LETTER

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

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Abstract

Although there is compelling evidence that tree diversity has an overall positive effect on forest productivity, there are important divergences among studies on the nature and strength of these diversity effects and their timing during forest stand development. To clarify conflicting results related to stand developmental stage, we explored how diversity effects on productivity change through time in a diversity experiment spanning 11 years. We show that the strength of diversity effects on productivity progressively increases through time, becoming significantly positive after 9 years. Moreover, we demonstrate that the strengthening of diversity effects is driven primarily by gradual increases in complementarity. We also show that mixing species with contrasting resource-acquisition strategies, and the dominance of deciduous, fast-developing species, promote positive diversity effects on productivity. Our results suggest that the canopy closure and subsequent stem exclusion phase are key for promoting niche complementarity in diverse tree communities.

KEYWORDS
biodiversity-ecosystem functioning, functional diversity, functional identity, functional traits, IDENT, life-history strategy, long-term diversity effects, productivity, resource partitioning, tree diversity experiment

INTRODUCTION

Recent decades have seen a large number of studies, both observational and experimental, investigating the diversity–productivity relationship (hereafter DPR) in forest ecosystems. As a result, there is now a general consensus that diverse tree communities, on average, promote higher biomass production than their species-poor counterparts (Liang et al., 2016; Paquette & Messier, 2011; Zhang et al., 2012). However, within this body of research, there are important divergences in the magnitude of diversity effects, with some studies reporting negligible or only marginal effects (e.g. Li et al., 2014; Tobner et al., 2016). While recent studies have demonstrated how complex interactions between abiotic factors and stand structure explain some of these divergences across different forest types (Forrester, 2014; Hulvey et al., 2013; Jucker et al., 2016), much less is known about the mechanisms driving the temporal dynamics of the strength of DPR over time during

forest development (Grossman et al., 2018; Huang et al., 2018; Jucker et al., 2020; Taylor et al., 2020). In particular, diversity effects are thought to be especially important during the early phases of forest development (i.e. stand establishment, canopy closure and stem exclusion), when competition for limited resources is the major driver determining the future forest structure and functioning (Fichtner et al., 2018).

Two main mechanisms have been proposed to explain positive diversity effects on productivity. The first is complementarity effects, which include niche partitioning and interspecific facilitation; and the second is selection effects, which are caused by the dominance of one or few species driving community's productivity (Loreau & Hector, 2001; Roscher et al., 2012). These depend, in turn, on species-specific functional traits. Functional traits define species' life-history strategies, thus determining their capacity to grow, survive and use resources in competitive environments (Violle et al., 2007). Two different approaches to measuring functional aspects of the community can provide mechanistic insights into DPRs as well as the underlying mechanisms at play. The first is functional identity (FI; selection effects) which allows the evaluation of the effect of dominant traits on productivity, whereas the second is functional diversity (FD; complementarity effects) which quantifies the effect of the variability in functional trait values on productivity (Grime, 1998; Morin et al., 2011; Roscher et al., 2012; Shipley et al., 2006). Long-term studies in grassland biodiversity experiments have already shown that the strength of diversity effects and the relative importance of complementarity over selection tend to increase over time (Reich et al., 2012). This observation explains the ability of functionally diverse communities to progressively optimise the use of limiting resources over time and to enhance soil fertility and nutrient availability (Reich et al., 2012).

Increasing importance of complementarity effects over time is expected in forest ecosystems as well (Huang et al., 2018). However, as community dynamics in forests are relatively slow compared to those in grassland ecosystems, complementarity effects driving mixtures' overyielding (i.e. when mixtures' productivity is higher than their components' respective monocultures) might take many years (e.g. a decade or more) to manifest following tree establishment (Huang et al., 2018; Jucker et al., 2020). This is because essential resources such as light and nutrients are normally abundant (relative to demand) in the early years following stand establishment, fulfilling trees' requirements to grow and survive. Consequently, competition among trees for resources is minimal during these early years. This reduces the likelihood of complementarity effects and increases the probability of sampling a dominant, high productive species with a specific set of functional traits driving community productivity (i.e. selection effects) as found by Tobner et al. (2016). However, as stands develop, trees progressively expand

