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RESEARCH ARTICLE

Evolutionary diversity impacts tropical forest biomass and productivity through disturbance-mediated ecological pathways

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Abstract

1. Significant research efforts have been made to uncover links between biodiversity and biomass productivity in forest ecosystems. However, the causal link between these two ecosystem components, and the underlying mediation role of disturbance, are yet poorly understood for hyper-diverse tropical forests, because multiple ecological mechanisms are sequentially or simultaneously in play, leading to contradictory results in observational studies.
2. Here, we introduce a novel framework for inferring the expected effects of evolutionary diversity on biomass stocks and productivity within forest ecosystems using observational field data. This framework involves an analytical decomposition of stand biomass into three key components: the number of trees, the mean size of trees and the mean wood density. Through this approach, we can distinguish structure- and compositional-based diversity effects, which likely have distinct ecological origins. We tested this framework in one of the oldest tropical forest experiments, where different levels of silvicultural disturbances were applied in the 1980s, with regular monitoring since then.
3. Our results revealed that disturbance history mediates the effect of evolutionary diversity on forest biomass dynamics and that several Biodiversity Ecosystem Function (BEF) relationships may be hidden behind the composite biomass variable. We specifically found an overall significant negative relationship between evolutionary diversity and biomass productivity soon after disturbances (~5–8 years), mostly via mean tree size, despite a positive evolutionary diversity

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effect on mean wood density. This result reflects that the productivity of disturbed forests is driven by a few dominant and disturbance-prone species with low wood density and large potential stature, and not by niche complementarity among species. However, these effects rapidly vanished with time, with non-significant overall effect of evolutionary diversity on productivity both ~30 years after disturbance and in the undisturbed plots.

4. *Synthesis*. By disentangling the effects of evolutionary diversity on the different components of forest biomass, our framework unveiled how evolutionary diversity impacts forest productivity through different ecological mechanisms, and suggests that it plays a major role, albeit mainly negative, only soon after a disturbance.

KEYWORDS
above-ground biomass, canopy packing, phylogenetic diversity, sampling effect, silviculture, tree-packing

1 | INTRODUCTION

Biodiversity ecosystem function (BEF) relationships aim to elucidate the ecological mechanisms underlying the impact of diversity on ecosystem functioning, such as productivity, stability and nutrient dynamics (Tilman et al., 2014). Specifically, understanding the importance of biodiversity in supporting biomass dynamics is critical for anticipating the impacts of biodiversity loss on the terrestrial carbon balance (Pan et al., 2011; Sullivan et al., 2017) and assessing potential co-benefits in conservation planning (Mori et al., 2021; Osuri et al., 2020). However, the causal link between these two ecosystem components has not yet been completely resolved for a range of ecosystems (van der Plas, 2019), such as hyper-diverse tropical forests, which constitute an ideal study case given their outstanding diversity and biomass stock.

Initial BEF models proposed the existence of a positive correlation between diversity and resource-use intensity (Loreau, 1998; Tilman et al., 1997). These theoretical studies were validated by experimental research conducted in simplified systems, where multispecies polycultures were shown to have higher biomass productivity than monocultures (Cadotte, 2013, 2017; Loreau & Hector, 2001). Despite the great contributions of these pioneering studies, the strength and direction of BEF relationships were found to vary strongly among natural communities (van der Plas, 2019). In particular, observational (non-manipulative) studies examining the direct influence of diversity on productivity and biomass accumulation have reported divergent results in forested ecosystems (Borges et al., 2021; Lasky et al., 2014; Morin, 2015; Morin et al., 2011; Satdichanh et al., 2018). Different ecological mechanisms are expected to generate positive associations between diversity and productivity. One important class of studies explores species niche differences and predicts that plant communities consisting of multiple species that occupy different niches can partition limited resources more efficiently, providing greater productivity than that expected from monocultures (Hector et al., 1999; Hooper & Dukes, 2004; Van de Peer et al., 2018). For instance, light is the main limiting resource in forests (Terborgh, 1985; Wright & van Schaik, 1994) and diverse communities are expected to better occupy different forest strata, leading to improved light interception, reduced competition and increased stand volume and productivity (Duarte et al., 2021; Guillemot et al., 2020). This more efficient use of the canopy space modifies the forest structure, allowing trees to pack more densely (Jucker et al., 2015) and is therefore hereafter referred to as 'tree-packing effects'. Another type of biodiversity effect on productivity is that hyper-diverse communities have a greater chance of containing species with high-performance traits that could become dominant (due to large fitness differences) and drive ecosystem functioning (Hector et al., 2002; Huang et al., 2020; Loreau & Hector, 2001) through the mass-ratio effect (i.e., biomass productivity driven by the functional identity of the most dominant species; Grime, 1998). This biodiversity effect is hereafter referred to as 'sampling effect' (previously also referred to as selection probability effects; Huston, 1997). However, the relative importance of the ecological mechanisms driving BEF relationships in natural communities remains largely unknown (Cavanaugh et al., 2014; Finegan et al., 2015; Grace et al., 2016; Luo et al., 2019).

Here, we assumed that diversity acts in forest biomass and productivity through different pathways and that their joint effects can be disentangled by disaggregating forest biomass into its components: the number of trees, the tree volume and the wood density. Most BEF studies indeed ignored the fact that there are several ways to build forest biomass at the stand level, that is, with a higher number of trees, with larger trees or with higher wood density. Because diversity may act separately and simultaneously on each of the biomass components through different ecological mechanisms, these different effects may add up to each other, potentially leading to confounding effects.

Previous studies conducted on forest ecosystems have suggested that the effect of diversity on biomass and productivity is context-dependent, because of differences in environmental and historical contexts (Van de Peer et al., 2018). In particular, forest disturbances cause shifts in species diversity and composition and generally reduce the mean wood density and volume in the short term, which alters competitive interactions between individuals and allows competitors to coexist where they would normally be excluded (Carreño-Rocabado et al., 2012; Slik et al., 2008). These shifts are mainly caused by increased light availability in the understory following forest structure modifications (Yamamoto, 1992), which may alter the BEF relationship observed in undisturbed communities. Given the rapid erosion of biodiversity (IPBES, 2019) and loss of undisturbed tropical forests (Vancutsem et al., 2021), it is important to understand if and how the relationship between diversity and ecosystem functioning is altered in second-growth tropical forests, which are currently estimated to represent half of the global tropical forests (FAO, 2020).

