RESEARCH ARTICLE

Climate interacts with the trait structure of tree communities to influence forest productivity

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Abstract

1. Tree functional diversity can increase forest productivity by enhancing species interactions and providing greater growth stability. However, very few studies have examined the influence of tree community trait structure on survivor growth, recruitment and mortality simultaneously, which are the main drivers of forest population dynamics.

2. Here, we explore the interactions among functional diversity, productivity and climate to investigate the role of the trait structure of communities on forest productivity and to determine under what circumstances functional diversity should be promoted to ensure forest adaptive capacity under future climate.

3. Using random-forest modelling and a network of permanent sample plots covering a broad gradient of climatic conditions, we isolated the effects of functional diversity—described as the distribution of trait values in a community—and climate variables on net forest productivity (NFP), survivor growth, recruitment and mortality.

4. Based on our findings, community-level trait structure affects forest productivity in different ways. NFP was influenced by three traits from three different plant strategy dimensions, whereas survivor growth and recruitment were strongly correlated with leaf and resource acquisition traits, and tree mortality with a mix of traits reflecting various plant strategies.

5. We also observed climate interactions with the functional trait structure of tree communities. For instance, we observed an interaction between drought tolerance and mean annual temperature: At low temperatures, NFP biomass accumulation increased with the value of the drought tolerance trait; however, at higher temperatures, the opposite pattern was observed. However, we found contrasting patterns of population response to climate variability, depending on their functional diversity. Greater functional diversity does not necessarily increase biomass accumulation under different climatic conditions.

6. *Synthesis.* As all components of forest productivity contribute to NFP, studies on forest productivity should consider not only survivor growth but also recruitment and mortality. Each component responds differently in terms of biomass changes in climatic variation, according to the trait structure of tree communities. This

study provides a framework to identify the trait structure that should be targeted under different climate scenarios to anticipate change and help strengthen forest response capacity to climate change.

1 | INTRODUCTION

Diverse forests can be more productive than species-poor ones (Forrester, 2017; Liang et al., 2007, 2016; Paquette & Messier, 2011; Pretzsch, del Río, et al., 2015; Pretzsch, Forrester, et al., 2015; Zhang et al., 2012; Zheng et al., 2021). The positive mixing effects may reflect complementarity interactions, such as niche differentiation (i.e. where two or more species occupy distinct spatial niches enhancing collective performance) and facilitation (i.e. where one species positively influences another, directly or indirectly, by increasing its growth or survival) (Callaway, 1995; Loreau, 2000; Loreau & Hector, 2001). Competition between two species can be reduced if they differ in their use of a resource, for example one being adapted to the use of light found in the understorey, while another is specialized in the use of light higher up in the canopy (Man & Lieffers, 1999; Pretzsch, del Río, et al., 2015; Pretzsch, Forrester, et al., 2015) or one species can increase the amount of nitrogen available for another by increasing litter decomposition rates (del Río & Sterba, 2009; Man & Lieffers, 1999). The differential sensitivity of species to specific disturbance agents (e.g. diseases, pathogens, defoliation and climate) could also contribute to the positive mixing effect (Jucker et al., 2016; Pretzsch, 2005; Sousa-Silva et al., 2018). By studying the trait structure of communities, more attention is paid to the role of each organism in the ecosystem and to the attributes needed to maintain ecosystem functioning (Reiss et al., 2009). A trait can be defined as *'a measurable characteristic (morphological, phenological, physiological, behavioural, or cultural) of an individual organism that is measured at either the individual or other relevant level of organizational'* (Dawson et al., 2021). One of the fundamental advantages of their use is that they can provide generalizations across species and taxa, revealing the different ecological strategies involved in species assemblages (Dawson et al., 2021; Kraft et al., 2015; Shipley et al., 2016), and as such, inferences are more generalizable beyond the immediate study system. Thus, this approach enables the study of the mechanisms underlying the diversity–ecosystem function relationships and recognizes that some mixtures can be more complementary than others (Lavorel et al., 2008). Forest productivity can be studied as a net value (i.e. net forest productivity, NFP), defined as the biomass remaining after subtracting the losses through tree mortality (i.e. trees that have died between two measurements) from the gain of survivor growth (i.e. growth of trees that survived between two consecutive plot measurements) and tree recruitment (i.e. trees that reach 9.1 cm DBH between two measurements)

(Pretzsch, 2009). However, relatively few studies have examined the effect of the trait structure of tree communities on forest productivity in relation to demographic processes, namely survivor growth, recruitment and mortality, which all contribute to forest population dynamics (Condés & del Río, 2015; Liang et al., 2007; Looney et al., 2021).

Along with the trait structure, climate also represents a major determinant of forest productivity (Ammer, 2019). As reported by the Intergovernmental Panel on Climate Change (IPCC), global temperatures in the northern midlatitudes are projected to increase by 1.5–2°C and temperature extremes by 3–4°C, depending on the scenario (Allen et al., 2019; Ammer, 2019; Kirilenko & Sedjo, 2007), increases that will undoubtedly affect many forest ecosystems. As disturbances become more frequent or more intense (Dale et al., 2001), interactions among species will be altered. These changes will affect population dynamics and, therefore, ecosystem functions and services, of which productivity is a key feature (Ammer, 2019; Silva Pedro et al., 2016).

Currently, promoting tree diversity is seen as a promising avenue to adapt to climate change in current forestry practices (Ammer, 2019; Kolström et al., 2011; Looney et al., 2021; Pretzsch, del Río, et al., 2015; Pretzsch, Forrester, et al., 2015). A combination of different approaches can be used to help an ecosystem to functionally recover after changes (Thompson et al., 2009), either through resistance (i.e. the absence of change), resilience (i.e. the return to the initial state after a disturbance) or response (i.e. strengthening the capacity of forests respond to change) (Hörl et al., 2020; Malmsheimer et al., 2008; Millar et al., 2007). However, recent studies have shown contrasting patterns concerning the effect of tree diversity on the ability of some stands to maintain their productivity when subjected to climate change (CC) (Jucker et al., 2016; Paquette et al., 2017). Mitigating the effects of CC on forests requires identifying and understanding the circumstances under which tree species diversity has the utmost potential to positively influence forest productivity and its components, information that has important implications for forest management and forest conservation.

Our study had two goals. The first one was to understand how the structure of traits within tree communities influences the different components of forest productivity (survivor growth, recruitment of new trees and mortality) over a wide latitudinal and longitudinal gradient in northeastern North America. We proposed to address this question by using trait values from the literature to analyse the trait structure of tree communities within a large network of

periodically measured permanent sample plots (PSP). It can be assumed that the trait structure of communities affects each component of forest productivity differently. Indeed, it is expected that (i) leaf traits are associated with survivor growth because they are important for overall plant functioning, whereas (ii) traits related to resource acquisition have the largest impact on tree recruitment, and (iii) those related to competition and survival strategies play a more notable role in tree mortality. Our second goal was related to the effects of CC on forest productivity and motivated by this question: Does the trait structure of a community influence its ability to respond to climatic variations? We hypothesized that (iv) forests with the highest functional diversity have better adaptive capacity to an altered climate than those with the lowest diversity. To do this, we used annual temperature and precipitation to investigate how tree communities responded to a range of climatic conditions. The relationships between trait structure, productivity and climate may provide insights to evaluate under which circumstances tree species diversity can enhance forest productivity under CC.

2 | MATERIALS AND METHODS

2.1 | Study area

The PSPs used in the study cover a latitudinal and longitudinal gradient (45°–52.5°N and 55°W–80°W), stretching from the western border of the province of Quebec (QC) to the Atlantic coast of the province of Newfoundland (NL) (Figure 1). The ecozone covered by the PSP network extends from the Mixedwood Plains in the south to the Taiga Shield in the north, passing through the Atlantic Maritime, Hudson Plains, and Boreal Shield ecozones (Government of Canada, 2018). The dominant tree species in the Mixedwood Plains and Atlantic Maritime ecozones are sugar maple (*Acer saccharum*

Marsh.), and a mixture of boreal species, including balsam fir (*Abies balsamea* [L.] Mill.) and black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb.), and southern species, including yellow birch (*Betula alleghaniensis* Britt.). The Boreal Shield and the Hudson Plains ecozones are dominated by black spruce and white spruce (*Picea glauca* [Moench] Voss), balsam fir and eastern larch (*Larix laricina* [Du Roi] K. Koch). White birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsamifera* L.) and trembling aspen (*Populus tremuloides* Michx.) are also present in smaller proportions in this ecozone.

2.2 | Forest inventory

The QC permanent sample plot network, established in 1970 and still monitored today (Duchesne & Ouimet, 2008; Gouvernement du Québec, 2019), has more than 12,500 randomly distributed circular sample plots (400 m²). In each plot, trees with diameter at breast height (DBH; measured at 1.3 m above-ground) larger than 9.0 cm are numbered, and their DBH and status (alive, dead or harvested) are recorded at each survey. Recruits, living trees that reach the threshold of 9.1 cm DBH between two measurements, are numbered and their DBH recorded. Tree height is measured on a subsample of nine trees per plots (MRNF, 2022). For trees with missing height, it was predicted using species-specific models of height–diameter relationships (Auger, 2016). The PSPs are remeasured approximately every 10 years, with some plots having up to six measurements in total.