their crowns (i.e. canopy closure), gradually intensifying competition for light and growing space. This, in turn, might increase the importance of complementarity effects driving DPR, as is expected under harsher conditions (Searle & Chen, 2020; Paquette & Messier, 2011; Callaway et al., 2002; but see Belluau et al., 2021). For example mixing species with contrasting life strategies promotes a better use of canopy space (Jucker et al., 2015). This, in turn, reduces competition for light and allows diverse communities to intercept a greater proportion of incoming light and grow faster compared to their respective monocultures (Jucker et al., 2015; Kunz et al., 2019; Pretzsch, 2014; Sapijanskas et al., 2014). This helps explain why, in contrast to studies carried out in the early years of tree diversity experiments where negligible or only marginal positive DPRs were found (Healy et al., 2008; Li et al., 2014; Tobner et al., 2016; Verheyen et al., 2015), recent studies conducted many years after stand establishment highlighted strong positive diversity effects on productivity (Schnabel et al., 2019; Huang et al., 2018; Van de Peer et al., 2017).

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

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

MATERIALS AND METHODS

Site description

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

In the spring of 2009, an area of 0.6 ha was planted with 1- or 2-year-old tree seedlings (Tobner et al., 2014). The experiment includes 12 North American temperate forest species—five broad-leaf species and seven conifers (Table S1). This experiment is part of the 'International Diversity Experiment Network with Trees' (IDENT) that includes several sites in North America, Europe and Africa (Verheyen et al., 2015).

Experimental design

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

Trees were planted in square plots of 8 x 8 individuals (i.e. 64 trees), with 50-cm spacing among trees and 1.25 m between plots to allow movement and minimise inter plot interactions (Tobner al., 2014). The experiment includes monocultures of all 12 species, 14 combinations of two-species mixtures, 10 combinations of four-species mixtures and one mixture including all 12 species (Tobner et al., 2014) for a total of 37 different tree communities (i.e. unique species composition). Each community was replicated four times in a randomised block design for a total of 148 plots and 9472 trees (note that the site includes more plots addressing other questions that were not used in this experiment) (Tobner et al., 2014). The proportion of species within plots was equal and their distribution randomised with restrictions to prevent monospecific patches (see Tobner et al., 2014 for details). The distribution of trees within the plots remained constant in all the blocks; however, the distribution of plots within blocks was randomised.

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

Cumulative productivity as measured by tree basal area

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

DATA ANALYSIS

Quantification of the diversity effects and its underlying mechanisms

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

$$NE = YO - YE = CE + SE$$
$$= N\overline{\Delta RYM} + N\text{cov}(\Delta RY, M) \tag{1}$$

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

$$\Delta RY = \frac{yieldA\,(\text{Mixture})}{yieldA\,(\text{Monoculture})} - P_A, \tag{2}$$

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

CE is the mean of the deviation from the expected relative yield of each species in the mixture ($\overline{\Delta RY}$) multiplied by the mean of each species' yields in monoculture ($\overline{M}$) and by the number of species (N). Therefore, CE averages positive and negative diversity effects of all species in the mixture. On the other hand, SE is the covariance between species' relative (ΔRY) and monoculture yields (M) multiplied by the number of species in the mixture (N). SE is positive when the most productive species in monoculture performs better in the mixture. Alternatively, SE is negative when the less productive species in monoculture overyield in the mixture. In case of both high and low productive species in monocultures overyielding in the mixture, SE can be positive or negative depending on the stronger effect.

Trait data collection and calculation of functional composition

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

The first two principal components explained 80% of the variance in traits. The first principal component (PC1) was correlated to wood density (WD), leaf nitrogen content by unit mass (LNmass), specific leaf area (SLA) and specific root length (SRL), clearly separating gymnosperms from angiosperms (Table S2). These functional traits are involved in the acquisition, processing and conservation of resources and, hence, define species' life-history strategy largely by influencing growth versus survival trade-offs (Reich, 2014). It is worth noting that WD is a highly phylogenetically conserved trait (i.e. less variable within phylogenetic groups than expected by chance) with angiosperms typically having significantly denser wood than gymnosperms (Zhang et al., 2021), as evidenced in our PCA, with that factor overwhelming the typical within-group association of high WD with slow