Quantitative information on species traits and phylogeny is known to better predict ecosystem functions than more commonly used metrics of diversity such as species richness (Potter & Woodall, 2014). Indeed, communities with functionally dissimilar species tend to have greater resource-use complementarity and reduced competition (van der Plas, 2019). In this regard, evolutionary distances are known to correlate with multidimensional phenotypic differences among species, because phylogenetic diversity encapsulates a wide range of information about species complementarity across space and time (Faith, 1992). Evolutionary diversity was even shown to be a better predictor of productivity than some easily measured, or 'soft', functional traits (e.g. specific leaf area, seed weight and height). This suggests that unmeasured traits that are significantly related to phylogenetic relationships, such as root architecture, root morphology, resource requirements or other critical physiological differences, could contribute to maximizing productivity (Cadotte et al., 2009; Tucker et al., 2018). Besides, experimental evidence also suggests that the effect of phylogenetic diversity on productivity is likely to be a result of increased functional complementarity among lineages (Cadotte, 2013; Huang et al., 2020). Indeed, many studies have revealed that phylogenetic diversity can explain ecosystem function (biomass accumulation), stability and community biomass productivity better than measures of species richness (Coelho de Souza et al., 2019; Lasky et al., 2014; Paquette et al., 2015; Potter & Woodall, 2014; Rodríguez-Hernández et al., 2021; Satdichanh et al., 2018; Yuan et al., 2020) and better than functional diversity (Flynn et al., 2011; Larkin et al., 2015) based on the hypothesis that relevant traits are phylogenetically conserved (Coelho de Souza et al., 2016; Srivastava et al., 2012).

Here, we used an experimental site established in 1982 in the Central African Republic to assess the effect of evolutionary diversity on forest biomass and productivity in different disturbance contexts. We specifically aimed to (1) disentangle the effects of diversity on different biomass components to better understand if and how different ecological mechanisms jointly determine the diversity-productivity relationship in natural tropical forests and (2) test whether historical disturbances influence the effect of diversity on biomass and biomass productivity. We predicted that the effect of diversity on biomass productivity varies between undisturbed and disturbed forests. In disturbed forests, overwhelming fitness differences could prevent complementarity due to the dominance of a few resource-acquisitive and highly productive species (Jucker et al., 2020; Reich et al., 2012; Tobner et al., 2016) while undisturbed forests are often characterized by more diverse tree communities that compete under resource-limiting conditions (Lohbeck, Poorter, et al., 2015; Pacala & Tilman, 2001).

2 | MATERIALS AND METHODS

2.1 | Building a conceptual model

To analyse the separate influence of diversity on each biomass component, we conceptualized plausible causal pathways in a structural equation model (SEM) based on theoretical considerations and prior empirical results. As a starting point, we used the approach developed by Vincent et al. (2014), in which the stand-level AGB (or $\mathrm{AGB}_{\mathrm{plot}}$) estimate, that is, the sum of all individual tree AGB estimates, is analytically disaggregated into three components: the number of trees (N) times the mean individual tree above-ground volume ($\mathrm{AGV} = \sum_i^N \mathrm{AGV}_i / N$, in m^3) times the mean volume-weighted wood density ($\mathrm{WD}_v = \sum_i^N \mathrm{AGV}_i \times \mathrm{WD}_i / \mathrm{AGV}$, in kg m^{-3}). After log transformation, we obtain the following additive model:

$$\log\left(\mathrm{AGB}_{\mathrm{plot}}\right) = \log(N) + \log(\mathrm{AGV}) + \log\left(\mathrm{WD}_v\right).$$

As an exact (analytical) relationship, this part of the SEM has known coefficient values of 1 between each component and $\mathrm{AGB}_{\mathrm{plot}}$ (no estimation is required here; Figure 1).

We argue that diversity could impact biomass through different ecological mechanisms involving different biomass components. Because these effects may add up to each other, their respective role in BEF relationships are often challenging to infer due to confounding effects. Here, disaggregating biomass and its components allows the comprehension of the dissociating independent diversity effect, such as the tree packing and the sampling effects, which are expected to act through different biomass components or set of components. The first effect of diversity, namely the 'tree-packing effect' would act on the community structure components of AGB (number of individuals and their mean above-ground volume). Indeed, the positive effect of diversity on canopy packing is often invoked as a mechanism that explains positive diversity–productivity relationships in forests as more diverse forests utilize canopy space more efficiently (Jucker et al., 2015; Morin et al., 2011). Here, we specifically argue that canopy packing can be increased by increasing the number of trees and/or their mean above-ground volume (Tatsumi & Loreau, 2023; Urgoiti et al., 2023). The second effect of diversity, the 'sampling effect' would operate on the composition of the tree community, more specifically through the mean wood density and the maximum potential size, as hyper-diverse communities have a greater chance of containing species with high-performance

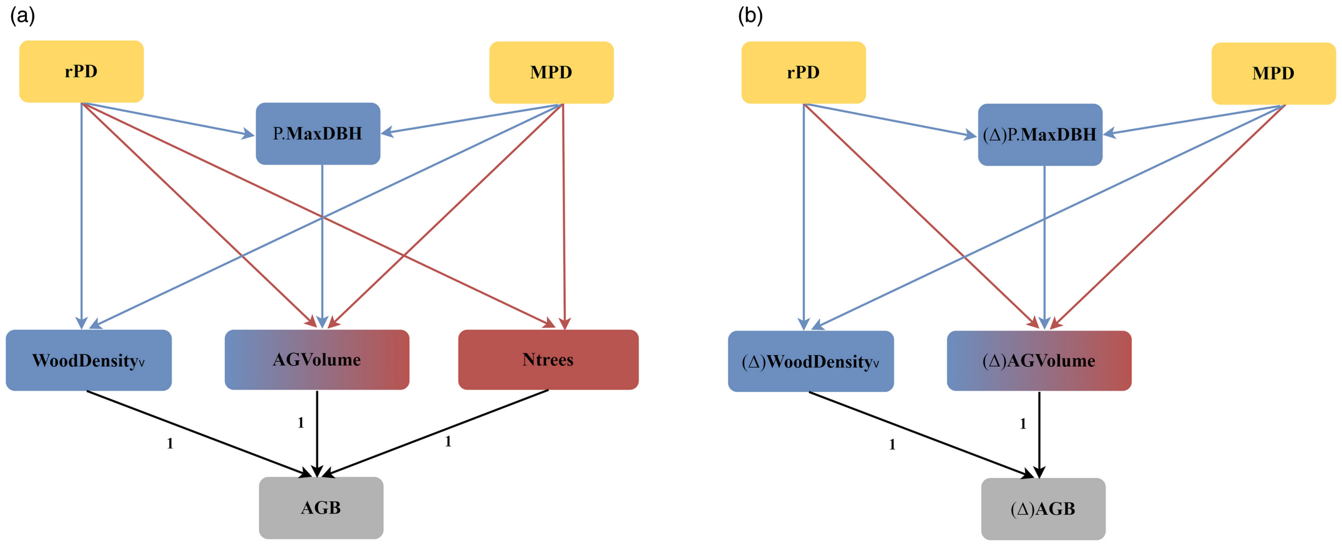

FIGURE 1 Conceptual model of the expected role of the sampling effect (blue paths) and the tree-packing effect (red paths) on AGB (a) and ΔAGB (b) components. AGB, log transformed above-ground biomass; AGV, log transformed mean individual above-ground volume; MPD, mean pairwise distance; Ntrees, log transformed number of trees; P.MaxDBH, potential maximum diameter; rPD, rarefied phylogenetic diversity; WD, log transformed mean wood density weighted by AGV; Δ, Net change.