Data from NL were also collected from 400 m² circular sample plots established by the Canadian Forest Service of Natural Resources Canada from 1987, and plots have been remeasured every 3–5 years (up to eight measurements in total) (Government of Newfoundland and Labrador, 2022). The inventory protocol is similar to that of QC PSPs. Tree species, DBH at 1.3 m, tree height and status of all trees with DBH larger than 9.0 cm are recorded. The

FIGURE 1 Map of permanent sample plots and their distribution across eastern Canadian terrestrial ecozones, with the three reference climatic zones for the regionalized climate simulations in Quebec and the Maritimes (see Ouranos (2015) for details). Map lines delineate study areas and do not necessarily depict accepted national boundaries.
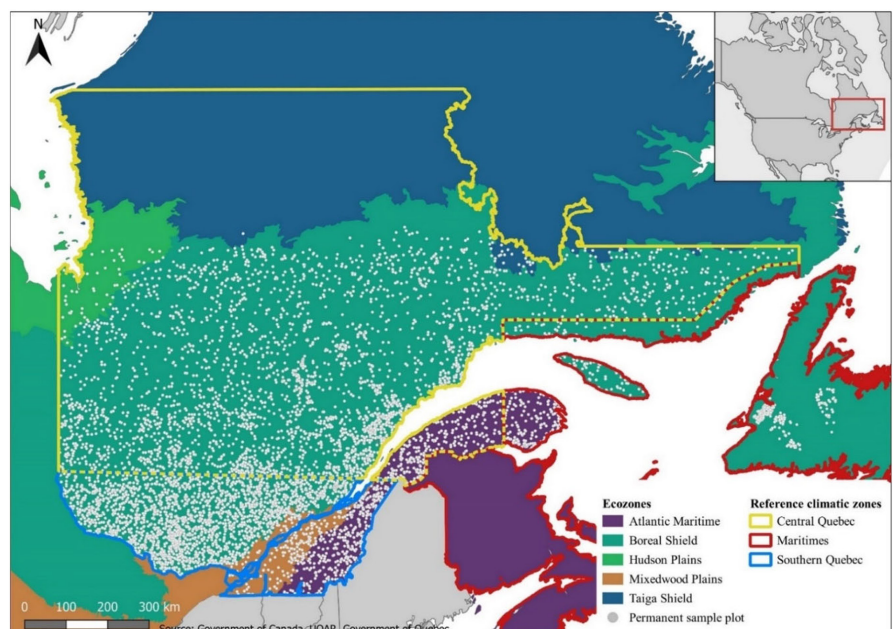
height of tree was measured using the *height vertex* feature of the Postex®, and models of height–diameter relationships were used to impute missing heights (Mehtätalo et al., 2015; van Lier et al., 2022).

After screening the two data sets for plots containing trees of merchantable species (i.e. trees with a commercial value) with a DBH over 9 cm and at least two consecutive measurements, we retained 11,835 different plots (Table 1), for a total of 30,799 pairs (30,037 QC, 762 NL) of plot measurements representing growth periods (i.e. a growth period consists of two consecutive measurements of a plot) to estimate changes in biomass at the plot level. We proceeded as follows. The total above-ground biomass of individual trees was predicted using previously published models of biomass (Lambert et al., 2005) using DBH and height as predictors. Then, the net forest productivity was divided into survivor growth SG (growth of trees that survived between two consecutive plot measurements), recruitment R (trees that reach 9.1 cm DBH between two measurements) and mortality M (trees that have died between two measurements). The trees that were harvested or thinned were recorded with a distinct code in the database and consequently were not included in the calculation of mortality. More precisely, these different components were calculated as follows for each pair of measurements:

$$SG_{ik} = \frac{\sum_{j \in sg} b_{ijk+1} - b_{ijk}}{t_{ik+1} - t_{ik}}, \quad (1)$$

$$R_{ik} = \frac{\sum_{j \in r} b_{ijk+1}}{t_{ik+1} - t_{ik}}, \quad (2)$$

$$M_{ik} = \frac{\sum_{j \in m} b_{ijk}}{t_{ik+1} - t_{ik}}, \quad (3)$$

$$Y_{ik} = SG_{ik} + R_{ik} - M_{ik}, \quad (4)$$

where sg, r and m are the sets of trees that survived, were recruited and died, respectively, SG_{ik} is the survivor growth in biomass b for all the survivor trees in plot i, over the interval that goes from measurement k to measurement $k+1$, tree recruitment R_{ik} is defined as the above-ground biomass b of the trees that were recruited between measurements, and tree mortality M_{ik} is defined as the above-ground biomass b of a tree that died between measurements k and $k+1$. Net forest productivity Y is expressed as total living above-ground biomass increments (Mg ha^{-1} year^{-1} of dry biomass) in plot i between measurements k and $k+1$. Mortality does not consider the growth of dead trees (growth between the last plot measurement when the tree is alive and the moment of its death) since dead trees are not measured. A tree was noted as a recruit once it achieved merchantable size (i.e. DBH >9 cm).

2.3 | Explanatory variables

We used a series of 37 explanatory variables to account for between-plot differences (Table 1). Among these, five described the forest structure, six described the environment, and 26 described the trait structure of tree communities.

2.3.1 | Forest structure

Forest structure was characterized by five variables that were computed at the initial measurement of each interval. Competition was quantified using merchantable basal area (m^2 ha^{-1}, i.e. calculated with trees with a DBH over 9 cm and a commercial value). Plot ontogeny was estimated using dominant height (average height of the four thickest trees in the plot) as proxy. Stand composition was assessed with the dominant species and with the basal area of the dominant species (m^2 ha^{-1}). The plot's total biomass (Mg ha^{-1} of dry biomass) was also included.

2.3.2 | Environment

Six environmental descriptors of local biophysical conditions and climate were included. Topographic position index (TPI) and topographic wetness index (TWI) (20 m resolution) were used as proxies for biophysical conditions (De Reu et al., 2013; Kopecký et al., 2021) and calculated once for each plot. The mean and minimum total annual precipitation (mm) and the mean and maximum annual temperatures (°C) of each interval were used as climatic variables and were obtained using the BioSIM software v.10.2.4.20 (Régnière et al., 2014).

2.3.3 | Trait structure of communities

The last set of variables was to evaluate the trait structure of the plots at the initial measurement of each interval. As has been done in other studies (Díaz et al., 2007; Mokany et al., 2008; Paquette & Messier, 2011), we characterized the trait structure of communities to assess which trait or group of traits drives each component of forest productivity. It is possible to characterize the trait structure of communities using a variety of indices (Dias et al., 2021). We assembled a table of traits from published sources for the 38 merchantable tree species observed in our data set (Aubin et al., 2020; Paquette & Messier, 2011) (see Table S1 for more details regarding the dataset) as well as a table of species abundance (i.e. total species basal area m^2 ha^{-1}) by plot. Several community functional structure indices were then computed using the *FD* (Laliberté et al., 2014) and *SYNCSA* (Debastiani & Pillar, 2012) R packages (see Table S2): functional dispersion (FD$_{is}$) (Laliberté & Legendre, 2010), community-level weighted means of trait values (CWM) (Laliberté & Legendre, 2010; Lavorel et al., 2008), functional redundancy index (FR) (de Bello et al., 2007; Pillar et al., 2013), a posteriori functional group richness (FGR) (Laliberté & Legendre, 2010), Rao's quadratic entropy (Q) (Laliberté & Legendre, 2010; Rao, 1982) and Gini–Simpson index (D) (Simpson, 1949). Two more traditional diversity indices based on species abundance only (i.e. without traits) were computed for comparison: Shannon–Wiener diversity index (H′, e$^{H'}$) (Burks, 1951; Shannon, 1948; Shannon & Weaver, 1949) and species richness (N) (Spellerberg & Fedor, 2003).

TABLE 1 Description of the study data set per eastern Canadian terrestrial ecozone.

	Atlantic maritime	Boreal shield	Hudson Plains	Mixedwood Plains	Taiga shield
Number of plots	1556	9721	103	386	69
Number of pairs of measurements	3869	25,544	228	986	172
Mean net forest productivity increment (Mg ha^{-1} year^{-1})	2.6±2.0 (0.3–4.9)	1.7±1.7 (0.0–3.8)	0.2±1.1 (−0.4–1.2)	3.3±1.7 (1.1–5.3)	0.4±0.7 (0.0–1.0)
Mean survivor growth increment (Mg ha^{-1} year^{-1})	2.2±1.5 (0.2–4.2)	1.6±1.3 (0.1–3.4)	0.3±0.5 (0.0–0.9)	2.8±1.6 (0.6–4.9)	0.4±0.3 (0.1–0.8)
Mean tree recruitment increment (Mg ha^{-1} year^{-1})	0.7±0.9 (0.0–1.8)	0.5±0.7 (0.0–1.4)	0.2±0.3 (0.0–0.5)	0.8±0.8 (0.0–1.8)	0.3±0.2 (0.0–0.6)
Mean tree mortality loss (Mg ha^{-1} year^{-1})	0.4±0.9 (0.0–1.0)	0.4±0.9 (0.0–1.3)	0.4±0.9 (0.0–0.7)	0.3±0.7 (0.0–0.9)	0.3±0.6 (0.0–0.7)
Mean net biomass (Mg ha^{-1})	86.7±62.0 (12.6–163.9)	80.9±58.3 (12.8–157.3)	40.2±41.4 (2.5–95.5)	110.1±68.4 (27.2–199.8)	40.5±26.5 (8.4–71.8)
Basal area (m^2 ha^{-1})	22.1±12.9 (4.7–38.2)	20.3±12.2 (4.3–36.1)	11.2±9.6 (1.4–23.5)	25.4±12.7 (8.7–41.8)	13.4±7.7 (3.5–22.9)
Dominant height (m)	17.1±4.2 (11.4–22.4)	16.9±4.5 (10.9–22.7)	12.6±3.1 (9.0–16.5)	19.9±4.3 (14.2–25.2)	12.5±2.3 (9.4–15.3)
Three most-dominant species	Abies balsamea Acer saccharum Acer rubrum	Picea mariana Abies balsamea Betula papyrifera	Picea mariana Pinus banksiana Larix laricina	Acer rubrum Acer saccharum Abies balsamea	Picea mariana Pinus banksiana Abies balsamea
Dominant species basal area (m^2 ha^{-1})	13.0±9.0 (2.8–25.6)	12.4±8.4 (2.9–23.4)	9.9±8.3 (1.2–21.4)	13.5±7.9 (4.6–23.8)	10.9±5.6 (3.3–17.7)
Mean topographic position index (TPI)	3 (1–5)	3 (1–5)	2 (2–5)	3 (1–5)	3 (1–5)
Mean topographic wetness index (TWI)	7.1±1.6 (5.4–9.4)	6.9±1.6 (5.3–9.0)	9.2±1.8 (6.9–11.8)	7.3±1.4 (5.9–9.6)	7.8±1.3 (6.3–9.1)
Mean annual temperature (°C)	3.2±1.1 (1.7–4.6)	1.6±1.9 (−1.1–4.0)	−0.3±0.7 (−1.3–0.6)	5.1±0.9 (4.0–6.3)	−2.3±1.0 (−3.5 to 1.1)
Mean annual total precipitations (mm)	1139.5±105.3 (1002.7–1271.2)	1007.0±141.8 (870.4–1187.0)	785.6±36.5 (742.3–848.7)	1090.3±84.9 (978.7–1200.4)	822.7±68.2 (739.6–913.5)
Species richness (SR)	4.0±1.7 (1–14)	3.5±1.8 (1–14)	1.5±0.7 (1–5)	4.8±1.9 (1–10)	1.9±0.6 (1–3)
Proportion of plots with low SR (no. species <4)	40.6%	56.7%	97.3%	27.9%	100.0%
Functional dispersion (FDis index, with all traits)	0.1049±0.0514 (0.0224–0.1637)	0.0891±0.0546 (0.0000–0.1569)	0.0262±0.0422 (0.0000–0.1066)	0.1198±0.0492 (0.0451–0.1723)	0.0369±0.0319 (0.0000–0.0759)