growth (Swenson & Enquist, 2007). As a result of this strong phylogenetic conservatism, high WD—a 'slow' trait—is positively correlated with high values of 'fast' leaf traits among the studied species, which is different than the general pattern observed in nature (Reich, 2014). The second principal component (PC2) was related only to seed mass (Table S2). Seed mass is considered as an indicator of the trade-off between colonisation (early vs. late successional species) and competitive capacity (Turnbull et al., 2004). For example small-seeded species are typically better colonisers but less shade tolerant and thus, lesser competitors. Using the species scores over these two life-history axes (i.e. principal components), we calculated the communities' FD and FI using functional dispersion (Fdis, Laliberté & Legendre, 2010) and community weighted means (CWMs, Lavorel et al., 2008) respectively (i.e. $Fdis_{PC1}$, $Fdis_{PC2}$, CWM_{PC1} and CWM_{PC2}). Functional dispersion is the mean distance in a multidimensional trait space of each species to the centre of mass of all species, weighted by their relative abundances (Laliberté & Legendre, 2010). We calculated the Fdis for all possible species combinations of 2, 4 and 12 species. CWM values were computed for the two principal components collecting the variance of functional traits following Lavorel et al. (2008). CWMs are, thus, the mean value of each principal component of all species present in a community weighted by their relative abundance. We used the R package FD to calculate CWM and Fdis (Laliberté & Legendre, 2010).

Statistical analysis

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

$$
\begin{aligned}
NE = \ &Year + Fdis_{PC1} + Fdis_{PC2} + CWM_{PC1} + CWM_{PC2} + \\
&Year \times Fdis_{PC1} + Year \times Fdis_{PC2} + \\
&Year \times CWM_{PC1} + Year \times CWM_{PC2} + \\
&Plot(R) + Block(R) + \varepsilon
\end{aligned}
\tag{3}
$$

where '$Fdis$' is functional dispersion, and 'CWM' community weighed means. The subscripts 'PC1' and 'PC2' refer to the principal components obtained from the PCA previously done on the functional trait values that represent two axes of life-history strategies. The best model was selected based on AIC. We ran a variance-based sensitivity analysis from the best model to estimate the deviance explained by each predictor of the model.

We subsequently explored the effects of FD and FI on NE over time. We performed independent cluster analyses for each of the diversity parameters of the best model (i.e. $Fdis_{PC1}$, CWM_{PC1} and CWM_{PC2}). The cluster
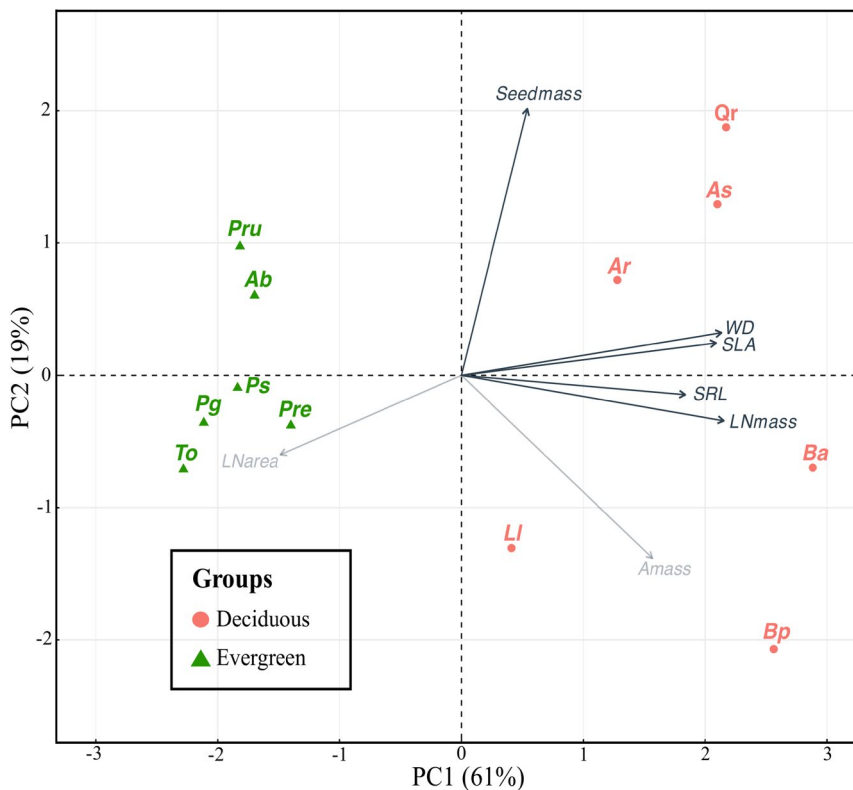
FIGURE 1 Principal Component Analysis of the functional trait values used to characterise the species of the experiment. The first Principal Component (i.e. PC1) is explained mostly by Wood Density (i.e. WD), Specific Leaf Area (i.e. SLA), Specific Root Length (i.e. SRL) and Leaf Nitrogen Mass (i.e. LNmass). And the second Principal Component (i.e. PC2) is explained primarily by Seed Mass (i.e. Seedmass). Leaf Nitrogen Area (i.e. LNarea) and net maximum photosynthesis per unit leaf mass (i.e. Amass) were not correlated with any of the two principal components. Species codes are: Ab, *Abies balsamea*; Ar, *Acer rubrum*; As, *Acer saccharum*; Ba, *Betula alleghaniensis*; Bp, *Betula papyrifera*; Ll, *Larix laricina*; Pg, *Picea glauca*; Pru, *Picea rubens*; Pre, *Pinus resinosa*; Ps, *Pinus strobus*; Qr, *Quercus rubra*; To, *Thuja occidentalis*

