \times 0.58 \times$
252 c_i , where θ_i is gravel (>2 mm) content at sample location i (%), ρ_i is soil bulk density
253 in the surface layer (g cm^3), and c_i is organic matter content in the i th soil sample (g
254 kg^{-1}).

255 Litter biomass (Mg hm^{-2}) was determined through the collection of the intact
256 litter layer above soil mineral horizons with a hand spade, after removing the surface
257 dried twigs and herbs. The water-holding capacity (WHC, Mg hm^{-2}) of litters and
258 soils were determined using full drainage methods (Naeth, Bailey, Chanasyk, & Pluth,
259 1991). Soil N (g kg^{-1}) was determined following the Kjeldahl method. Soil P (g kg^{-1})
260 was measured by molybdate colorimetry, after digestion in $\text{H}_2\text{SO}_4\text{-HClO}_4$. Total K (g
261 kg^{-1}) was derived using atomic absorption spectrometry. Available N was alkali
262 digested and was detected using hydrochloric acid titration method, whereas available
263 P was extracted following the method of Mehlich 1 (Nelson, Mehlich, & Winters,
264 1953). Soil available K was obtained with detection by atomic absorption
265 spectrometry (AAS). Please see detailed measurement approaches in Appendix B.

266 All individual functions were z -scored (standardized deviates) and averaged to
267 calculate the forest ecosystem multifunctionality index (EMF_A) (J. E. K. Byrnes et al.,
268 2014). We also evaluated whether multiple functions are simultaneously performing
269 at a high level using the multiple threshold approach, which calculates the number of
270 functions that reach a given threshold (i.e. the percent of the maximum value of each
271 of the functions measured in the dataset). This maximum is defined as the mean of the

272 five highest values for each function observed across all study plots. We used
273 multifunctionality-threshold values of 25% (EMF_{T25}), 50% (EMF_{T50}) and 75%
274 (EMF_{T75}).

275

276 *Statistical analyses*

277 We first conducted a principal component analysis (PCA) to reduce the
278 multicollinearity in CWM indices and climate variables, separately. The result
279 indicated that the first axis of PCA on CWM indices (CWM_{PC1}) explained 56.9% of
280 the total variation in CWM variables, mainly reflecting taller trees (high CWM of
281 height) but lower CWM of SLA and LNC (i.e., conservative strategy). The first axis
282 of PCA on climate variables ($Clim_{PC1}$) accounted for 67.1% of the variation
283 representing increasing temperature and precipitation gradients (Table S2).

284 We tested the effects of disturbance on EMF and individual functions separately,
285 as well as on above- (i.e. taxonomic, phylogenetic, functional and stand structure) and
286 below-ground (i.e. soil bacterial and fungal diversity) diversity indices using two-way
287 ANOVA models. A Post-hoc Tukey's test was used to assess the significant
288 differences among disturbance levels.

289 We used multiple linear regression models to evaluate the effects of the multiple
290 predictors considered on EMF. However, before conducting regression analysis, we
291 removed the highly correlated predictors (i.e., $r > 0.7$), such as H_S and PD, H_D and
292 CV_D , to avoid multicollinearity issues (see Fig. S2). Hence, nine variables including
293 five above-ground diversity indices (H_S , PD_F , FD, CV_D , and CWM_{PC1}), two

294 below-ground diversity indices (H_B and H_F), one composite climate variable ($Clim_{PC1}$),
295 and disturbance levels were included into the multiple regression models for
296 predicting EMF. The disturbance levels were treated as an ordinal categorical variable
297 (i.e. a regular numeric variable) and were coded as 1 (low), 2 (medium), and 3 (high).
298 Since all predictors and response variables were standardized after min-max
299 normalization, an analogue of the variance decomposition analysis was applied to
300 obtain the relative importance of each predictor on a comparable scale, which can be
301 simply calculated as the ratio between its standardized regression coefficient and the
302 sum of all coefficients, and expressed in % (Le Bagousse-Pinguet et al., 2019). The
303 obtained relative importance of predictors was grouped into five identifiable variance
304 fractions: (i) above-ground diversity, (ii) below-ground diversity, (iii) climate, (iv)
305 disturbance levels and (v) unexplained variance.