Note: Mean±standard deviation is provided for continuous variables, followed by the range. Values were scaled to 1 ha from the original 400 m^2 plot size, and ranges are the 10th and 90th percentiles.

To obtain the best possible community trait structure indices, several combinations of traits were used to calculate the indices. First, indices based on all available traits and individual traits were calculated. Second, based on Westoby's (1998) proposed scheme to classify species strategies, we categorized those traits grouped along different dimensions. If multiple traits are related to the same ecological strategies or are part of a group that characterizes similar functions, they can be said to be part of the same plant strategy dimension or the same functional group dimension (Wright et al., 2007). We separated the available traits into three plant strategy dimensions: (1) resource acquisition; (2) competition/survival; and (3) reproduction; and in a second manner, into five functional group dimensions: (1) tree stature; (2) dispersal, germination, and seedling development; (3) stress tolerance/environment; (4) underground; and (5) leaf (see Table S1). Diversity indices were then built with all the traits categorized in these various dimensions and with all possible combinations of either three or five traits for plant strategy dimensions and functional group dimensions, respectively. The details of these indices are presented in Table S3.

Finally, to reduce the dimensionality of the trait structure index matrix, we applied a clustering approach to group the indices into homogeneous clusters such that each cluster was composed of indices yielding similar information (Chavent et al., 2011). To evaluate the feasibility of the clustering analysis (i.e. non-random structures), we computed the Hopkins statistic (H) with R's *factoextra* package (Kassambara & Mundt, 2017). A value of H greater than 0.75 indicates a tendency to cluster at the 90% confidence level (Table S4). To then assess the optimal number of clusters k (Table S4), we used the variance explained, silhouette and AIC criterion with R's *ClusterR* package (Mouselimis, 2022). Clustering analyses were performed on (1) indices built with all traits; (2) indices built with individual traits; (3) indices built with traits grouped into dimensions; (4) indices built with a combination of three traits; and (5) indices built with a combination of five traits. The index retained for each cluster was that closest to the central synthetic variable, the medoid (Table S4.). We thus reached a final set of 26 indices to account for differences in trait structure of the plots: two indices calculated with species abundance only (e^H and N added for comparison), three indices calculated with all the traits (D, FDis, FGR), three community-weighted mean indices (CWM.SeFreq, CWM.TolD, CWM.LMA), eight functional dispersion indices (FDis.Pb, FDis.Nmass, FDis.WDR, FDis.Leaf, FDis.Eco296, FDis.3, FDis.5, FDis.Logi2106), three Gini–Simpson indices (D.Tree, D.Eco1, D.Logi1), four Rao's quadratic entropy index (Q.Eco242, Q.Eco277, Q.Eco506, Q.Logi354) and three functional redundancy indices (FR.Eco5, FR.Logi394, FR.Logi1252) (see Table S5 for details).

2.4 | Analysis

The set of 37 field-measured attributes related to forest structure, environment and trait structure of communities was then included in a random-forest (RF) analysis. Random-forest regression is an effective prediction method when the number of predictors is high and when interactions and correlations among them are numerous and complex (Breiman, 2001; Strobl et al., 2008; Svetnik et al., 2003). The RF algorithm finds the optimal combination of explanatory variables (Kuhn & Johnson, 2013) to reduce the number of predictors and maximize model performance. The RF modelling was performed using the recursive feature elimination algorithm from the *caret* package (Kuhn, 2020) in R. The RF was calculated to find the best subset of predictors—from a model having a single explanatory variable to a model using all explanatory variables—that generates the lowest root mean square error (RMSE) with a tolerance of 3% (3% more error than the model with the lowest RMSE) and with 50 repetitions of 10-fold cross-validation. We used the above-mentioned 37 explanatory variables describing forest structure, environment and trait structure to predict NFP and the above-ground biomass increment attributed to survivor growth, recruitment and mortality. The optimal model was recalibrated using the *randomForest* package (Liaw & Wiener, 2002) in R, with the number of features sampled at each split set to the default value for regression (i.e. $p/3$ where p is number of variables) and the number of random trees set to 20,000. To understand how each feature contributes to the model's predictive performance, we used the per cent increase in mean square error (MSE) to determine variable importance (Kuhn & Johnson, 2013). This method is the most robust and informative measure and is based on the average decrease in the precision of the predictions of the out-of-bag samples—data used by the algorithm to incorporate a validation step within the fitting procedure—when a given variable is excluded from the model (Attanasi et al., 2020; Liaw & Wiener, 2002). As the per cent in MSE for a given variable becomes greater, so does the importance of this variable. In addition to looking at the RF model's performance as RMSE, the percentage of the explained variance (R^2) was also calculated. Serial and spatial correlations among the residuals were checked and found to be small or negligible, indicating very limited impact on the statistical inference (Aarts et al., 2014) (see SI Appendix text and Tables S6 and S7 for details).

3 | RESULTS

3.1 | Important variables linked to forest productivity

Survivor growth explained an average 63% of total forest productivity (see SI Appendix text and Figure S1 for details), whereas tree recruitment and tree mortality were responsible for 26% and 10% of total forest productivity, respectively (Figure S1). In our models, all the explanatory variables, including those describing the trait structure of tree communities, explained 53% of the variance in plot NFP, 78% of the survivor growth contribution to NFP, 55% of tree recruitment contribution to NFP and 13% of the tree mortality of contribution to NFP (Figure 2).
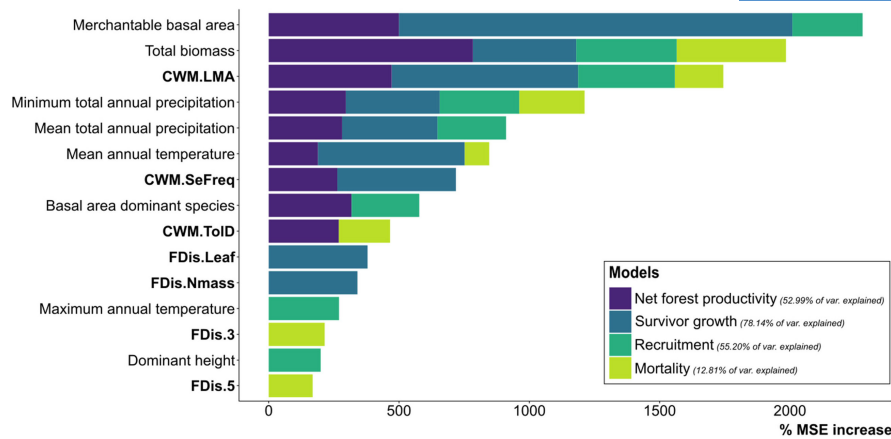
FIGURE 2 Important variables for net forest productivity (52.99% of variance explained), survivor growth (78.14% of variance explained), recruitment (55.20% of variance explained) and mortality (12.81% of variance explained) models. Important diversity features are in bold: the community-weighted means of leaf mass per area (CWM.LMA), seed frequency (CWM.SeFreq), and drought tolerance (CWM.TolD), the functional dispersion index based on leaf traits (FDis.Leaf; i.e. leaf size, leaf longevity, leaf mass per area, and nitrogen content per leaf mass unit), the functional dispersion index based only on the leaf nitrogen content trait (FDis.Nmass), the functional dispersion index based on three traits (FDis.3, i.e., ectomycorrhiza, wood decay resistance, and vegetative reproduction), and the functional dispersion index based on five traits (FDis.5, i.e. average maximum height, frequency of a good crop year, drought tolerance, root depth, and leaf longevity).