analysis classifies the different mixtures of the experiment into similarity groups (i.e. clusters) according to a defined distance measure based on their Fdis and CWM values. The cluster analyses performed on the diversity components grouped the different mixtures of the experiment into (1) plots with high (no. of plots 16) and low (9) functional diversity on the resource-use strategy axis (i.e. $Fdis_{PC1}$); (2) plots with high (5), medium (16) and low (4) mean values on the resource-use strategy axis (i.e. CWM_{PC1}) and (3) plots with high (9), medium (12) and low (4) mean values on the colonisation strategy axis (i.e. CWM_{PC2}). We then extracted the fitted NE values from the model (Equation 3) and plotted them 1) against the measured CE and SE over time to observe the temporal dynamics of the forces driving the NE and 2) against the different Fdis and CWM groups generated by the cluster analyses.

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

RESULTS

Our results show a nonlinear increase in net diversity effects (NE) over time (Figure 2; Table 1). Net diversity effects were negative from year 3 to 6 after the establishment of the experiment, became positive after year 8, and then significantly so from year 9 onward (Figure 2). This strengthening of the net diversity effect was primarily driven by gradual increases in complementarity effects as stands developed (notably > year 5), while during the first years, negative selection effects (which peaked in year 6) were more common in driving the net diversity effects (Figure 2). In the last year of the experiment (year 11), net diversity effects had accumulated enough through time to be easily detected looking at plot total G, with six mixtures overyielding their component monocultures, and four even showing transgressive overyielding (Figure S5).

Further analysis of the effect of tree communities' functional trait-based composition on productivity
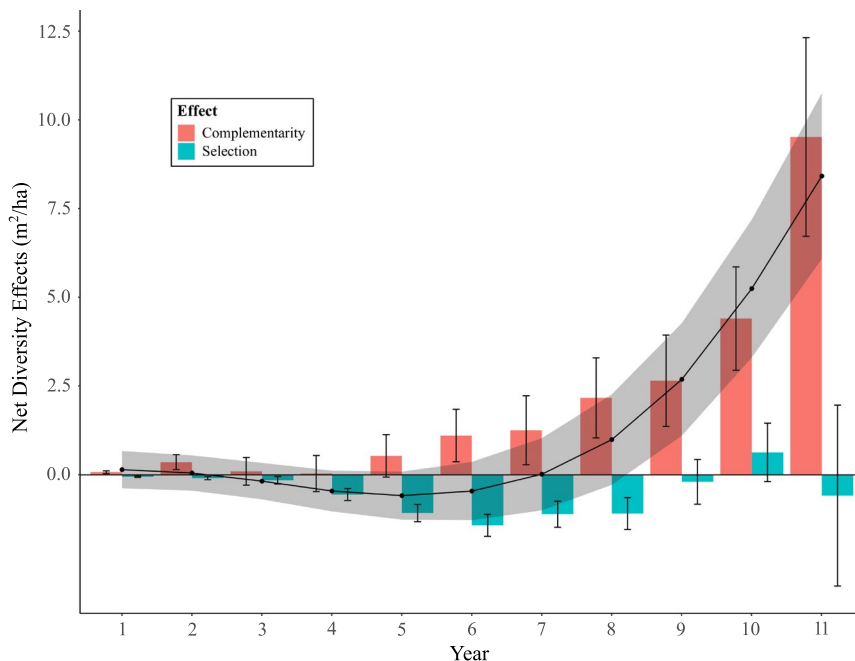
FIGURE 2 Fitted (Equation 3) Net Diversity Effects (NE; Black line ± confidence interval 95% across mixtures and blocks; $N = 1100$) on G (m^2/ha) over time driven by complementarity and selection effects (red and blue bars respectively ± standard error)