traits. To understand the relative influence of these two potential effects, we designed two different pathways in our conceptual model (Figure 1). We considered evolutionary diversity metrics since they mirror diversification in species traits and have been shown to best capture BEF relationships (Cadotte, 2013; Coelho de Souza et al., 2019; Huang et al., 2020). To navigate the multitude of phylogenetic indices available in the literature, we adopted a two-step approach. Initially, we turned to the classification provided by Tucker et al. (2017), wherein 70 existing phylogenetic indices were organized into three main groups: how much, how different and how regular. Our focus was on the first two groups, which were expected to influence sampling and tree-packing effects in BEF relationships, respectively. Our final metric selection was then informed by an extensive review of the literature. We ultimately chose two metrics, namely Faith's phylogenetic diversity (PD; Faith, 1992) and the phylogenetic Mean Pairwise Distance (MPD; Webb et al., 2002). This selection was based on their widespread usage and demonstrated effectiveness in capturing biodiversity effects on productivity in both experimental studies (Cadotte, 2013; Huang et al., 2020) and observational studies (Lasky et al., 2014; Satdichanh et al., 2018). In forest ecosystems, the sampling effect of diversity would operate on functional traits that promote forest biomass, thus favouring hard-wooded or large tree species (Huston, 1997). Both metrics (wood density and potential maximum tree size) are here considered species-specific functional traits relevant to species standing biomass (Lohbeck, Lebrija-trejos, & Martínez-ramos, 2015; Pérez-Harguindeguy et al., 2013). Thus, we introduced in our SEM direct pathways from MPD and rPD (rarefied PD, see Section 2.4 below) towards log(WD_v), and indirect pathways towards log(AGV) through the mean maximum potential stem diameter weighted by tree basal area $P.MaxDBH = \sum_i P.MaxDBH_i \times BA_i / \sum_i BA_i$, where BA_i is the basal area of tree i and $P.MaxDBH_i$ is the potential maximum diameter that can be reached by the species to which tree i belongs, estimated as the 98th percentile of the observed DBH distribution per species in our dataset to avoid the effect of unrepresentative exceptionally large trees. On the other hand, the tree-packing effect represents the role of diversity in forest biomass and productivity in maximizing the number and the size of coexisting trees (Jucker et al., 2015; Morin et al., 2011; Tatsumi & Loreau, 2023; Urgoiti et al., 2023). Thus, we introduced direct pathways from MPD and rPD towards log(N) and log(AGV) in our SEM. The relationships representing the sampling and the tree-packing effects in our SEM are illustrated in blue and red, respectively, in Figure 1.

2.2 | Study sites and forest inventory data

The study was conducted at the M'Baïki Experimental Station (3°900′N, 17°930′E), located in the Lobaye Province of the Central African Republic, 110 km southwest of the capital of Bangui (Figure S1). The experimental site was established in 1982 in protected forests with no logging history (Gourlet-Fleury et al., 2013). The climate is humid tropical, with an average annual rainfall of 1700 mm and an annual average monthly temperature of 25°C (range of 19.6–30.2°C; WorldClim dataset; Fick & Hijmans, 2017). The plots are located within a 10 km radius on a large plateau (500–600 m a.s.l.) with a generally flat topography and deep ferritic soils, classified as acrisols (FAO Soils, 2014). The vegetation belongs to the northern margin semideciduous forest type (Réjou-Méchain et al., 2021).

We used forest inventory data from nine 4-ha (200 × 200 m) permanent plots established in 1982 in an old-growth forest to monitor the effects of silvicultural treatments (Gourlet-Fleury et al., 2013). A tenth 4-ha plot was available but discarded in the present study because it experienced a large fire event in 1983 and a second one in 1997 and floristic determination was not homogeneous with the other nine plots (Gourlet-Fleury et al., 2013). Based on preliminary vegetation surveys, plots were established in areas with similar vegetation types and topographies to minimize environmental effects such as soil fertility (often spatially associated with topography at the study scale). All trees with a diameter at breast height (DBH) ≥10 cm were individually marked, geo-referenced and botanically identified (94% at the species level). The plots have been monitored annually since 1982 (except for 1997, 1999 and 2001). Between 1984 and 1985, six plots were selectively logged: all trees from 16 timber species with a DBH ≥80 cm were harvested. Afterwards (1986–1987), three of the logged plots were additionally thinned, which consisted of poisoning all trees from non-timber species with a DBH ≥50 cm and systematically removing lianas to increase light penetration (Ouédraogo et al., 2011). Therefore, the nine 4-ha plots considered here were assigned to three different silvicultural treatments according to a random block design: control (three plots), logging (three plots) and logging-and-thinning (three plots), with removal of ~24% of the basal area per hectare in logging plots and ~36% in the logging-and-thinning plots. Each 4-ha plot was gridded into 20 × 20 m (0.04 ha) subplots from which 275 were excluded from the analysis due to fire events and an additional active removal of the entire population of *Musanga cecropioides* (as part of a different experiment), leading to a total sample of 625 subplots: 186 control, 218 logging and 168 logging-and-thinning. We also excluded subplots with fewer than 15 trees to ensure robust inferences, that is, from 16 to 53 extra subplots, depending on the census date considered. The choice of subplot size was based on previous findings where diversity-biomass relationships only occurred at a fine scale (0.04 ha; Chisholm et al., 2013; Sullivan et al., 2017). The highest probability of sampling species with high maximum diameter and wood density (therefore capturing the sampling effect) was found at 20-m resolution in a pantropical study (Sullivan et al., 2017), and individual biotic interactions, such as competition, are also expected to manifest at such a fine scale (Wang et al., 2010).

2.3 | Above-ground biomass disaggregation and net biomass change

The above-ground biomass (AGB) of individual trees was calculated using allometric equation 5 of Chave et al. (2014): $AGB = 0.0559 \times (WD \times DBH^2 \times H)$, which incorporates measures of DBH (in cm), height (H, in m) and species wood density (WD, in g cm^{-3}). In this equation the exponent was constrained to one, facilitating analytical disaggregation. This equation has been widely used and referenced in biomass studies. Wood density was extracted from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009) using the BIOMASS R package (Réjou-Méchain et al., 2017). When wood density was not available at the species level (33.2% of the individuals), we used genus- (22.1%) or stand-level (11.1%) averages, as recommended by (Flores & Coomes, 2011). Tree height was estimated using a regional (central Africa) diameter–height equation (Feldpausch et al., 2012).