In terms of the important explanatory variables related to forest structure, merchantable basal area, total biomass, basal area of the dominant species and dominant height were retained in at least one model. Total biomass at the beginning of the growing period was among the most important variables for the four models, increasing the mean square error (MSE) 784%, 397%, 385% and 419% if removed from the NFP, survivor growth, tree recruitment and tree mortality models, respectively. When total biomass was excluded, the merchantable basal area was important in the NFP (500% MSE increase if removed), survivor growth (1510% MSE increase if removed) and recruitment (270% MSE increase if removed). The basal area of the dominant species was important for both NFP and tree recruitment, increasing the MSE 318% and 260%, respectively, if removed. Finally, dominant height was only important in the tree recruitment model by increasing the MSE 199% when dropped from this model.

Among all the environment-related explanatory variables, climate variability emerged as an important variable in all four models (Figures 2 and 3). At least two of the following climatic variables explained the observed variation (calculated based on observed data range) in the four models: mean and/or minimum annual total precipitation and mean and/or maximum annual temperature.

The mean square error (MSE) increased by 189%, 563% and 94% when mean annual temperature was excluded from the NFP, survivor growth and tree mortality models, respectively. MSE increased by 270% when maximum annual temperature was excluded from the tree recruitment model. The variable importance plot (Figure 2) also illustrates that the MSE increased by 296% if minimum annual precipitation was dropped from the NFP model, by 360% in the survivor growth model, by 305% in the tree recruitment model and by 251% in the tree mortality model.

Finally, regarding the explanatory variables linked to the trait structure of communities, RF models showed several of these variables to be relevant for explaining the variability of NFP and each of its components (Figure 2). The community-weighted mean of leaf mass per area (CWM.LMA) was common to all four models and was always among the five most important variables. When CWM.LMA was excluded, the MSE increased by 472% for the NFP model, 716% for the survivor growth model, 371% for the tree recruitment model and 186% for the tree mortality model. For both NFP and tree mortality, the community-weighted mean of drought tolerance (TolD) was also an important trait, and the MSE increased by 269% when CWM.TolD was excluded from the NFP model and 196% from the tree mortality model. Moreover, the community-weighted mean of seed frequency (SeFreq) was an important trait for both the NFP and survivor growth models. The higher the seed frequency trait, the longer the period between two good mast years. The variable importance plot shows that the MSE would increase by 263% if CWM.SeFreq were to be dropped from the NFP model and 455% in the survivor growth model. The functional dispersion (FDis) index based on leaf traits (FDis.Leaf, i.e. leaf size, leaf longevity, leaf mass per area and nitrogen content per leaf mass unit) and the FDis based only on the leaf nitrogen content trait (FDis.Nmass) were both important functional diversity features in the survivor growth model. Moreover, both the functional dispersion index using three (FDis.3, i.e. ectomycorrhiza, wood decay resistance and vegetative reproduction) and five traits (FDis.5, i.e. average maximum height, frequency of a good crop year, drought tolerance, root depth and leaf longevity) entered the tree mortality model. The MSE would respectively increase by 379% and 340% if FDis.Leaf and FDis.Nmass were to be excluded from the survivor growth model. MSE would increase by 215% and 169%, respectively, if FDis.3 and FDis.5 were dropped from the tree mortality model.
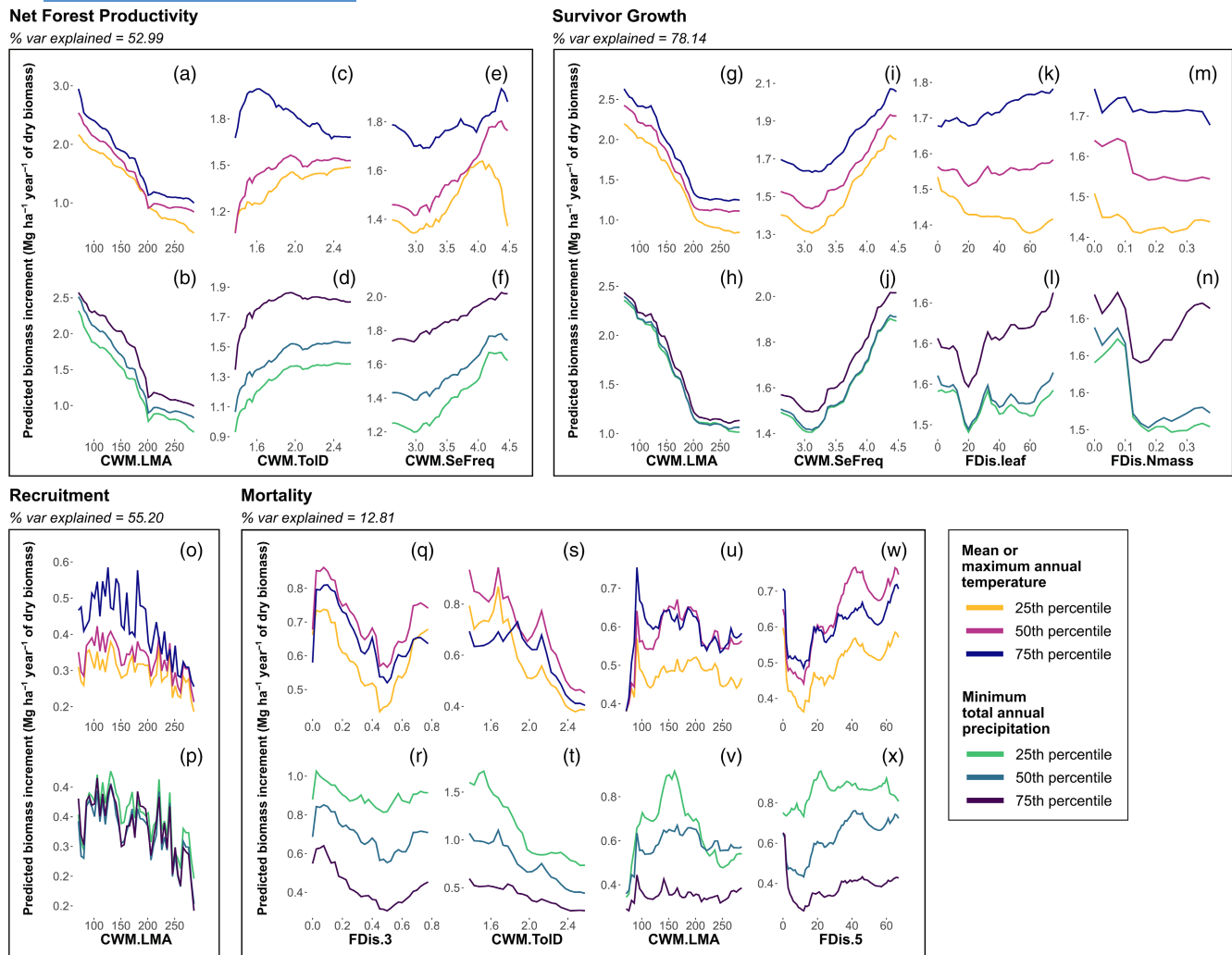
FIGURE 3 Predicted biomass increment (Mg ha^{-1} year^{-1} of dry biomass) as a function of important diversity features for net forest productivity, survivor growth, recruitment and mortality, with variations in mean or maximum annual temperature (°C) and minimum total annual precipitation (mm) calculated based on observed data range. Important diversity features are as follows: the community-weighted means of leaf mass per area (CWM.LMA), seed frequency (CWM.SeFreq) and drought tolerance (CWM.TolD), the functional dispersion index based on leaf traits (FDis.Leaf; i.e. leaf size, leaf longevity, leaf mass per area, and nitrogen content per leaf mass unit), the functional dispersion index based only on the leaf nitrogen content trait (FDis.Nmass), the functional dispersion index based on three traits (FDis.3, i.e. ectomycorrhiza, wood decay resistance and vegetative reproduction), and the functional dispersion index based on five traits (FDis.5, i.e. average maximum height, frequency of a good crop year, drought tolerance, root depth and leaf longevity). Diversity features are limited to between the 10th and 90th percentiles.

3.2 | Trait structure–productivity–climate interactions

When examining biomass accumulation against community's trait structure under climate variation (25th–75th percentiles), the predicted biomass increments in both the NFP, and survivor growth models were always greater at higher mean annual temperatures and higher minimum annual precipitation (Figure 3a–n). Predicted tree recruitment was greater at higher maximum annual temperatures (Figure 3o) and remained similar despite variation in minimum annual precipitation (Figure 3p). For tree mortality, the predicted biomass increment was similar between the 25th, 50th and 75th percentile of mean annual temperatures (Figure 3q,s)

but appeared slightly lower when temperatures were low (Figure 3u,w). However, when the minimum annual precipitation was low (25th percentile), mortality was higher than at high levels of minimum annual precipitation (75th percentile) (Figure 3r,t,v,x). The percentile values (25th, 50th and 75th) corresponding to the environmental descriptors of climate were, respectively, 0.6, 2.1 and 3.3°C for mean annual temperature, 7.7, 9.1 and 10.2°C for maximum annual temperature and 752, 834 and 918 mm for minimum total annual precipitation.