TABLE 1 Summary of the generalised additive model (REML estimation) of significant diversity indices on net diversity effects (NE; $N = 1100$) over time (fixed effects)

Effect	edf	DevExp	p-value
s(Year)	4.112	0.080	<0.001
s(Fdis_PC1)	2.698	0.012	<0.001
s(CWM_PC1)	1.111	0.016	<0.001
s(CWM_PC2)	1.102	0.019	<0.001
ti(Year, Fdis_PC1)	5.461	0.066	<0.001
ti(Year, CWM_PC1)	8.510	0.064	<0.001
ti(Year, CWM_PC2)	5.291	0.067	<0.001

Note: Summary includes estimated degrees of freedom (edf), deviance explained (DevExp) and *p*-values. When edf is close to 1, the effect on NE is linear; when edf is 2 or greater it is considered nonlinear. The model includes Block and Plot as random effects. The 's' and 'ti' are GAM-specific terms that mean smooth term (main effects) and tensor product (interactions) respectively. The coefficient of determination (R^2) for the whole model was 0.506.

shows that net diversity effects vary substantially among mixtures during the early stages of stand development (Table 1). We observed that mixtures characterised by species with contrasting resource-use strategies (i.e. high Fdis_PC1) performed similarly to their constituent monocultures during the first years of the experiment. However, starting in year 6, these tree communities progressively increased their productivity compared to their respective monocultures, increasingly overyielding from year 9 onwards (Figure 3). Mixtures characterised by species with similar resource-use strategies

(i.e. low Fdis_PC1) showed similar productivity to their monoculture counterparts during the whole experiment except for the last year when, in general, they slightly overyielded (Figure 3).

In addition, we also observed that the functional identity of tree communities (i.e. CWM_PC1 and CWM_PC2) had a substantial effect on mixtures' productivity over time. For instance mixtures with highly acquisitive resource economic traits (other than WD) (i.e. medium and high CWM_PC1) showed, in general, an increasing trend of diversity effects since year 6 that started to overyield from year 9 onwards (Figure 4). Conversely, mixtures in the 'slow' end (again, other than WD) of the resource economic spectrum (i.e. low CWM_PC1) showed, in general, negative diversity effects from year 8 onwards (i.e. negative NE; Figure 4). Seed mass CWM had a negative relationship with overyielding. In mixtures with low and medium values of seed mass, diversity effects tended to increase progressively over time, overyielding their constituent monocultures in the last 3 years (Figure 5). In contrast, mixtures dominated by late-successional species (i.e. high CWM values of seed mass) showed negligible or even negative diversity effects during the early stages of stand development except for the last year, where, in general, they slightly overyielded (Figure 5).