We considered two time periods along the forest dynamics trajectory, one relatively soon after the silvicultural treatments, from 1992 to 1998, and the other a few years later, from 2012 to 2018. For both periods, we computed initial AGB in 1992 and 2012 as baselines, and estimated productivity as AGB change (Δlog(AGB), hereafter ΔAGB) over each six-year monitoring interval, that is, the difference in AGB from the final date to the baseline. Because mortality and recruitment impacted ΔAGB with strong stochasticity components (Sheil et al., 2000), especially given that recruitment occurs at 10 cm DBH in our dataset, we computed ΔAGB only considering trees that were alive and measured in both censuses, as done in previous studies (Chisholm et al., 2013; Jucker et al., 2016; Yuan et al., 2016). Thus, we neglected transient contribution due to recruitment and mortality. As a consequence, ΔAGB was only disaggregated into ΔAGV, ΔWDv and ΔP.MaxDBH, as the number of trees remained constant between two censuses.

2.4 | Phylogenetic analysis

We used a recently published megaphylogeny (Janssens et al., 2020), based on two plastid markers (matK and rbcL) from 36,234 plant species distributed across 8357 genera, and calibrated with 52 plant fossils. Missing genera (9 out of 177) were manually added to the phylogeny based on phylogenetic hypotheses drawn from the literature (Table S1) and species included as polytomies within their genera using the R package spacodiR (Eastman et al., 2011). Finally, MPD (weighted by tree abundance) was estimated for all the 20-m subplots using the R package picante (Kembel, 2010). Just like species richness, PD increases monotonically with increasing sampling effort, creating a classic sampling curve that reaches an asymptote when all species (and branch segments) are represented. To control for this sampling effort, we computed the rarefied version of PD (rPD) using the R package PDcalc (Nipperess & Matsen, 2013), where authors derived the exact formulae for the mean and variance of PD under rarefaction. More details on the formulae index calculations can be found in Nipperess, 2016. Considering this approach, we randomly subsampled (rarefied) the pool of accumulation units to 15 individual trees to calculate rPD.

2.5 | Statistical analyses

We used structural equation modelling (SEM) to evaluate the strength and direction of individual pathways in our conceptual model. All predictors were standardized to have a mean of 0 and a standard deviation of 1. For the AGB model, P.MaxDBH was log-transformed before standardization to deal with positively-skewed data and improve normality of residuals. SEMs were fit using the 'sem' function of the lavaan package in R (Rosseel, 2012). The performance of the models was evaluated using a combination of the Bentler's comparative fit index (CFI), root mean square error of approximation (RMSEA) and standardized root mean square residual (SRMR). Indirect (mediated) effects of phylogenetic diversity metrics (rPD and MPD) were calculated by multiplying the coefficients of all paths linking them to each component of (Δ)AGB. For assessing the integrated effect of diversity on components due to multiple independent paths, for example, the effect of MPD on meanAGV mediated by P.MaxDBH, we summed all the involved indirect effects. To account for the non-independence of observations within large plots, a random intercept associated with the 4-ha plots to which each subplot belongs was accounted for using mixed linear models. This analysis was done using the piecewiseSEM R package that allows the inclusion of random effects with maximum likelihood estimators (Lefcheck, 2016). Model fitting performances were compared using likelihood ratio tests and Akaike information (AIC) and Bayesian information (BIC) criteria (Snijders & Bosker, 2012). Because models without random effects always had smaller AIC and BIC values (Table S3), we hereafter do not report results obtained with the mixed models. This result additionally confirms that there is no major spatial structure in our variable of interest at the 4-ha scale, suggesting that the design of the experimental sites was well optimized to maintain homogeneous conditions between plots (see study site description). Furthermore, because the correlation between MPD and rPD (Figure S2) may have induced collinearity issues, we tested additional SEM models replacing MPD by the model residuals of the MPD regression on rPD. The results showed that our conclusions remained unchanged and thus that our results were not impacted by any collinearity issue (Tables S4 and S5).

Analyses were run separately among the different silvicultural treatments (control, logging and logging-and-thinning plots) to assess whether the effects of diversity on biomass and biomass productivity depend on disturbance history. The effect of diversity on biomass (AGB) was, however, only reported for control plots (see Figure S3; Tables S6 and S7) as we observed that the losses of basal area due to the silvicultural treatments were not independent of the evolutionary diversity found before treatments, potentially generating biases in our results.

Since old clades may disproportionately contribute to the phylogenetic diversity estimates and, consequently, our final results, we recomputed MPD and rPD estimates after excluding the Magnoliales and Laurales clades. We then reran all analyses and reported any resulting changes in the results section.

The analyses were performed using the R programming language v.4.3.1 (R Core Team, 2023) and graphical representations were done using the ggplot2 R package (Wickham & Chang, 2016).

3 | RESULTS

3.1 | Tree stand dynamics

All silvicultural treatments (including control plots) experienced monotonic growth in AGB since 1992 (Figure 2a; Figure S4), indicating that, even unlogged, the forest in M'Baïki accumulated biomass during the studied period. However, the origin of this increase in AGB differed between the treatments. In the control plots, AGB increased over time due to an increase in its three components (AGV, Ntree and mostly wood density), without any gain in the basal area of the large-sized species (P.MaxDBH). In contrast, the increase in AGB over time in the logging and logging-and-thinning treatments was mostly due to a large increase in AGV, notably in large-sized species, compensating for the decreasing trend in wood density and globally stable number of trees. Plots that experienced logging or logging-and-thinning consistently had less AGB than the control plots in the two initial censuses, mostly due to lower AGV, that is, a smaller proportion of large trees that were preferentially harvested in 1986–87. However, the AGB of the last three censuses displayed no statistical differences between the control and disturbed plots owing to the rapid recovery in AGV (Table S8).

Concomitantly with AGB, phylogenetic diversity tended to increase over time in all silvicultural treatments, except for rPD in the control plots where values remained stable. The rPD values of logging and logging-and-thinning plots were initially significantly lower in the first two censuses, a pattern imputable to logging operations and then increased, reaching values not statistically different from those of control plots in the last two censuses due to regeneration. For MPD, all treatments revealed an increase in diversity over time, especially in the logged plots. However, the MPD values of the control and logging-and-thinning plots were very similar and both were significantly higher than the MPD values of the logged plots in the two oldest censuses (Figure 2g; Table S8).