306 Finally, we used a piecewise structural equation modeling (pSEM) to investigate
307 direct and biodiversity-mediated effects of disturbance intensities on the averaged
308 EMF-index, EMF-thresholds and individuals ecosystem functions. We used site (i.e.
309 11 plots) as a random factor in pSEM. Since we had multiple candidate variables to
310 use in pSEM, we included those variables of above- and below-ground diversity
311 which had the highest standardized effect on EMF in multiple linear regression
312 models. The model fit of pSEM was assessed using the Fisher's C statistic, i.e., the
313 model was considered to have adequate fit to the data when the model had a Fisher's
314 C statistic with $P > 0.05$ (Shiple, 2009). The conditional (R^2_c) and marginal R^2 (R^2_m)
315 were calculated for each of the dependent variables (Nakagawa & Schielzeth, 2013).

316 We computed the *Pearson* correlations between pairs of individuals functions
317 and their relationships with EMF_A , aiming to assess the synergies (positive) or
318 trade-offs (negative) between forest functions. All data analyses were conducted in R
319 3.6.0 (R Development Core Team, 2019). Phylogenetic and functional diversity
320 indices were calculated using the *picante* (Kembel et al., 2010) and *FD* packages
321 (Laliberte & Legendre, 2010), respectively. EMF indices were calculated using the
322 *multifunc* package (J. Byrnes, 2014). Multiple linear mixed models and pSEM
323 analyses were performed in *nlme* (Pinheiro et al., 2017) and *piecewise SEM*
324 (Lefcheck, 2016) packages, respectively.

325

326 **Results**

327 Highly disturbed plots exhibited the highest EMF, even at higher thresholds (Fig. 1A).
328 In addition, five of the nine individual functions (i.e., SOD, WHC_S , AN, AP, and AK)
329 measured in highly disturbed plots were significantly higher than in low disturbed
330 plots. In contrast, AGB_W was higher in low disturbed plots, whereas CWP, B_L , and
331 WHC_L did not show significant differences among the three levels of disturbance
332 (Fig. S3). As such, plant species richness (S), Shannon-Wiener diversity (H_S), Faith's
333 phylogenetic diversity (PD_F), and soil microbe diversity (H_B & H_F) were higher in
334 highly disturbed plots, whereas functional trait diversity (FD) and identity (CWM_{PC1})
335 and stand structural attributes (H_D and CV_D) were higher in low disturbed plots (Fig.
336 1B).

337 The multiple linear regressions models explained 68%, 56%, 58% and 26% of

338 the variations in EMF_A , EMF_{T25} , EMF_{T50} and EMF_{T75} , respectively (Fig.2). The
339 biodiversity indices explained 45% on average [26—58%] of the variations in EMF,
340 while climate and disturbance together explained on average 7% [0.4—15%]. The
341 cumulative above-and below-ground diversity accounted for about 26.0%
342 [17.5—39.4%] and 18.9% [8.1—28.8%] of the variations in EMF, respectively.
343 Individual tree size variation (CV_D) and soil bacterial diversity (H_B) were selected as
344 the best predictors of above- and below-ground diversity, explaining up to 11.3%
345 [4.6—19.7%] and 6.0% [2.0—9.9%] of the accounted variance, respectively (Fig.2).
346 Since there was no significant relationship between composite climate factors
347 ($Clim_{PC1}$) and EMF, and hence, we did not include $Clim_{PC1}$ in the pSEM analysis
348 (Fig.2).
349 The tested pSEM models showed that disturbance had significant positive direct
350 effects on EMF, irrespective of the EMF threshold considered (Fig. 3). However, our
351 models also showed opposite indirect effects of disturbances on EMF, highlighting
352 the occurrence of contrasting biodiversity-mediated pathways. While both above- and
353 belowground diversity attributes had direct positive effects on EMF, their mediating
354 effects were in partial contrast, i.e., negative for aboveground diversity and positive
355 for belowground diversity. Furthermore, the negative mediating effect of
356 aboveground diversity on EMF increased with higher thresholds ($\beta = 0.02$ to 0.19),
357 highlighting a stronger negative pathway occurring when functions performed at
358 higher rates (Fig. 3). In order to complement the results from main pSEMs (Fig. 3),
359 the correlation between forest functions is provided in Fig. S4, whereas pSEMs for

360 tested single forest functions are provided in Fig. S5.