Furthermore, the interaction of explanatory variables showed interesting variation patterns. First, we observed an interaction between drought tolerance CWM and mean annual temperature. With temperatures near the 25th and 50th percentiles, NFP biomass

accumulation increased with the value of the CWM.TolD; however, at higher temperatures (near the 75th percentile), we observed the opposite pattern (Figure 3c). Then, as seed frequency CWM values increased, biomass accumulation for NFP also increased as the climate warmed (50th and 75th percentiles). But, for communities that experienced a longer period between good mast years (4+ years) at low temperatures (25th percentile), NFP biomass accumulation dropped drastically (Figure 3e). As the temperature increased to the 50th percentile, these communities (high CWM.SeFreq) accumulated biomass at a similar amount as when the temperature approached the 75th percentile. Regarding survivor growth, FDis.Leaf showed an interaction with temperature and precipitation. Indeed, the greater the increase for FDis.Leaf, the more the precipitation and temperature curves diverged (Figure 3k). FDis.Nmass demonstrated the same pattern of divergence between precipitation curves for high-FDis.Nmass communities (Figure 3n), with survivors' growth increasing at 75th percentile and decreasing at 25th percentile of the climate variable. For tree recruitment, when CWM.LMA values were low, temperature curves diverged and tree recruitment was higher at the 75th percentile of temperature. Then, tree recruitment decreased and was similar at all temperatures as CWM.LMA values increased (Figure 3o). The CWM.TolD index showed a similar interaction with precipitation in regard to tree mortality. In communities having a low CWM.TolD, mortality diverged between the three precipitation curves and was higher at 25th percentile of precipitation, then converged as CWM.TolD increased (Figure 3t). Finally, we also observed some interactions between tree mortality and precipitation for the CWM.LMA index (Figure 3v). We noted that the lowest tree mortality occurred for communities with lower CWM.LMA values at high precipitation (75th percentile). However, at low precipitation, predicted biomass loss associated with tree mortality was at its highest for mid-CWM.LMA communities then dropped considerably for communities with a high CWM.LMA.

4 | DISCUSSION

Tree species diversity can enhance forest productivity by improving positive interactions between species and providing greater growth stability (Ammer, 2019; Looney et al., 2021; Paquette & Messier, 2011). Very few studies have, however, explored the influence of the trait structure of tree communities on survivor growth, recruitment and mortality, which are the main drivers of species population dynamics in forests not subject to thinning or harvesting (Liang et al., 2007; Looney et al., 2021). Using RF models and PSP data covering a wide gradient of climatic conditions, we isolated the effects of the trait structure and climate variables on NFP, survivor growth, recruitment and mortality. Our analysis of the interactions between trait structure, productivity and climate made it possible to evaluate the contribution of the trait structure of tree communities to forest productivity and to determine the trait, group of traits or functional diversity indices that can improve the capacity of communities to respond to future climate conditions.

4.1 | Communities' trait structure influences each component of forest productivity

Although it is well known that tree species diversity has an effect on productivity, our results lead to a better understanding of the aspects of functional diversity that influence the underlying components of overall productivity. Examining forest productivity purely from the perspective of survivor growth cannot reveal the full extent to which tree functional diversity affects forest dynamics. By examining the patterns of biomass increment in relation to the trait or indices that are common among our models, we managed to assess the contribution of each component to NFP.

Our models explained 53% of the variance in plot NFP, and respectively, 78%, 55% and 13% of the survivor growth, tree recruitment and tree mortality contribution to NFP. These findings align with prior research, showcasing the intricate relationship between diversity, environmental conditions and forest productivity. Even though they were relying on different environmental variables and diversity indices, many studies on forest productivity report similar percentages of variance explanation (Hao et al., 2018; Healy et al., 2008; Liang et al., 2007; Looney et al., 2021; Morin et al., 2018; Paquette & Messier, 2011; Silva Pedro et al., 2016; Zhang et al., 2012). For example, Hao et al. (2018) reported that 45% of the above-ground biomass variation was accounted for by their model, with 24% attributable to biodiversity and environmental conditions and Silva Pedro et al. (2016) that the influence of diversity on forest productivity accounted for up to 54.2% of the variance.

The relationships between NFP and the trait structure of the communities were similar to those observed for the survivor growth component. This pattern is corroborated by our results for the contribution proportion of each component to total forest productivity (see SI Appendix text and Figure S1 for details for details), which showed that survivor growth was the component that most contributed to NFP. The second-most important contributor to total forest productivity was recruitment, supported by tree recruitment being driven by LMA (quantified by the community-weighted mean of leaf mass per area, CWM.LMA) in the same manner as NFP. Finally, mortality influenced NFP through the drought-tolerance trait but contributed the least to total forest productivity. The results of our study demonstrate that all three components contribute to forest productivity, but above all that some components have a stronger impact than others. Future forest productivity studies should therefore consider all components.

To address our first research question, our results first highlight how each of NFP components are influenced by the trait structure of communities. Three traits were important in predicting NFP and are each from a different plant strategy dimension (Westoby et al., 2002; Wright et al., 2007). Those traits cover all life-history strategies that contribute to overall plant fitness: resource acquisition (LMA), competition/survival (ToID) and reproduction (SeFreq). High NFP was indeed linked to low-LMA communities (i.e. species that acquire resources rapidly and have high growth rates (Poorter et al., 2009)). It was also associated with

both drought-tolerant communities (quantified by the community-weighted mean of drought tolerance, CWM.TolD) and communities with long period between two good mast years (quantified by the community-weighted mean of seed frequency, CWM.SeFreq). Our results confirm that a single dimension is not sufficient to fully capture the effects of functional diversity on forest productivity. Moreover, our results confirm that Westoby's three-way scheme can more accurately capture all aspects of plant strategies (Westoby, 1998; Westoby et al., 2002).

Then, considering each component separately, survivor growth was first strongly linked to leaf traits, as expected and thus, to resource acquisition. Of the four important explanatory variables related to the structure of traits of communities, three were calculated from leaf traits (i.e. CWM.LMA, FDis.Nmass—the functional dispersion index based on the leaf nitrogen content trait, and FDis.leaf—the functional dispersion index based on leaf traits: leaf size, leaf longevity, leaf mass per area and nitrogen content per leaf mass unit), thus corroborating our first hypothesis. High survivor growth was, as with NFP, linked to low-LMA communities. Higher growth was also associated with more diversity among leaf traits, but with less diversity among Nmass traits. Survivor growth was also positively correlated to the seed frequency trait (CWM.SeFreq), which is an indicator of resource allocation for the plant. The longer the period between two good mast years, the lower the cost associated with reproduction, leaving more resources available for growth during that time, as observed for evergreen trees (Tumajer & Lehejček, 2019; Vergotti et al., 2019).

The interaction between seed production, seed germination, seedling survival and growth to the sapling stage, and subsequent sapling survival and growth to the pole stage are all key aspects of tree recruitment. The dynamics prior to the pole stage, however, were unknown. Tree recruitment only had one trait associated with resource acquisition (leaf mass per area, CWM.LMA) as its main feature, supporting our second hypothesis. As with NFP and survivor growth, tree recruitment was higher for low-LMA communities. Recent studies also showed that LMA was negatively correlated with recruitment and was explained by the fact that plant carbon gain and allocation are strongly influenced by leaf economic traits (He et al., 2022; Wright et al., 2004). Low-LMA pioneer species are prompt to colonize disturbed stands. Because of an increase in resource availability, rapid growth and tree turnover rates are indeed observed in recently disturbed areas (Blundo et al., 2015; Poorter et al., 2009; Sui et al., 2017), where species compete for light and nutrients for increased colonization probability (He et al., 2022; Qi et al., 2021).

Finally, although a trait related to competition and survival (drought tolerance, CWM.TolD) drove tree mortality as expected by our third hypothesis, tree mortality was also influenced by a mixture of traits reflecting various plant strategies and functional groups. This suggests that a three- or five-way scheme would be better to understand the effect of functional diversity on tree mortality. Mortality, however, was highly stochastic and the least well-explained component by our models. High mortality has nonetheless been linked to communities with low drought-tolerance, explaining low NFP of these communities. The trend of the relationships with the two functional dispersion indices (FDis.3—the functional dispersion index based on three traits: ectomycorrhiza, wood decay resistance, vegetative reproduction; and FDis.5—the functional dispersion index based on five traits: average maximum height, frequency of a good crop year, drought tolerance, root depth, leaf longevity) are, however, unexpectedly contrasting, showing respectively a negative and a positive correlation. Predicting tree mortality is challenging and environment alone (i.e. mainly edaphic variables) can explain nearly twice as much variability as diversity and can be more important for tree mortality than for net productivity (Healy et al., 2008; Hooper et al., 2005). In our study however, when plots were established in the field, ecotones with greater variation in edaphic conditions (e.g. plots crossing boundaries between wetland and upland forests) were avoided.

A few things should be considered when studying the effects of functional community structure on forest productivity. First, regarding how to quantify the trait structure of communities, many traits and indices of functional diversity have been introduced in the last decades. A lot of studies are using the FD_{is} (Bell et al., 2023; Hao et al., 2018; Looney et al., 2023; Morin et al., 2011; Paquette & Messier, 2011). However, our results showed that other indices such as the CWM or single traits (e.g. LMA, TolD and SeFreq) seemed to better capture the variability of forest productivity and each of its components. Also, to properly test our traits matrix according to Westoby's three traits scheme, an enormous number of indexes would need to be tested to determine which mix of traits is the best among all possible iterations of three traits. Moreover, working at large scale is very limiting in terms of data availability, especially on traits which are difficult to find (large-scale databases are just beginning to be compiled) and very laborious to quantify when working on several species. Qualitative traits, like relative shade tolerance, are more common in the literature and databases than quantitative traits. Some trait classes are underrepresented, for example, frost-related or underground traits that are difficult to collect. A fully comprehensive analysis is then hard to perform. As a result of this lack of data, we worked with trait averages across Canada, which fail to account for intraspecific variability and to assess changes in trait values along gradients. Consequently, species-specific trends may be hidden behind these averaged traits. Our results should therefore be interpreted with caution, as they are representative of the mean and trait value measurements could be biased in favour of populated and accessible areas. Also, as the trait structure of the plots was evaluated at the initial measurement of each interval, it may not fully capture stand conditions throughout the whole interval, especially when heavy tree mortality or recruitment occurs. Furthermore, as species traits vary between sites, they will change in divergent ways in the face of climate change. It is also worth mentioning that we were also limited by the forest inventory data for the choice of explanatory variables (i.e. forest attributes and environment). Among other things, we did not have enough information on past

disturbances, which could have had an impact on forest productivity and species composition in these forests. Our study also relies solely on the examination of merchantable trees, leaving a portion of the total biomass unexplored. The biomass of saplings should, however, be low, as a study conducted in softwood forests found that saplings accounted for a mere 5% of the total biomass in locations with a stand volume of $100\,m^3\,ha^{-1}$ (Boudewyn et al., 2007). This condition was observed in around 61% of the forests that were part of the research. Finally, the findings hold relevance for the studied forests, it should be borne in mind that they may not hold the same weight if applied to more diverse forest ecosystems.