3.2 | Effects of diversity on AGB stocks

The SEM results for 1992 (Figure 3) and 2012 (Table S7) indicate that evolutionary diversity had both significant positive and negative effects on the components of AGB. MPD had a positive effect on the number of trees, suggesting higher tree-packing effect over the different forest strata. We consistently found a concomitant negative effect of MPD on AGV, but this effect was no longer significant when we recomputed MPD and rPD estimates after excluding old clades (Magnoliales and Laurales). P.MaxDBH emerged as a significant mediator of rPD's effect on AGV even though a substantial proportion of P.MaxDBH did not originate from rPD and the rPD's effect on P.MaxDBH was also no longer significant when excluding old clades. The variation in mean wood density appeared largely independent of evolutionary diversity, suggesting that there was no sampling effect of diversity on this trait at our study site. Overall, the SEM for 1992 predicted 64% of the variance in mean AGV, 0.6% in mean wood density, 64% in mean AGV and 13.7% in Ntree (see Table S7 for 2012 similar results). Because positive and negative effects averaged up to the final AGB variable (after summing all indirect effects), we did not detect any significant overall effect of phylogenetic diversity on AGB, despite several intermediate paths within the SEM with significant effects (Figure S5).

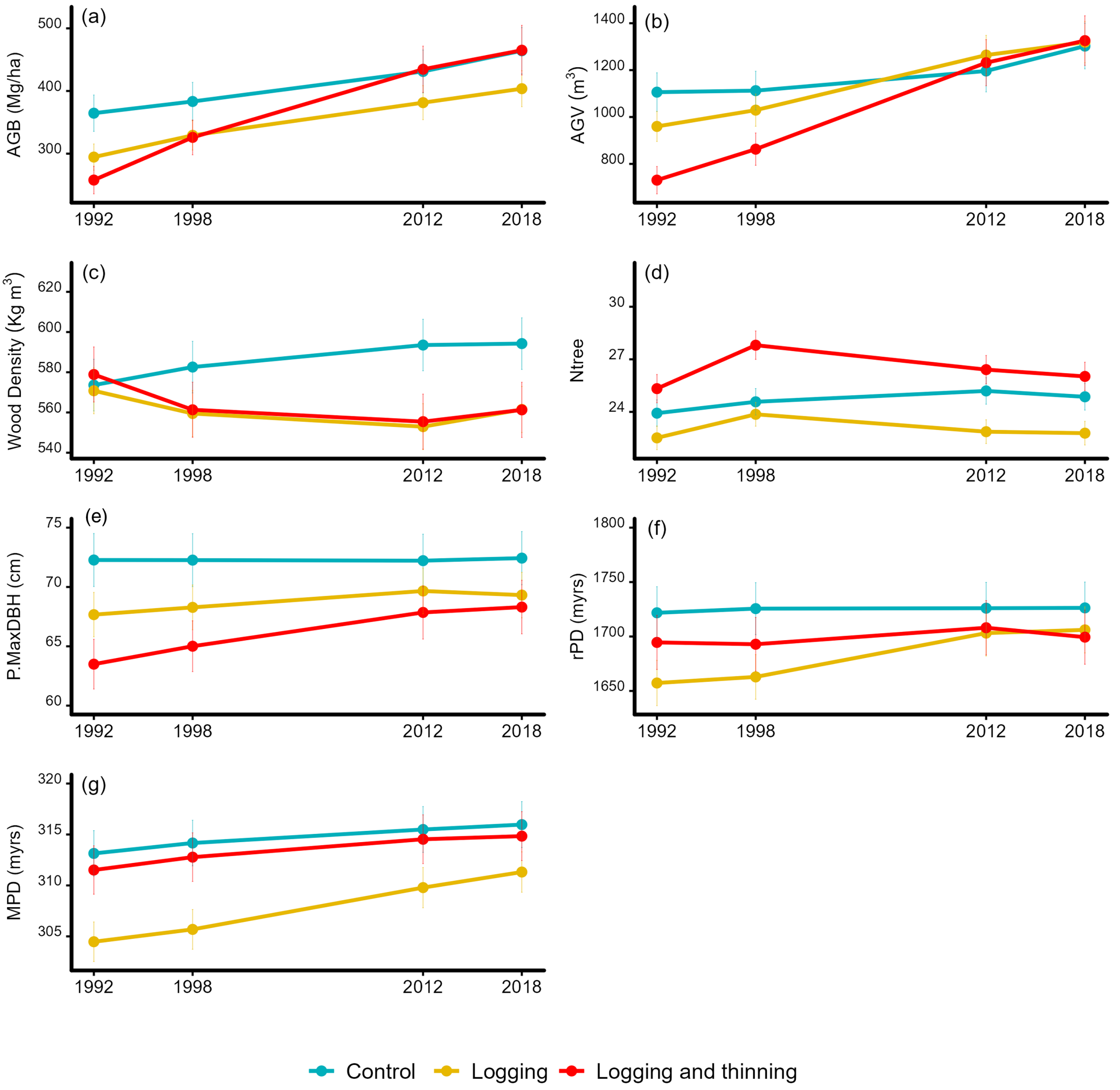

FIGURE 2 Effects of disturbance (silvicultural treatments) on tree stand structure and diversity over time. Above-ground biomass (AGB, a), mean individual tree above-ground volume (AGV, b), mean wood density (WD, c), number of trees (Ntree, d), potential maximum tree diameter (P.MaxDBH, e), rarefied phylogenetic diversity (rPD, f) and mean pairwise distance (MPD, g) are reported for the four census dates. Error bars represent 95% confidence interval.

3.3 | Effects of diversity on AGB productivity

The effects of evolutionary diversity on biomass productivity (ΔAGB) varied among sylvicultural treatments (Figure 4). As observed for the AGB model, we found a significant impact of ΔP.MaxDBH on ΔAGV in all models, explaining 33.5% to 55% of the variance in AGV net change, depending on the treatment (Tables S9 and S10). This indicates that the differential allocation of growth in small- or large-sized trees is, in any case, an important driver of above-ground volume, and thus of forest productivity, though not generally controlled by evolutionary diversity (except for logging plots in 2012–2018, Figure 4e). rPD also showed a weak positive effect on ΔWD in the control plots for the period 2012–2018. However, this effect should be approached with caution because it was not significant during the first period (1992–98, Figure 4a–c) nor when we excluded old clades. Overall, we did not detect any significant tree-packing nor sampling effects of evolutionary diversity on AGB net change in the control plots (Figure 5).