361 **Discussion**

362 Our study offers an integrative framework aimed at exploring how multiple attributes
363 of above-ground (taxonomic, phylogenetic, functional, and stand structure) and
364 below-ground (soil bacterial and fungal diversities) biodiversities simultaneously
365 influence the EMF of temperate forests recovering from post-logging disturbances.
366 The effects of biodiversity on EMF were two-fold higher than those of both climate
367 and disturbances together, expanding to previous findings on individual function such
368 as productivity to EMF (Duffy et al. 2017). However, our results also show evidence
369 for divergent above- and below-ground biodiversity pathways in mediating
370 disturbance impacts on EMF. Hence, this study highlights the necessity of considering
371 the multi-dimensional role of biodiversity to better grasp its complex effects on the
372 functioning of terrestrial ecosystems in a changing world.

373 Maximum EMF was found in disturbed forests rather than relatively undisturbed
374 mature forests. Our result thus departs from the MacArthur's (1970) minimisation
375 principle, suggesting that more mature and late-stage communities should become
376 more efficient by minimising energy wastage and thus maximizing ecosystem
377 functioning. Rather, our result reminds the recent study of (Ghedini et al., 2018) who
378 observed that mid-stage communities could be more efficient at utilizing resources.
379 Specifically, forest canopy removal by sawlogs and timber harvesting indeed could
380 result in tree density and forest biomass decline (Yuan et al., 2018), but our finding
381 shows that relatively high disturbed forests could promote EMF by increasing soil

382 carbon storage, nutrient availability, and water retention capability, and hence,
383 supporting the notion that suitable forest practice such as thinning could achieve the
384 best combination of high wood yield and nutrients reserves (Gong, Tan, Liu, & Xu,
385 2021; Schwaiger, Poschenrieder, Biber, & Pretzsch, 2019; Thornley & Cannell,
386 2000). One possible mechanistic explanation is that timber harvest will lead to more
387 plant residues entering the soil, and more light and precipitation to reach the floor,
388 which in turn may increase the litter decomposition rate and nutrient cycling (Huang,
389 Li, & Su, 2020; Simonin, Kolb, Montes-Helu, & Koch, 2007). However, there was no
390 significant difference in woody production among the three levels of disturbance,
391 implying that subsequent forest biomass recovers when emerging trees grow to
392 occupy the gaps created by the felled trees, and hence, the loss of forest biomass can
393 be compensated if the forests are left to recover, primarily depending on the
394 magnitude of disturbance intensity (Piponiot et al., 2016). Collectively, compared
395 with the relative pristine or unmanaged stands, the soil physicochemical properties,
396 such as organic matter and available nitrogen, maximal water retention, and total
397 porosity, of natural mixed stands with low and medium management intensities were
398 significantly increased after 10 years restoration (WU et al., 2008).

399 Stand structural diversity was the main above-ground biodiversity attribute to
400 promote EMF, particularly at higher multifunctionality-thresholds. This result
401 confirms the key role of stand structure for forest EMF, as previously shown for
402 individual functions (e.g. productivity) (Ali et al., 2016; Gough, Atkins, Fahey,
403 Hardiman, & LaRue, 2020). Forests with complex stand structure attribute such as

404 higher tree size variations, mainly reflecting the degree of heterogeneity in vegetation
405 density, could sustain higher EMF likely through optimizing space, resources and
406 understory microclimatic conditions (Hardiman et al., 2013; Jucker, Bouriaud,
407 Coomes, & Baltzer, 2015). For instance, higher individual size inequality (CV_D)
408 could promote heterogeneity in branch and leaf density and morphology, resulting in
409 higher light use efficiency (Ali, 2019; Yachi & Loreau, 2007). For instance, our
410 analysis also indicates that more complex communities could lead to faster shrub
411 species growth and biomass accumulation (Fig.S5B).

412 Considering multiple above-ground biodiversity attributes showed contrasted
413 responses to post-logging disturbance, ultimately leading to positive, neutral and
414 negative effects on EMF (Le Bagousse-Pinguet et al., 2019). Although timber
415 harvesting could cause a reduction in stand structural diversity due to large stems
416 removal, it could promote species diversity by creating forest gaps in which higher
417 light resources might be available for saplings or colonizing seedlings (Molino &
418 Sabatier, 2001). Gaps could promote higher tree species diversity through the niche
419 partitioning of more greatly contrasting and frequently created resources and/or
420 density effect (Sipe & Bazzaz, 1995). These gaps are expected to be occupied by
421 early-successional, light-demanding species (Poorter & Bongers, 2006). Generally,
422 forest gaps are also expected to be primarily filled by the inclusion of by chance
423 species rather than by best-adapted species because of the stochastic availability of
424 gaps and limited recruitment of juveniles leading to slow competitive exclusion and
425 enable the coexistence of more plant species (Brokaw & Busing, 2000). Interestingly,