DISCUSSION

Here we present the results of what is, to the best of our knowledge, the first study with trees to test the temporal
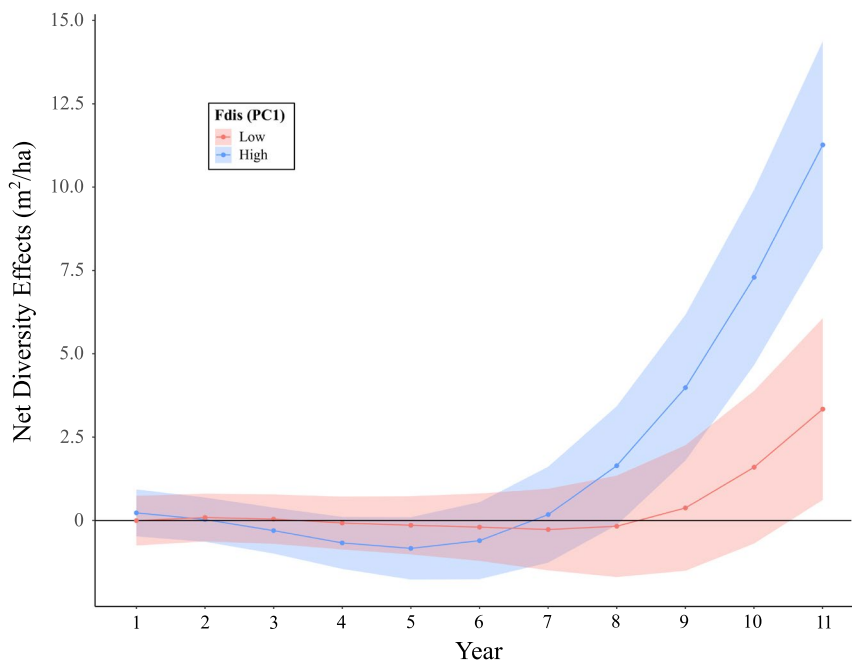
FIGURE 3 Fitted (Equation 3) Net Diversity Effects (NE) on G (m^2/ha) over time for high and low diversity mixtures grouped by the first principal component (i.e. resource-use strategy, PC1). The graph shows that plots with high diversity in resource-use strategy (blue line ± confident interval 95%, $N = 704$) overyielded as stands developed. In contrast, plots with low diversity in resource-use strategy (red line ± confident interval 95%, $N = 396$) showed negligible diversity effects over time, except the last year, when they slightly overyielded
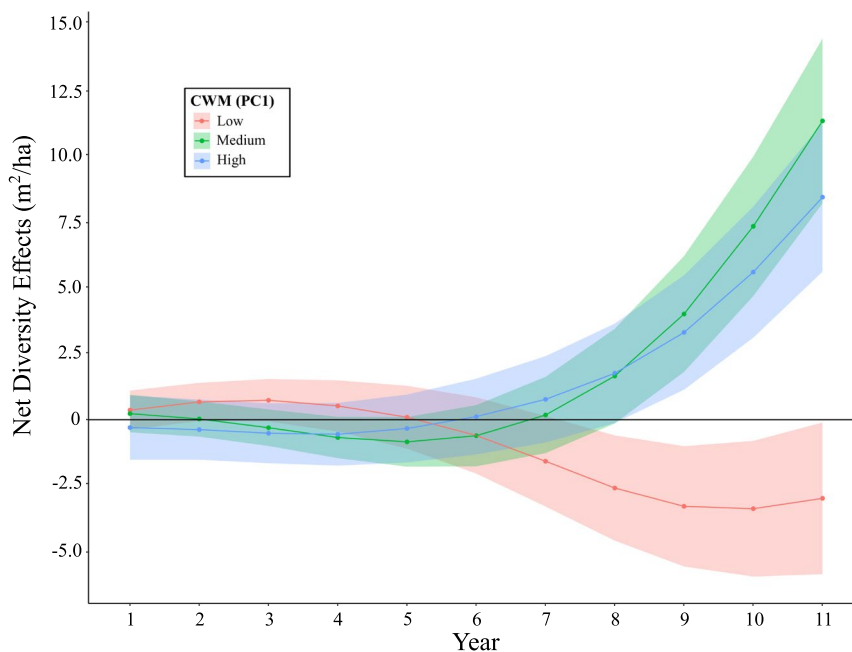
FIGURE 4 Fitted Net Diversity Effects (NE) on G (m^2/ha) over time for mixtures with high, medium and low values over the first principal component (i.e. resource-use strategy, PC1). The graph shows that mixtures with high and medium values in the resource-use strategy (blue and green line respectively ± confidence interval 95%, $N = 220$ and 704 respectively) overyielded over time. Conversely, mixtures with low values (red line ± confidence interval 95%, $N = 176$) showed negative diversity effects over time