Contrary to control plots, logging and logging-and-thinning plots systematically revealed a significant negative effect of MPD on

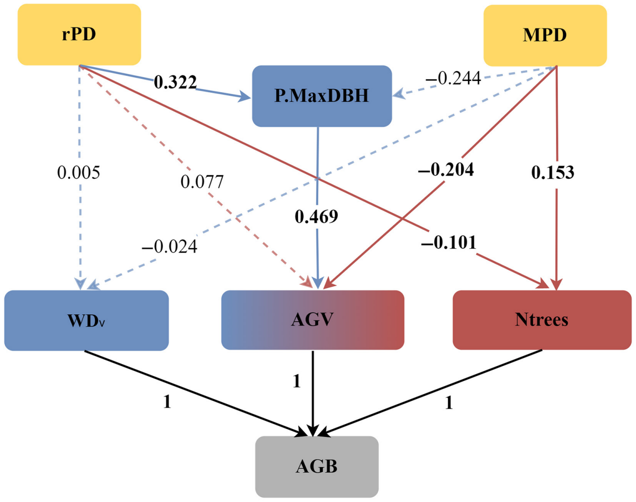

FIGURE 3 Results of the structural equation models for the effect of phylogenetic diversity on above-ground biomass (AGB) components via the sampling effect (in blue) and the tree-packing effect (in red) in 1992. AGV, log transformed mean individual above-ground volume; MPD, mean pairwise distance; Ntrees, log transformed stem density; P.MaxDBH, potential maximum tree diameter; rPD, rarefied phylogenetic diversity; WDv, log transformed mean wood density weighted by AGV. Bold arrows and numbers represent significant effects ($p < 0.05$) and light-dotted arrows represent non-significant effects. Standardized regression coefficients are given for all paths. Model fit statistics are provided in Table S6.

ΔAGV and a weaker positive effect on ΔWD for the first interval (1992–1998, Figure 4a–c), leading to an overall negative effect of phylogenetic diversity on ΔAGB (Figure 5). As an illustration, ΔAGB was ca. three times higher for the smallest observed MPD or rPD values than for the largest ones during this interval. The negative effect of MPD on ΔAGV was stronger for logging-and-thinning plots, but overall, the pathways associated with the tree-packing effect on ΔAGB were strongly negative in both logging treatments (Figure 5). Thus, despite a slightly positive sampling effect, a global negative BEF relationship occurred in disturbed plots for the first period. For the second interval (2012–2018, Figure 4d–f), phylogenetic diversity effects were mostly null in all treatments, except for a slightly positive sampling effect that remained in logging-and-thinning plots. In summary, while control plots showed no overall diversity effect on ΔAGB for both intervals (Figure 5), biomass productivity in disturbed plots seemed to be driven by species dominance.

4 | DISCUSSION

Using one of the oldest long-term tropical forest experiments, we developed a conceptual framework and revealed that evolutionary diversity impacts forest biomass and productivity through different ecological pathways. The 'tree-packing effect' influences the structural components of AGB, such as the number of individuals and their mean sizes, thereby allowing trees to grow more densely packed. Conversely, the 'sampling effect' is expected to operate on mean wood density and maximum potential size, as hyper-diverse communities have a greater chance of containing species with high-performance traits. Our results showed that, in the absence of disturbance, the change in forest biomass (AGB) or productivity (ΔAGB) was unaffected by diversity, despite the existence of underlying significant effects of evolutionary diversity on some AGB components. Furthermore, our findings partially support our overall hypothesis that fitness differences among species lead to a marked role of species dominance in promoting productivity (ΔAGB) in recently disturbed forests, aligning with recent results from European grassland communities (Brun et al., 2022; Lisner et al., 2023).

4.1 | Observed trends in community dynamics in natural and disturbed forests

As observed in several mature central African forests (Hubau et al., 2020), undisturbed (control) plots experienced an increase in AGB during the study period, mostly due to an increase in wood density, mean tree volume and, to a lesser extent, in the number of trees (Figure 2b–d). The reason for this biomass increase is still under debate (Baker et al., 2003). Gourlet-Fleury et al. (2013) found unusual mortality of large light-demanding species between 1987 and 2011 in the same plots, suggesting that these forests were still recovering from ancient large-scale disturbances caused by human occupation, drought or fires in the last 500 years, as has often been reported for tropical African forests (Brncic et al., 2009; Van Gemerden et al., 2003; White & Oates, 1999). Another hypothesis is that the global rise in atmospheric CO_2 concentration, or more generally recent changes in climatic conditions, positively affects the forest carbon balance of tropical forests (McDowell et al., 2020).

As expected, the disturbed forests experienced a marked increase in AGB over time, illustrating the forest recovery process. The impact of logging was mostly seen on the maximum potential size of species (P.MaxDBH) and wood density (WD), with the latter showing no full recovery after 30 years of disturbance. Previous results consistently showed that selectively logged tropical forests showed a decrease in wood density, even 20 years after exploitation (Baraloto et al., 2012; Carreño-Rocabado et al., 2012). African forests affected by human-induced disturbances are known to be dominated by long-lived pioneer species characterized by low WD but high potential maximum stature (Réjou-Méchain et al., 2021), which outcompete species with conservative strategies where resource availability is high (Grime, 1998; Rüger et al., 2020). The increase in P.MaxDBH from 1998 to 2012 in disturbed plots probably illustrates both the importance of these long-lived pioneer species in forest volume recovery and the high death rates of the medium-sized abundant pioneer species *Musanga cecropioides* R. Br. (Urticaceae) during the first few decades post-disturbance (Sanchez & Lindsell, 2016). By disaggregating AGB into its different components, our results illustrate that the biomass accumulation over time observed in disturbed and undisturbed forests has different origins: undisturbed forests tend to accumulate biomass mostly through a higher volume growth in hard-wooded species, whereas disturbed