426 our results show that the disturbance-induced increase in species richness does not
427 lead to higher functional trait diversity, implying the high functional redundancy in
428 the above-ground species composition. Therefore, ignoring the contrasting effects of
429 land-use impacts on a variety of biodiversity attributes, such as taxonomic,
430 phylogenetic, functional, and stand structural diversity, will likely bias our ability to
431 predict the functional consequences of biodiversity decline (Le Bagousse-Pinguet et
432 al., 2019). In contrast of the above-ground biodiversity attributes considered, high soil
433 bacterial diversity consistently promoted EMF irrespective of the
434 multifunctionality-threshold considered, while soil diversity is often viewed to drive
435 EMF mainly at low thresholds (M. Delgado-Baquerizo et al., 2016; Wagg et al.,
436 2014). Soil bacteria diversity is a main driver for maintaining EMF in many terrestrial
437 ecosystems (M. Delgado-Baquerizo et al., 2016; Wagg et al., 2014; Wang et al., 2019;
438 Yuan et al., 2020) through maintaining key ecological processes such as nutrient
439 cycling and decomposition (Manuel Delgado-Baquerizo et al., 2020; Van Der Heijden
440 et al., 2008). A recent global survey and microcosm experiment revealed that the
441 positive impact of soil biodiversity on EMF can be maintained across biomes after
442 accounting for important ecosystem factors such as climate and plant attributes
443 (Manuel Delgado-Baquerizo et al., 2020). Higher diversity of soil organisms, such as
444 bacteria and fungi, are the major controllers of EMF by fine-tuning nutrient supply
445 and the distribution of resources, thereby promoting high rates of material processing
446 in terrestrial ecosystems which supplies substrate to other important soil organisms
447 involved in nutrient cycling and releases soil nutrients to above-ground communities

448 (Maron et al., 2018; Wardle et al., 2004). One of the important findings of this study
449 is that the relative contribution of stand structural attributes on EMF increased with
450 the increasing thresholds levels of EMF, which can be viewed as a superior predictor
451 of ecosystem functioning, as has been shown for individual functions (e.g.
452 productivity) (Ali et al., 2016; Gough et al., 2020). Forests with complex stand
453 structure attribute such as higher tree size variations, mainly reflecting the degree of
454 heterogeneity in vegetation density, sustaining higher EMF likely through optimizing
455 space and understory microclimatic conditions (Hardiman et al., 2013; Jucker et al.,
456 2015). As the individual size inequality (CV_D) increases, niche differentiation among
457 and plasticity within trees probably augment heterogeneity in branch and leaf density
458 and morphology, resulting in more efficient light intercept and utilize across a range
459 of light conditions (Ali, 2019; Yachi & Loreau, 2007). For instance, our analysis also
460 indicates that more complex communities could lead to faster shrub species growth
461 and biomass accumulation (Fig.S5B).

462 Our study provides observational evidence that post-logging disturbances (from
463 low to high level) could enhance forest multifunctionality and below-ground
464 biodiversity, while simultaneously declining above-ground biodiversity. While certain
465 attributes of above-ground plant diversity can impede EMF, above-ground stand
466 structural and soil microbial diversity attributes appears as important biodiversity
467 facets to promote forest ecosystem multifunctionality. Hence, managing forest
468 ecosystems to maximize above-ground biodiversity, such as higher species richness,
469 may not necessarily maximize a particular subset of functions. In other words,

470 ecosystem service provisioning cannot be solely replaced by the protection of a high
471 above-ground stand diversity (Felipe-Lucia et al., 2018; Meyer et al., 2018). This
472 study underlines that maintaining multifunctional forests through a suitable level of
473 management or disturbance intensity may allow for higher biodiversity and ecosystem
474 services on which human beings are dependent. Hence, we argue that the inclusion of
475 soil biodiversity and disturbance levels should be considered as decisive components
476 of the management decision-making policies (Manuel Delgado-Baquerizo et al.,
477 2020; Huang et al., 2020).