dynamics of both net diversity effects and its component mechanisms, complementarity and selection, on cumulative productivity during the first decade of stand development. Our results support the widespread evidence from prior studies that mixtures are, on average, more productive than monocultures of their constituent species. Our study brings new insight into the temporal changes of such effects; showing that the strength of net diversity effects on cumulative productivity is nonlinear during the first phases of stand development, taking
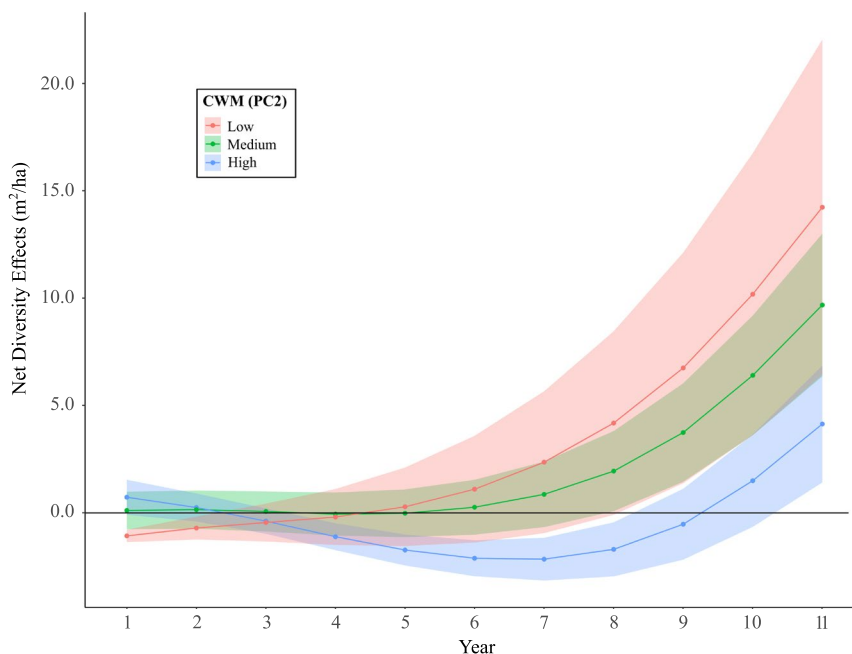
FIGURE 5 Fitted Net Diversity Effects (NE) on G (m^2/ha) over time for plots with high, medium and low CWM values over the second principal component (i.e. colonisation strategy, PC2). The graph shows that mixtures with low and medium values in the colonisation strategy (red and green lines ± confidence interval 95%, N = 176 and 528 respectively) progressively overyielded as stands developed. However, mixtures with high values (blue line ± confidence interval 95%, N = 396) showed negative diversity effects, except the last year where they also overyielded

many years to appear (Figure 2). While an earlier study of the same experiment found, on average, a negligible net diversity effect on cumulative productivity by year 4 (i.e. Tobner et al., 2016), these updated results over a longer temporal scale show i) that the strength of the net diversity effects on cumulative productivity increases throughout early stand development (Jucker et al., 2020; Taylor et al., 2020), and that ii) this is driven by gradual increases of complementarity (Huang et al., 2018; Sapijanskas et al., 2014). Previous studies have shown how complex interactions between resource availability, climatic conditions and stand structures can explain some of the variation in the strength of net diversity effects on productivity across different forest ecosystems (Forrester, 2014; Jucker et al., 2014, 2016; Mori, 2017). Our results mirror several long-term studies in grasslands (Guerrero-Ramírez et al., 2017; Reich et al., 2012) and forest ecosystems (Huang et al., 2018). They show that changes in the relative importance of complementarity and selection effects during the first stages of stand development strongly influence net diversity effects on productivity over time.

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

During the first years following stand establishment we found that, on average, net diversity effects were driven

by opposing forces of complementarity and selection (i.e. negligible net diversity effects; Figure 2). This is consistent with our expectations that in years immediately following stand establishment, high resource availability eliminates or reduces the opportunity for complementarity to have much of an impact on productivity (Forrester, 2014; Paquette & Messier, 2011; Taylor et al., 2020; Zhang et al., 2012). Instead during this phase, selection effects have more impact on productivity (Tobner et al., 2016).