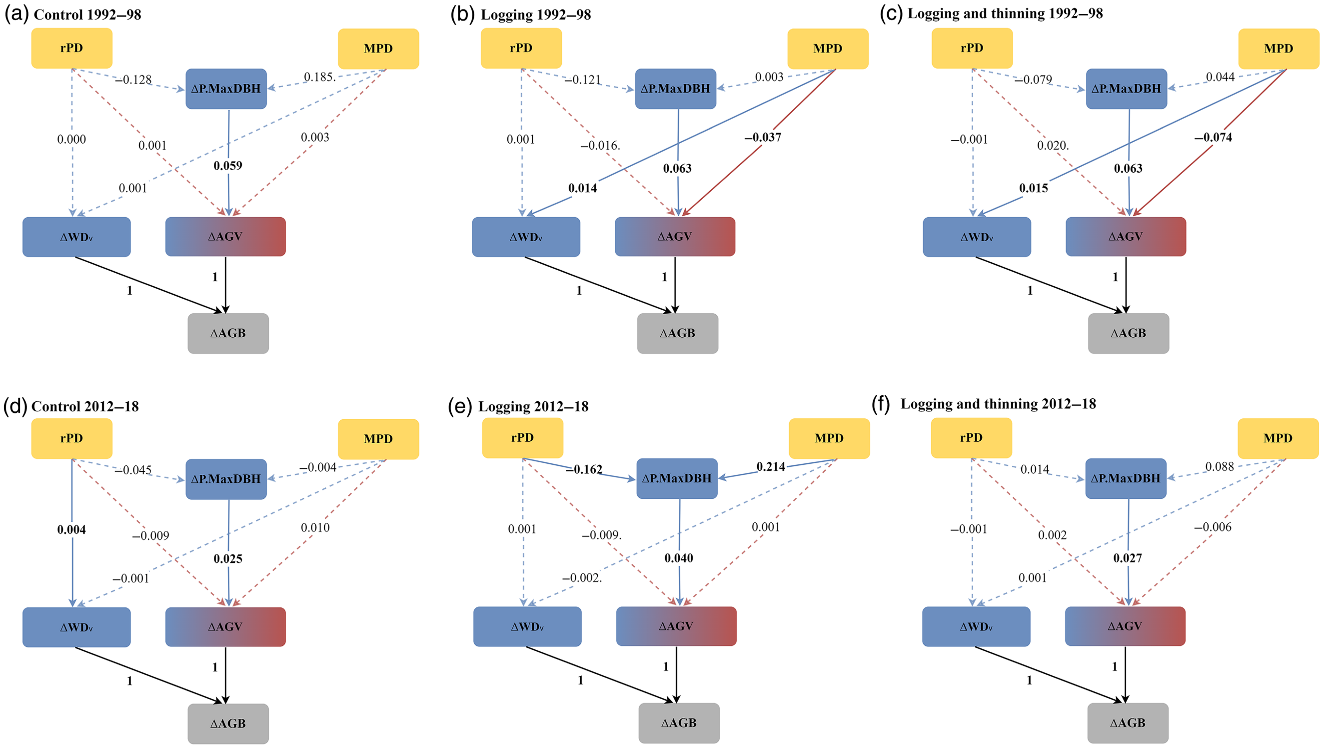

FIGURE 4 Results of the structural equation models for the effect of phylogenetic diversity on above-ground biomass productivity (ΔAGB) components via the sampling effect (in blue) and the tree-packing effect (in red) for the first (1992–1998, a–c) and second monitoring period (2012–2018, d–f). MPD, mean pairwise distance; rPD, rarefied phylogenetic diversity; ΔAGV, change in log transformed mean individual above-ground volume; ΔP.MaxDBH, change in potential maximum tree diameter; ΔWDv, change in log transformed mean wood density weighted by AGV. Bold arrows and numbers represent significant effects ($p < 0.05$), and light-dotted arrows represent non-significant effects. Standardized regression coefficients are given for all paths. The model fit statistics are presented in Tables S9 and S10.

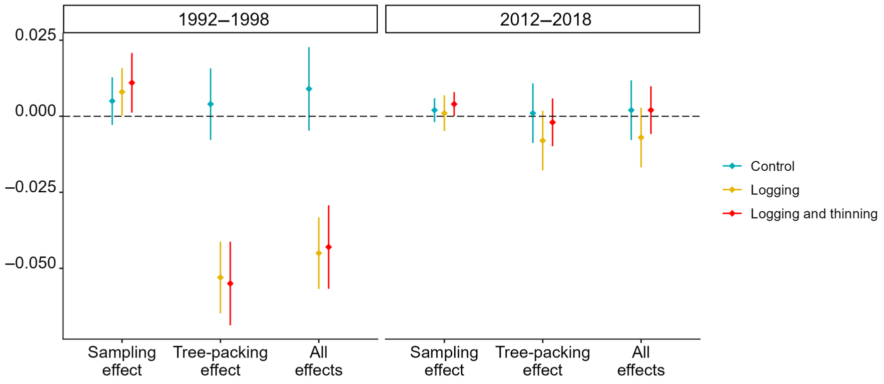

FIGURE 5 Model coefficients for the effects of diversity on ΔAGB via the sampling and the tree-packing effects. 'All effects' represents the sum of all effects in the SEM pathways. A standardized slope estimate is considered as significant if the 95% confidence interval does not intersect zero.

forests tend to accumulate biomass mostly through the recruitment and volume growth of large, light-wooded species. These results, which are generally hidden behind the composite biomass variable, indicate that the effects of diversity on forest biomass dynamics potentially operate through different ecological pathways.

4.2 | Effects of evolutionary diversity on AGB and productivity

When summing all indirect effects, we found no overall effect of evolutionary diversity on biomass (AGB) and productivity (ΔAGB) in control plots, despite significant individual effects of diversity on biomass components. Contradicting the results obtained in manipulative experiments, the absence of the effect of evolutionary diversity on ecosystem functioning has been repeatedly observed in natural systems (Lasky et al., 2014; Satdichanh et al., 2018; van der Sande et al., 2017). At least two explanations are possible for these contradictory results. First, BEF is expected to saturate towards an asymptote for high diversity values (Liang et al., 2016); thus, there is no apparent effect of evolutionary diversity on biomass and productivity once all available niches are filled. Second, contrary to manipulative experiments, the original diversity, that is, the pool of species available during the colonization phase, is unknown in natural systems because abiotic and biotic filters already operated and impacted the local diversity, potentially blurring existing positive BEF relationships in observational data (Hagan et al., 2021).

However, careful examination of the impact of rPD and MPD on biomass components revealed significant effects of evolutionary diversity on ecosystem functioning, even if some of them seem to be overinfluenced by old clades. Regardless of the silvicultural treatment, (Δ)P.MaxDBH had a strong and positive effect on (Δ)AGV and consequently on (Δ)AGB. The differential allocation of forest volume in large and small-sized trees thus plays a predominant role in the spatio-temporal dynamics of forest biomass, supporting the mass-ratio hypothesis and confirming previous results on the importance of maximum tree size for forest biomass dynamics (Banin et al., 2012; Brun et al., 2022; Finegan et al., 2015; Hu et al., 2020; Lohbeck, Poorter, et al., 2015; Prado-Junior et al., 2016; Slik et al., 2013). However, evolutionary diversity explained only a small share of the variation in P.MaxDBH, calling for additional studies to understand the ecological drivers of this important trait at the community level. We also found a significant positive effect of MPD on the number of trees. This result indicates that higher evolutionary diversity is associated with a higher tree packing through an increased density of small-statured trees in the intermediate forest strata (see Figure 2d). Given that the studied traits, P.MaxDBH and wood density, displayed phylogenetic conservatism (Table S2), a higher MPD indeed indicates greater functional complementarity for these, and probably many other, traits. This result is in line with the expected positive effect of diversity on biomass through niche complementarity effects, where more diverse communities partition limited resources more efficiently and can thus store more biomass (Hector et al., 1999; Hooper & Dukes, 2004; Van de Peer et al., 2018). By maximizing the number and/or the size of coexisting trees, that is, tree packing, diversity is expected to increase biomass (Duarte et al., 2021; Guillemot et al., 2020). However, this positive effect of MPD on the number of trees was partly counterbalanced by a negative effect of MPD on the mean tree volume because tree packing involves that the space is filled by more small trees, even if this negative effect was no longer significant when old clades were discarded. Yet, we consistently found a negative effect of MPD on the temporal change in mean tree volume (ΔAGV) but only in forests that experienced recent disturbances.