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693

694 **Figures captions**

695 **Fig 1.** The effect of disturbance intensity on forest ecosystem multifunctionality (A)
696 and above-and below-ground biodiversity (B). Ecosystem multifunctionality includes
697 averaged (FEM_A), 25% (FEM_{T25}), 50% (FEM_{T50}) and 75% threshold levels (FEM_{T75}).
698 Above-ground diversity includes species richness (S), Shannon-Wiener diversity of
699 tree species (H_S), Faith's phylogenetic diversity (PD_F), phylogenetic species
700 variability (PSV), functional dispersion of functional traits (FD), the first PCA axis of
701 the community-weighted mean of six functional traits (CWM_{PC1}), Shannon-Wiener
702 diversity of tree size variation (H_D), and the coefficient of variation for tree DBH
703 (CV_D); the below-ground diversity includes, Shannon-Wiener diversity of soil
704 bacteria (H_B), and Shannon-Wiener diversity of fungi (H_F). Different lowercase letters
705 within each panel indicate significant ($P < 0.5$) differences between treatment means,
706 after using Tukey's method to correct for multiple comparisons. Error bars represent
707 $\pm 1SE$.

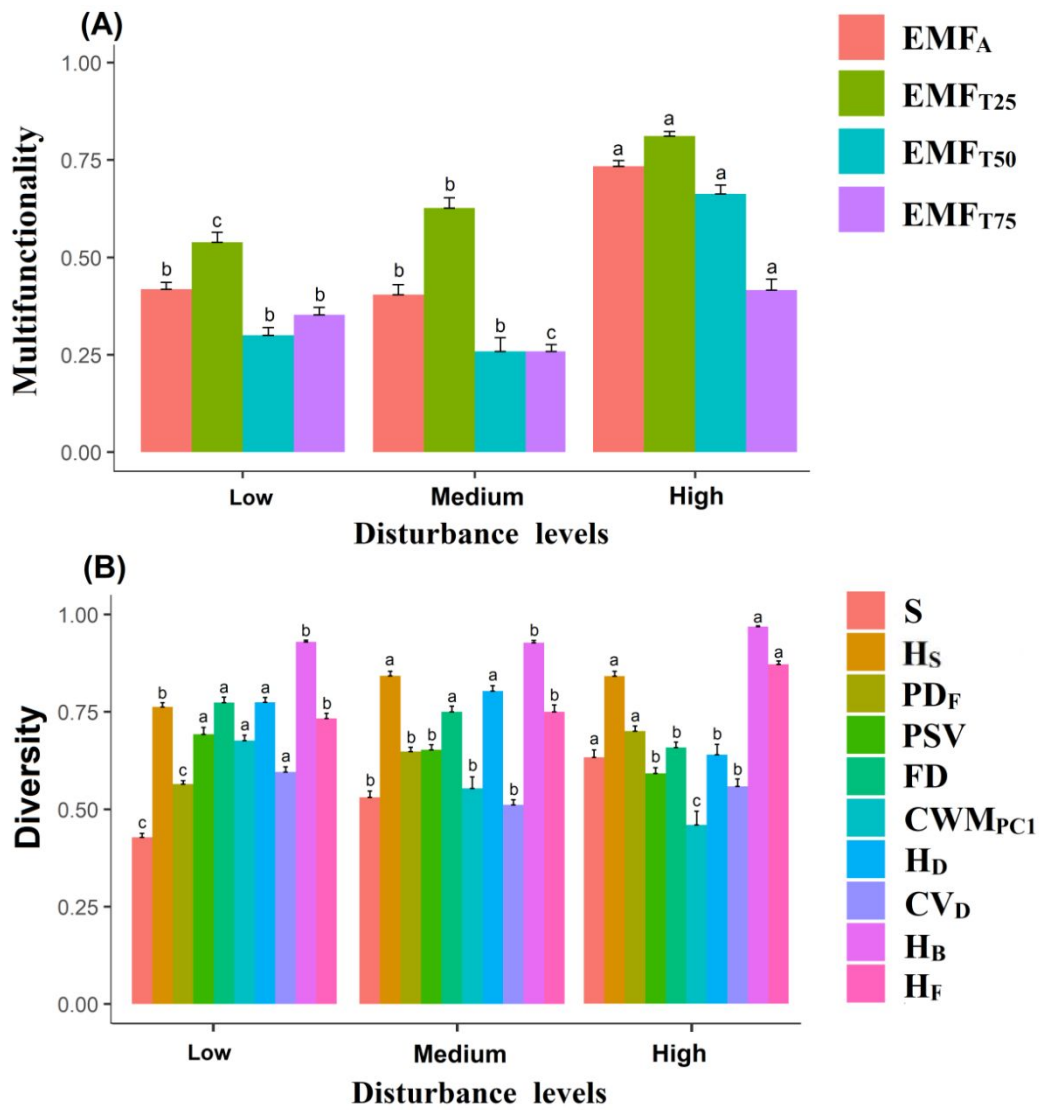
708 **Fig. 2.** Effects of post-logging disturbances, climate, and above- and below-ground
709 biodiversity on averaged ecosystem multifunctionality (A), 25% threshold-based (B),
710 50% threshold-based (C), and 75% threshold-based ecosystem multifunctionality (D).
711 Standardized regression coefficients of model predictors, the associated 95%
712 confidence intervals, and the relative importance of each factor (expressed as the
713 percentage of explained variance) are shown. The $adj.R^2$ of the models and the
714 P -value of each predictor are given as: * $P < 0.05$, ** $P < 0.01$. Dist, the disturbance
715 levels; $Clim_{PC1}$, the first axis of 19 climate variables, whereas other abbreviations are