4.2 | Climate variability influences biomass accumulation of communities through their trait structure

To answer our second research question, we investigated the interactions between biomass accumulation, trait structure of tree communities and climate. We found that forest communities generally experienced a positive response to higher annual temperatures and total precipitation. Our results showed that communities subject to higher temperatures and precipitation can absorb these disturbances and maintain similar or even enhanced functioning. This is in line with recent global forests analysis that found a positive relationship between species richness and mean annual temperature and total annual precipitation increases (Liang et al., 2022).

In the survivor growth, recruitment and mortality models, LMA (CWM.LMA) contributed to the overall NFP, even though the climate interaction was weak. Low-LMA species tend to be present when resources are abundant and are generally associated with productive ecosystems (Poorter et al., 2009). As presented above, LMA showed clear interactions with temperature for recruitment. A rise of maximum temperature of 1.1°C (9.1 to 10.2°C, i.e. from the 50th to the 75th percentile) increased tree recruitment by approximately $0.15\,Mg\,ha^{-1}year^{-1}$ of dry biomass, especially for communities with lower LMA values. Tree recruitment is highly dependent on environmental conditions (Blundo et al., 2015), and because low-LMA communities are characterized by greater resource availability, recruitment is greater (Poorter et al., 2009). In addition, increased temperatures and the often-resulting water deficit can alter population dynamics. Following droughts, tree mortality is higher, creating gaps in the canopy and increasing resource availability and light availability and, in turn, increasing tree recruitment (Anderegg et al., 2019; Chen et al., 2019). This sequence can explain our observed higher tree recruitment under warmer temperatures. Moreover, during drier years, trees experience increased stress and mortality (Anderegg et al., 2019; Trugman et al., 2019), as we observed for average-LMA communities at the lowest precipitation in the mortality model. If minimum total annual precipitation is reduced of 82mm (834 to 752mm, i.e. from the 50th to the 25th percentile), predicted mortality increased from approximately 0.6 to about $0.9\,Mg\,ha^{-1}year^{-1}$ of

dry biomass. To optimize their functioning under an altered climate, trees can demonstrate high plasticity in their leaf characteristics to reduce water loss and buffer the impact of tree mortality (Cui et al., 2020; Huang et al., 2019).

In addition to the above, our findings on drought tolerance (CWM.TolD) hint that low drought tolerance relates to low net plot productivity and can be explained by high tree mortality when precipitation is less abundant. Tree mortality related to drought or low annual precipitation is well-documented (Aleixo et al., 2019; Anderegg et al., 2019), although the underlying mechanisms are only beginning to be understood (Liu et al., 2021). During a drought, trees face a trade-off between carbon gain and water loss, as canopy evaporation demand increases beyond the sapwood supply capacity (Lopez-Iglesias et al., 2014; Trugman et al., 2019). Decreased transpiration through stomatal closure can prevent hydraulic failure in the xylem but can induce metabolic stress, hydraulic damage and reduced survivor growth that contribute to lower NFP and higher tree mortality (Chauvin et al., 2019; Trugman et al., 2019). Drought-intolerant communities experienced an increase of predicted tree mortality of $0.5\,Mg\,ha^{-1}year^{-1}$ of dry biomass when minimum total annual precipitation changes from 834mm (50th percentile) to 752mm (25th percentile). Moreover, as tree growth rate is strongly related to water supply and xylem-specific hydraulic conductivity (He et al., 2022; Poorter et al., 2010; Qi et al., 2021), it is plausible that the increase in minimum total annual precipitation from 834mm (50th percentile) to 918mm (75th percentile) contributes to the rise in NFP of drought-tolerant communities from approximately 1.5 to $1.8\,Mg\,ha^{-1}year^{-1}$. Thus, tree response to drought variability is important for understanding forest vulnerability to climate- and drought-induced mortality events (Anderegg et al., 2019).

We also observed that the longer the period between two good mast years (quantified by the community-weighted mean of seed frequency, CWM.SeFreq), survivor growth increased by about $0.1\,Mg\,ha^{-1}year^{-1}$ and NFP by $0.2\,Mg\,ha^{-1}year^{-1}$ when temperature and precipitation increased, respectively, from 2.1 to 3.3° and 834 to 918mm (50th to the 75th percentile). Seed frequency relates to both reproduction and growth (Greene & Johnson, 2004; Lambers et al., 2008), because, as mentioned above, the time between good mast years is a great indicator of resource allocation for the plant. Most species do not produce frequent mast years for reasons such as climatic conditions, photosynthate production, pollination success and/or predation (Greene & Johnson, 2004; Lambers et al., 2008). In North America, climate has been found to play a role in the masting behaviour of conifer species (Redmond et al., 2012; Wion et al., 2023). This observation is consistent with our results, as we noted an obvious effect of this trait in the survivor growth and NFP models.

Lastly, there are contrasting patterns of climate response shown by the four functional dispersion indices. In warmer and wetter conditions (i.e. increase of 1.2°C and 84mm, 50th to the 75th percentile), higher FDis.Leaf and FDis.3 promoted, respectively, higher survivor growth (increase of $0.1–0.2\,Mg\,ha^{-1}year^{-1}$ for high-FDis. Leaf communities) and lower mortality biomass loss (decrease of

about $0.2\,\mathrm{Mg\,ha^{-1}\,year^{-1}}$ in high-FDis.3 communities). However, FDis.Nmass and FDis.5 displayed the opposite patterns. Therefore, we cannot corroborate our fourth hypothesis that communities with higher functional diversity should have a better ability to respond to climatic variations. This is counterintuitive, as several studies have reported that greater functional diversity should enhance forest resilience (Ammer, 2019; Hisano et al., 2018; Morin et al., 2018), and, contrary to our expectations, we found that high FDis of some traits could increase mortality and reduce growth. This latter finding is, however, consistent with those of previous studies that found commonly mixed support for forest diversity positively modulating climate impacts (Ammer, 2019; Grossiord, 2020; Paquette et al., 2017).

4.3 | Perspectives

Regarding future climate, Eastern Canadian forests will be impacted by global change, according to regionalized climate simulations for Quebec (QC) and the Maritimes (produced with four representative concentration pathway emission scenarios, RCPs (Allen et al., 2019; Ouranos, 2015)): annual temperatures and precipitation are increasing, and this trend will continue (Ouranos, 2015). By combining these climate scenarios with our results on climate and functional diversity interactions, promoting particular functional diversity attributes could help strengthen forest response capacity to CC and reinforce forest resistance and resilience (Hörl et al., 2020; Millar et al., 2007). Management strategies to maintain existing species while facilitating the transition to future climate-adapted communities (e.g. assisted migration and the selection of adapted species and genetics) could help mitigate CC effects in the long term (Hörl et al., 2020; Looney et al., 2021; Millar et al., 2007). Given our findings, a few avenues could be considered by forest managers. For instance, with the projected temperature increase, promoting fast resource-acquisition and fast-growing species (low-LMA) might be a good strategy to increase tree recruitment in southern and central QC and the Maritimes, especially in more stressful environments, that is harsh climate and/or nutrient-poor, or in recently disturbed forests (Blundo et al., 2015; Poorter et al., 2009; Westoby, 1998). Also, promoting drought semi-tolerant to drought-tolerant species could help alleviate drought-induced mortality, even under the future drier conditions expected in southern QC. High species diversity, with diverse drought-tolerant traits, may enhance tree survival during severe or recurrent droughts, boosting forest communities' capacity to tolerate new environmental conditions (Anderegg et al., 2019; Trugman et al., 2019). In eastern North America, while most studied deciduous trees reduced growth during droughts, some species with drought-tolerant traits showed increased growth, but compensating mechanisms identified in a recent meta-analysis were insufficient to protect drought-prone populations from higher death rates (Anderegg et al., 2019; McGregor et al., 2021). In warmer climates with normal precipitation, good drought tolerance does not necessarily increase NFP, indicating water as a more limiting factor than temperature, as observed in southern boreal forests where increased water availability, rather than temperature, positively affects growth (D'Orangeville et al., 2016). Regarding good mast years, promoting moderate to high SeFreq communities might boost NFP and survivor growth under higher temperatures and precipitation. Even in the drier continental climate, biomass accumulation of communities with greater SeFreq values has the potential to be higher. However, it is highly possible that climate change will impact the masting frequency.