Although evolutionary diversity has been widely used in BEF studies, the presence of species from old clades, which are known to disproportionately contribute to phylogenetic metrics, should be controlled for. Here, we showed that removing taxa from the Magnoliales and Laurales orders in our dataset had some impact on certain results. Therefore, these results should be interpreted with caution, even though they did not change the main overall result of our study.

4.3 | Effects of disturbances on evolutionary diversity-productivity relationship

Our results showed that disturbance history mediates the relationship between evolutionary diversity and biomass productivity, as reported by Lasky et al. (2014). As initially hypothesized, we found evidence of significant and positive sampling effects in disturbed forests, but not in undisturbed forests (Figure 5). These sampling effects were first driven by the positive influence of evolutionary diversity on ΔWD (wood density net change) during the early post-disturbance period (first studied interval) and on ΔP.MaxDBH later on (second studied interval; Figure 4; Figure S3). Note that WD decreased in disturbed plots during the first interval (1992–98), even though AGB increased over the years (Figure 2a,c), corroborating that the dominance of early successional species with acquisitive traits (low wood density) drives productivity in recently disturbed forests (Rüger et al., 2020). By contrast, paths associated with the tree-packing effect had a strong negative impact on biomass productivity soon after disturbance, leading to a total negative balance of BEF relationships, which vanishes 30 years after disturbance (no overall BEF relationships in the second time period). More specifically, MPD had a negative effect on the net change in mean tree volume (ΔAGV) soon after disturbance (first interval), indicating that the relative contribution of small-sized trees to biomass productivity is larger in more diverse communities, resulting in smaller biomass gain than in less diverse communities (Figure S6).

The negative effect of evolutionary diversity on the net change in above-ground biomass (ΔAGB) found for the recently disturbed plots could be explained by the niche overlap (or functional redundancy) observed in recently disturbed tree communities. Indeed, increased light availability after logging causes environmental filtering, that narrows down the species able to efficiently use the available resources (fast-growing species) and drive biomass productivity (Rüger et al., 2020; Van de Peer et al., 2018). High biomass productivity is thus driven by a few functionally similar (or phylogenetically closer) dominant pioneer and light-demanding species. Indeed, we found that four phylogenetically closely related (Figure S7) pioneer and light-demanding species (*Musanga cecropioides*, *Trilepisium madagascariense*, *Celtis zenkeri* and *Celtis tessmannii*) disproportionally contributed to productivity (~50% of ΔAGV for the logging plots) resulting in a negative impact of evolutionary diversity on biomass productivity soon after disturbances. Therefore, our findings suggest that rather than a high trait diversity, a narrow range of trait values (traits that dominate in disturbed plots, such as high tree size and low wood density) from lineages separated by low mean distances increases productivity (Cadotte, 2017). However, this scenario seems to change rapidly, as in the next monitoring interval (~30 years after disturbance), the negative effect is no longer significant, suggesting a short-term effect of disturbance on the diversity-productivity relationships.

Our findings indicate that, in the absence of disturbance, evolutionary diversity does not directly impact changes in forest biomass or productivity, despite the presence of underlying relationships between evolutionary diversity and ecosystem functioning at intermediate levels. However, we found that disturbance plays a pivotal role in shaping the strength and direction of BEF relationships. In recently disturbed forests, where there are significant fitness differences among species, complementarity effects are hindered and species dominance becomes a key driver of productivity.

AUTHOR CONTRIBUTIONS

Erica Rievrs Borges, Maxime Réjou-Méchain and Raphaël Pélissier conceived the study. Sylvie Gourlet-Fleury, Guillaume Cornu, Fidèle Baya and Félix Allah-Barem provided the data from M'Baïki experimental design. Erica Rievrs Borges and Maxime Réjou-Méchain performed data analysis and interpreted the results along with Sylvie Gourlet-Fleury, Raphaël Pélissier, Grégoire Vincent, Frédéric Mortier and Xaxier Bry provided support to design the conceptual model and perform the statistical analyses. Erica Rievrs Borges, Maxime Réjou-Méchain and Raphaël Pélissier wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available on the CIRAD Dataverse: https://doi.org/10.18167/DVN1/FBYOBP (Borges et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Sources of the phylogenetic hypothesis for the missing genera manually added to the phylogenetic tree.

Table S2: To test whether wood density and P.MaxDBH were structured by plant phylogeny we checked for phylogenetic signal (Münkemüller et al., 2012).

Table S3: AIC (Akaike information) and BIC (Bayesian information) for models with and without random effect.

Table S4: Results of the structural equation models for aboveground biomass productivity (1992-1998) with the model residuals of the regression of MPD on rPD.

Table S5: Results of the structural equation models for aboveground biomass productivity (2012-2018) with the model residuals of the regression of MPD on rPD.

Table S6: Results of the structural equation models for aboveground biomass (1992).
Table S7: Results of the structural equation models for aboveground biomass (2012).
Table S8: Effect of silvicultural treatments on aboveground biomass (AGB, Mg), potential maximum tree size (P.MaxDBH, cm), rarefied phylogenetic diversity (rPD, myrs), aboveground volume (AGV, m^3), mean pairwise distance (MPD, myrs), wood density (WD, kg/m^3), and number of trees (Ntree) throughout monitoring intervals after disturbance.
Table S9: Results of the structural equation models for aboveground biomass productivity (1992–1998).
Table S10: Results of the structural equation models for aboveground biomass productivity (2012–2018).
Figure S1: Location of the study site in Central Africa and spatial distribution of the three treatments.
Figure S2: Pearson's correlation coefficients between the all variable.
Figure S3: Results of the structural equation models for the effect of phylogenetic diversity on aboveground biomass (AGB) components via the sampling effect (in blue) and the tree-packing effect (in red).
Figure S4: Effects of disturbance (silvicultural treatments) on tree stand structure and diversity over time among replicate plots.
Figure S5: Model coefficients for the total effects of diversity on aboveground biomass (AGB) for the control plots via the sampling effect and the tree-packing effect.
Figure S6: Bivariate relationships between aboveground biomass productivity (ΔAGB) model variables in 1992–1998.
Figure S7: Phylogeny of 321 Central African tree species in M'Baiki experimental station.

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