716 explained in Fig. 1.

717 **Fig.3** Results from the piece-wise structural equation models (pSEMs) exploring the
718 direct and indirect effects of disturbance levels on forest multifunctionality at
719 averaged (A) and three threshold levels (B-D) via above-ground diversity and
720 below-ground diversity. Numbers adjacent to arrows are indicative of the effect size
721 of the relationship. Continuous and dashed arrows indicate positive and negative
722 relationships, respectively. For all relations, standardized regression coefficients and
723 significance are given (* <0.05 , ** <0.01). The width of the arrows is proportional to
724 the strength of path coefficients. R^2 denotes the proportion of variance explained and
725 model-fit statistics for each pSEM are given.

726

727 **Fig. 1**

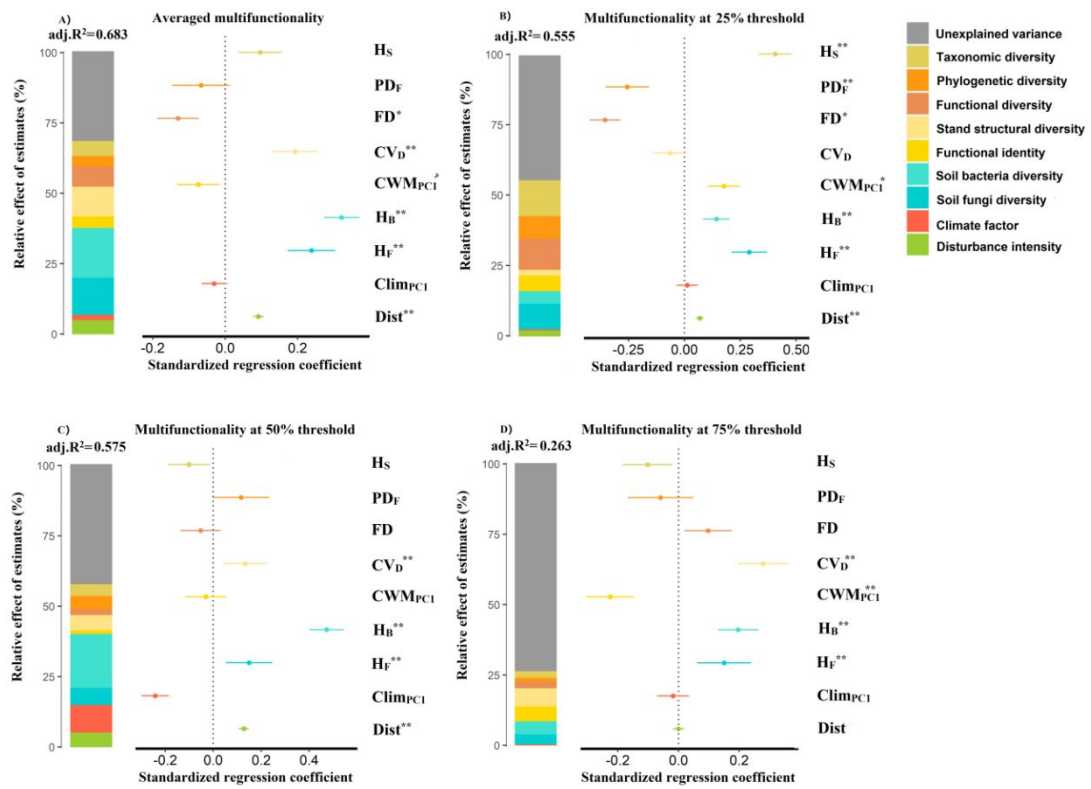


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730

731 **Fig. 2**

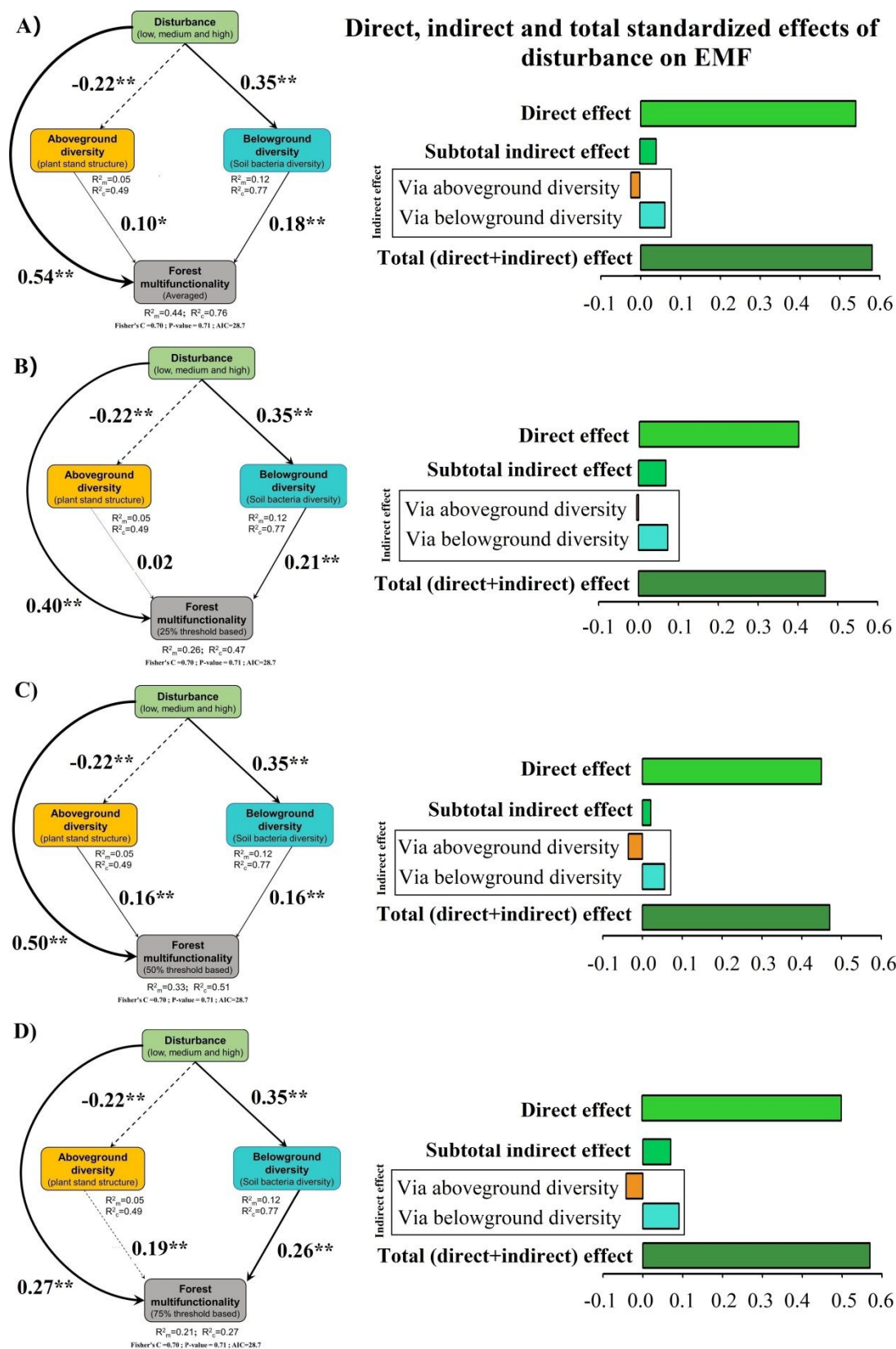


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734 **Fig. 3**



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