Net diversity effects were negligible at first due to negative selection effects being larger than initially weak (but positive) complementarity effects. This means that, overall, the species with relatively high monoculture productivity had lower performances in mixtures. The opposite was true for species with relatively low monoculture productivity. Selection effects have been hypothesised to be more important in more stable and productive environments, whereas in more stressful environments complementarity effects are expected to be more important (the stress gradient hypothesis, Bertness & Callaway, 1994; but see Belluau et al., 2021). In this study, the intense agricultural activity at the study site prior to the experiment establishment, and the complete removal of herbaceous competition during the first years, resulted in resource-abundant conditions for trees, possibly favouring selection effects initially (Tobner et al., 2016). However, as stands underwent canopy closure and entered the stem exclusion phase, resource competition among trees intensified (c. year 5 or 6; Figure S4). In diverse

stands, the impact of competition may have been reduced since the likelihood of two individuals competing for the same niche decreases; this then allows for the emergence of complementarity, and consequently, positive net diversity effects. These strong positive effects must have been driven by the faster growth of surviving trees within mixtures because tree survival rates remained similar between monocultures and mixtures (Figure S6). Numerous studies have shown that different mechanisms can explain positive diversity effects on productivity, including reduced pest and pathogen loads, or improved resource uptake belowground (Ammer, 2019). However, arguably the most important one is the ability of diverse communities to fill canopy space more efficiently than their species-poor counterparts (Jucker et al., 2015; Pretzsch, 2014). This reduces competition for light and allows these communities to grow faster overall, compared to their respective monocultures (Jucker et al., 2015; Sapijanskas et al., 2014). Therefore, the increase in competition associated with the canopy closure and stem exclusion phases seems to be a key factor in allowing conditions for mixtures to overyield through niche partitioning or facilitation (Jucker et al., 2020).

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

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

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

In addition, we show that, functional identity also plays an important role in driving diversity effects over time. We found that the dominance by slow-developing conifers reduced mixture productivity, compared to more mixed stands and stands dominated by fast-developing deciduous species. Therefore, our study suggests that complementarity effects are also driven by functional identity of specific species (i.e. life-history strategies) that are able to take advantage of diverse conditions, thus leading to overyielding at the community level (Grossman et al., 2018; Zheng et al., 2021). Specifically, our results suggest that effective light acquisition of tree communities dominated by deciduous 'fast' developing early-successional species allow these communities to grow faster (Hisano & Chen, 2020; Zheng et al., 2021). Fast growth (and consequently better access to light) has been linked to a reduced ability to tolerate competitive pressures such as shading from others (Kunstler et al., 2015). Indeed, all the mixtures that overyielded were mixtures of deciduous and evergreen species (except for one) and all but one contained *B.papyrifera* (Figure S5). In other words, this light-demanding pioneer species (the most productive monoculture) probably benefited from reduced competition when growing in mixtures, ultimately dominating them and overyielding at the community level. This could promote niche partitioning through the development of multilayered canopies over time, where shade-tolerant species grow under taller, light-demanding pioneers (Jucker et al., 2015; Niinemets, 2010). Therefore, these results show that both functional diversity and identity of tree communities play important roles in driving positive complementarity

effects, thus promoting net diversity effects on productivity in the mid-term (Zheng et al., 2021; Grossman et al., 2018; Van de Peer et al., 2017)—whether complementarity among initially slower growing species would catch up over time remains unknown.

CONCLUSION

Analysing 11 years of growth records from a tree diversity experiment, we show that diversity effects on productivity strengthen progressively during the early stages of stand development driven by gradual increases of complementarity. While previous studies have shown how abiotic factors and forest structure can explain a considerable amount of variation in the strength of DPR across space, this study highlights that changes in the relative importance of complementarity and selection effects during stand development also play an important role in determining the strength of these relationships over time. This pattern seems to be related to the progression into the canopy closure and stem exclusion phase of stand development, where increasing competition for resources allows positive complementarity effects to develop, and ultimately determines more diverse communities' success in the long term. Moreover, our study highlights that diversity effects on productivity are affected by both functional diversity and identity. We show that mixing species with contrasting resource-acquisition strategies, and the dominance of deciduous, fast-developing species promote positive diversity effects on productivity during the initial phases of stand development.

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

AUTHOR CONTRIBUTIONS
A.P., P.R. and C.M. designed the IDENT-MTL tree diversity experiment; A.P. and C.M. were in charge of the experiment; W.S.K. contributed to conceptualisation and J.U. collected the data during the last 3 years of the experiment. Many grad students, postdocs and interns who worked on the IDENT-MTL experiment collected the data. J.U. performed the analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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