5 | CONCLUSIONS

Currently, forest ecosystem adaptation to climate change is the greatest challenge to forest managers. The reorganization of species assemblages in natural forests will take centuries, and some species are unlikely to successfully migrate to new habitats at a sufficient pace without proper management (Ammer, 2019; Wang et al., 2017). Consequently, understanding trait structure–productivity–climate relationships for ecosystem services and functions are of primary interest to know whether diverse forests can truly be more resilient than species-poor ones. Net productivity, survival growth, recruitment and mortality are influenced by either the community-weighted mean of certain traits, or by functional diversity of several traits. Three traits from three different plant strategy dimensions that contribute to overall plant fitness were the most important for NFP. Survivor growth, on the other hand, was strongly linked to leaf traits, whereas tree recruitment only had a trait associated with resource acquisition as its main feature. Although traits related to competition and survival drove tree mortality as expected, tree mortality was also influenced by a mixture of traits reflecting various plant strategies and functional groups. Then, our results demonstrate strong climate interactions with the trait structure of tree communities. However, and contrary to our expectations, we found contrasting patterns of plot response to changes in climate related to the functional diversity of the studied communities. Depending on the studied group of traits, greater functional diversity did not necessarily positively affect biomass accumulation in response to shifts in climate. This observation may be considered a further validation of already published work showing contrasting patterns concerning the effect of tree species diversity on the ability of certain stands to maintain their productivity when subjected to climate change. The results of our study provide avenues to assess under which circumstances tree species diversity has the utmost potential to positively influence forest productivity under climate change to help anticipate changes and to sustainably promote forest health in the context of a changing climate.

AUTHOR CONTRIBUTIONS
Laurie Dupont-Leduc, Robert Schneider and Hugues Power conceived the ideas and designed methodology. Laurie Dupont-Leduc carried out the data analysis and led the writing of the manuscript. All authors discussed the results, read, contributed and agreed to the final manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. The funders had no role in the design of the study, the collection, analyses, or interpretation of data, the writing of the manuscript, or the decision to publish the results.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data supporting the results of this paper are available at: https://doi.org/10.5061/dryad.n5tb2rc41 (Dupont-Leduc, 2024). Data were derived from the following resources available in the public domain: Québec permanent sample plot forest inventory (https://www.donneesquebec.ca/recherche/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui/resource/ccf8d0d7-85fe-49b0-a965-e914b2395fb7), Newfoundland and Labrador Department of Fisheries, Farming and Natural Resources (https://www.gov.nl.ca/ffa/programs-and-funding/forestry-programs-and-funding/managing/inv-plan/). Functional diversity indices and traits data were derived from the TOPIC database with the permission from TOPIC (Aubin et al., 2020). Traits data from Paquette and Messier (2011) were also used.

STATEMENT ON INCLUSION

No local data collection was conducted in this study, as it relied on a meta-analysis of secondary data. The team of authors and collaborators, however, is representative of the main regions covered by the meta-analysis, ensuring appropriate interpretation of the data and results from the studied regions.

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REFERENCES

Aarts, E., Verhage, M., Veenvliet, J. V., Dolan, C. V., & Van Der Sluis, S. (2014). A solution to dependency: Using multilevel analysis to accommodate nested data. *Nature Neuroscience*, 17, 491–496.

Aleixo, I., Norris, D., Hemerik, L., Barbosa, A., Prata, E., Costa, F., & Poorter, L. (2019). Amazonian rainforest tree mortality driven by climate and functional traits. *Nature Climate Change*, 9, 384–388.

Allen, M., Antwi-Agyei, P., Aragon-Durand, F., Babiker, M., Bertoldi, P., Bind, M., Brown, S., Buckeridge, M., Camilloni, I., & Cartwright, A. (2019). *Technical summary: Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. IPCC.

Ammer, C. (2019). Diversity and forest productivity in a changing climate. *New Phytologist*, 221, 50–66.

Anderegg, W. R., Anderegg, L. D., Kerr, K. L., & Trugman, A. T. (2019). Widespread drought-induced tree mortality at dry range edges indicates that climate stress exceeds species' compensating mechanisms. *Global Change Biology*, 25, 3793–3802.

Attanasi, E. D., Freeman, P. A., & Coburn, T. C. (2020). Well predictive performance of play-wide and subarea random forest models for Bakken productivity. *Journal of Petroleum Science and Engineering*, 191, 107150. https://doi.org/10.1016/j.petrol.2020.107150

Aubin, I., Cardou, F., Boisvert-Marsh, L., Garnier, E., Strukelj, M., & Munson, A. D. (2020). Managing data locally to answer questions globally: The role of collaborative science in ecology. *Journal of Vegetation Science*, 31, 509–517. https://doi.org/10.1111/jvs.12864

Auger, I. (2016). *Une nouvelle relation hauteur-diamètre tenant compte de l'influence de la station et du climat pour 27 essences commerciales du Québec*. Gouv. du Québec, Ministère des Fôrets, Direction de la Recherche.

Bell, F. W., Deighton, H. D., Dacosta, J., Aubin, I., Newmaster, S. G., Searle, E. B., & Hunt, S. (2023). Individual response traits of understory plants vary along linked-press and compounded-pulse disturbance gradients in northern temperate and boreal forests. *Forest Ecology and Management*, 540, 121021.

Blundo, C., Malizia, L. R., & González-Espinosa, M. (2015). Distribution of functional traits in subtropical trees across environmental and forest use gradients. *Acta Oecologica*, 69, 96–104.

Boudewyn, P. A., Song, X., Magnussen, S., & Gillis, M. D. (2007). *Model-based, volume-to-biomass conversion for forested and vegetated land in Canada*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Information Report BC-X-411.

Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32.

Burks, A. W. (1951). Review of the mathematical theory of communication. *The Philosophical Review*, 60, 398–400. https://doi.org/10.2307/2181879

Callaway, R. M. (1995). Positive interactions among plants. *The Botanical Review*, 61, 306–349.

Chauvin, T., Cochard, H., Segura, V., & Rozenberg, P. (2019). Native-source climate determines the Douglas-fir potential of adaptation to drought. *Forest Ecology and Management*, 444, 9–20. https://doi.org/10.1016/j.foreco.2019.03.054

Chavent, M., Kuentz, V., Liquet, B., & Saracco, L. (2011). ClustOfVar: An R package for the clustering of variables. *arXiv preprint*, arXiv:1112.0295. https://doi.org/10.48550/arXiv.1112.0295

Chen, Y., Uriarte, M., Wright, S. J., & Yu, S. (2019). Effects of neighborhood trait composition on tree survival differ between drought and post-drought periods. *Ecology*, *100*, e02766. https://doi.org/10.1002/ecy.2766

Condés, S., & del Río, M. (2015). Climate modifies tree interactions in terms of basal area growth and mortality in monospecific and mixed *Fagus sylvatica* and *Pinus sylvestris* forests. *European Journal of Forest Research*, *134*, 1095–1108. https://doi.org/10.1007/s10342-015-0912-0

Cui, E., Weng, E., Yan, E., & Xia, J. (2020). Robust leaf trait relationships across species under global environmental changes. *Nature Communications*, *11*, 2999. https://doi.org/10.1038/s41467-020-16839-9

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., & Peterson, C. J. (2001). Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience*, *51*, 723–734.

Dawson, S. K., Carmona, C. P., González-Suárez, M., Jönsson, M., Chichorro, F., Mallen-Cooper, M., Melero, Y., Moor, H., Simaika, J. P., & Duthie, A. B. (2021). The traits of "trait ecologists": An analysis of the use of trait and functional trait terminology. *Ecology and Evolution*, *11*, 16434–16445.

de Bello, F., Lepš, J., Lavorel, S., & Moretti, M. (2007). Importance of species abundance for assessment of trait composition: An example based on pollinator communities. *Community Ecology*, *8*, 163–170.

De Reu, J., Bourgeois, J., Bats, M., Zwertvaegher, A., Gelorini, V., De Smedt, P., Chu, W., Antrop, M., De Maeyer, P., & Finke, P. (2013). Application of the topographic position index to heterogeneous landscapes. *Geomorphology*, *186*, 39–49.

Debastiani, V. J., & Pillar, V. D. (2012). SYNCSA—R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. *Bioinformatics*, *28*, 2067–2068.

del Río, M., & Sterba, H. (2009). Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*. *Annals of Forest Science*, *66*, 502.

Dias, A. T. C., Carmona, C. P., de Bello, F., Götzenberger, L., Moretti, M., & Berg, M. P. (Eds.). (2021). Community metrics. In *Handbook of trait-based ecology: From theory to R tools* (pp. 75–104). Cambridge University Press. https://doi.org/10.1017/9781108628426.006

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, *104*, 20684–20689.

D'Orangeville, L., Duchesne, L., Houle, D., Kneeshaw, D., Côté, B., & Pederson, N. (2016). Northeastern North America as a potential refugium for boreal forests in a warming climate. *Science*, *352*, 1452–1455. https://doi.org/10.1126/science.aaf4951

Duchesne, L., & Ouimet, R. (2008). Population dynamics of tree species in southern Quebec, Canada: 1970–2005. *Forest Ecology and Management*, *255*, 3001–3012.

Dupont-Leduc, L. (2024). Data from: Climate interacts with the functional trait structure of tree communities to influence forest productivity. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.n5tb2rc41

Forrester, D. I. (2017). Ecological and physiological processes in mixed versus monospecific stands. In H. Pretzsch, D. Forrester, & J. Bauhus (Eds.), *Mixed-species forests* (pp. 73–115). Springer.

Gouvernement du Québec. (2019). *Forêt ouverte* [WWW Document]. Forêt ouverte. https://www.foretouverte.gouv.qc.ca/

Government of Canada. (2018). *Ecological Land Classification (ELC) 2017* [WWW Document]. https://www.statcan.gc.ca/eng/subjects/standard/environment/elc/elc2017

Government of Newfoundland and Labrador. (2022). *Forest inventory program* [WWW document]. Fisheries, Forestry and Agriculture. https://www.gov.nl.ca/ffa/programs-and-funding/forestry-programs-and-funding/managing/inv-plan/

Greene, D. F., & Johnson, E. A. (2004). Modelling the temporal variation in the seed production of North American trees. *Canadian Journal of Forest Research*, *34*, 65–75. https://doi.org/10.1139/x03-188

Grossiord, C. (2020). Having the right neighbors: How tree species diversity modulates drought impacts on forests. *New Phytologist*, *228*, 42–49. https://doi.org/10.1111/nph.15667

Hao, M., Zhang, C., Zhao, X., & Von Gadow, K. (2018). Functional and phylogenetic diversity determine woody productivity in a temperate forest. *Ecology and Evolution*, *8*, 2395–2406. https://doi.org/10.1002/ece3.3857

He, P., Lian, J., Ye, Q., Liu, H., Zheng, Y., Yu, K., Zhu, S., Li, R., Yin, D., & Ye, W. (2022). How do functional traits influence tree demographic properties in a subtropical monsoon forest? *Functional Ecology*, *36*, 3200–3210.

Healy, C., Gotelli, N. J., & Potvin, C. (2008). Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation. *Journal of Ecology*, *96*, 903–913. https://doi.org/10.1111/j.1365-2745.2008.01419.x

Hisano, M., Searle, E. B., & Chen, H. Y. (2018). Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biological Reviews*, *93*, 439–456.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*, 3–35. https://doi.org/10.1890/04-0922

Hörl, J., Keller, K., & Yousefpour, R. (2020). Reviewing the performance of adaptive forest management strategies with robustness analysis. *Forest Policy and Economics*, *119*, 102289. https://doi.org/10.1016/j.forpol.2020.102289

Huang, M., Piao, S., Ciais, P., Peñuelas, J., Wang, X., Keenan, T. F., Peng, S., Berry, J. A., Wang, K., & Mao, J. (2019). Air temperature optima of vegetation productivity across global biomes. *Nature Ecology & Evolution*, *3*, 772–779.

Jucker, T., Avăcăriței, D., Bărnoaiea, I., Duduman, G., Bouriaud, O., & Coomes, D. A. (2016). Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology*, *104*, 388–398.

Kassambara, A., & Mundt, F. (2017). Package "factoextra". *Extract and visualize the results of multivariate data analyses*, 76.

Kirilenko, A. P., & Sedjo, R. A. (2007). Climate change impacts on forestry. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19697–19702.

Kolström, M., Lindner, M., Vilén, T., Maroschek, M., Seidl, R., Lexer, M. J., Netherer, S., Kremer, A., Delzon, S., & Barbati, A. (2011). Reviewing the science and implementation of climate change adaptation measures in European forestry. *Forests*, *2*, 961–982.

Kopecký, M., Macek, M., & Wild, J. (2021). Topographic Wetness Index calculation guidelines based on measured soil moisture and plant species composition. *Science of the Total Environment*, *757*, 143785. https://doi.org/10.1016/j.scitotenv.2020.143785

Kraft, N. J., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 797–802.

Kuhn, M. (2020). *caret: Classification and regression training*. https://CRAN.R-project.org

Kuhn, M., & Johnson, K. (2013). *Applied predictive modeling*. Springer.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Lambers, H., Chapin, F. S., III, & Pons, T. L. (2008). *Plant physiological ecology.* Springer.

Lambert, M.-C., Ung, C.-H., & Raulier, F. (2005). Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research*, *35*, 1996–2018. https://doi.org/10.1139/x05-112

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., & Bonis, A. (2008). Assessing functional diversity in the field–methodology matters! *Functional Ecology*, *22*, 134–147.

Liang, J., Buongiorno, J., Monserud, R. A., Kruger, E. L., & Zhou, M. (2007). Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *Forest Ecology and Management*, *243*, 116–127.

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A. D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Herault, B., Scherer-Lorenzen, M., Barrett, C. B., Glick, H. B., Hengeveld, G. M., Nabuurs, G.-J., Pfautsch, S., … Reich, P. B. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, *354*, 8957.1–8957.12. https://doi.org/10.1126/science.aaf8957

Liang, J., Gamarra, J. G. P., Picard, N., Zhou, M., Pijanowski, B., Jacobs, D. F., Reich, P. B., Crowther, T. W., Nabuurs, G.-J., de-Miguel, S., Fang, J., Woodall, C. W., Svenning, J.-C., Jucker, T., Bastin, J.-F., Wiser, S. K., Slik, F., Hérault, B., Alberti, G., … Hui, C. (2022). Co-limitation towards lower latitudes shapes global forest diversity gradients. *Nature Ecology & Evolution*, *6*, 1423–1437. https://doi.org/10.1038/s41559-022-01831-x

Liaw, A., & Wiener, M. (2002). Classification and regression by random-Forest. *R News*, *2*, 18–22.

Liu, Q., Peng, C., Schneider, R., Cyr, D., Liu, Z., Zhou, X., & Kneeshaw, D. (2021). TRIPLEX-Mortality model for simulating drought-induced tree mortality in boreal forests: Model development and evaluation. *Ecological Modelling*, *455*, 109652.

Looney, C. E., Long, J. W., Fettig, C. J., Fried, J. S., Wood, K. E., & Audley, J. P. (2023). Functional diversity affects tree vigor, growth, and mortality in mixed-conifer/hardwood forests in California, USA, in the absence of fire. *Forest Ecology and Management*, *544*, 121135.

Looney, C. E., Previant, W. J., Bradford, J. B., & Nagel, L. M. (2021). Species mixture effects and climate influence growth, recruitment and mortality in interior West USA *Populus tremuloides*-conifer communities. *Journal of Ecology*, *109*, 2934–2949. https://doi.org/10.1111/1365-2745.13709

Lopez-Iglesias, B., Villar, R., & Poorter, L. (2014). Functional traits predict drought performance and distribution of Mediterranean woody species. *Acta Oecologica*, *56*, 10–18.

Loreau, M. (2000). Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos*, *91*, 3–17.

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, *412*, 72–76.

Malmsheimer, R. W., Heffernan, P., Brink, S., Crandall, D., Deneke, F., Galik, C., Gee, E., Helms, J. A., McClure, N., & Mortimer, M. (2008). Forest management solutions for mitigating climate change in the United States. *Journal of Forestry*, *106*, 115–173.

Man, R., & Lieffers, V. J. (1999). Are mixtures of aspen and white spruce more productive than single species stands? *The Forestry Chronicle*, *75*, 505–513.

McGregor, I. R., Helcoski, R., Kunert, N., Tepley, A. J., Gonzalez-Akre, E. B., Herrmann, V., Zailaa, J., Stovall, A. E. L., Bourg, N. A., McShea, W. J., Pederson, N., Sack, L., & Anderson-Teixeira, K. J. (2021). Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest. *New Phytologist*, *231*, 601–616. https://doi.org/10.1111/nph.16996

Mehtätalo, L., de-Miguel, S., & Gregoire, T. G. (2015). Modeling height-diameter curves for prediction. *Canadian Journal of Forest Research*, *45*, 826–837.

Millar, C. I., Stephenson, N. L., & Stephens, S. L. (2007). Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications*, *17*, 2145–2151. https://doi.org/10.1890/06-1715.1

Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, *96*, 884–893.

Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., & Bugmann, H. (2018). Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. *Scientific Reports*, *8*, 1–12.

Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, *14*, 1211–1219.

Mouselimis, L. (2022). *ClusterR: Gaussian mixture models, k-means, mini-batch-kmeans, k-medoids and affinity propagation clustering.*

MRNF. (2022). *Norme d'inventaire écoforestier—Placettes-échantillons permanentes (cinquième inventaire)*. Direction des inventaires forestiers, Gouvernement du Québec.

Ouranos. (2015). *Vers l'adaptation. Synthèse des connaissances sur les changements climatiques au Québec* (No. Édition 2015). Ouranos.

Paquette, A., & Messier, C. (2011). The effect of biodiversity on tree productivity: From temperate to boreal forests. *Global Ecology and Biogeography*, *20*, 170–180.

Paquette, A., Vayreda, J., Coll, L., Messier, C., & Retana, J. (2017). Climate change could negate positive tree diversity effects on forest productivity: A study across five climate types in Spain and Canada. *Ecosystems*, *21*, 1–11.

Pillar, V. D., Blanco, C. C., Müller, S. C., Sosinski, E. E., Joner, F., & Duarte, L. D. (2013). Functional redundancy and stability in plant communities. *Journal of Vegetation Science*, *24*, 963–974.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, *182*, 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Poorter, H., Niinemets, Ü., Walter, A., Fiorani, F., & Schurr, U. (2010). A method to construct dose–response curves for a wide range of environmental factors and plant traits by means of a meta-analysis of phenotypic data. *Journal of Experimental Botany*, *61*, 2043–2055. https://doi.org/10.1093/jxb/erp358

Pretzsch, H. (2005). Diversity and productivity in forests: Evidence from long-term experimental plots. In *Forest diversity and function* (pp. 41–64). Springer. https://doi.org/10.1007/3-540-26599-6_3

Pretzsch, H. (2009). Forest dynamics, growth, and yield. In *Forest dynamics, growth and yield* (pp. 1–39). Springer. https://doi.org/10.1007/978-3-540-88307-4_1

Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D. I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matovic, B., … Bravo-Oviedo, A. (2015). Growth and yield of mixed versus pure stands of scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *European Journal of Forest Research*, *134*, 927–947.

Pretzsch, H., Forrester, D. I., & Rötzer, T. (2015). Representation of species mixing in forest growth models. A review and perspective. *Ecological Modelling*, *313*, 276–292.

Qi, J.-H., Fan, Z.-X., Fu, P.-L., Zhang, Y.-J., & Sterck, F. (2021). Differential determinants of growth rates in subtropical evergreen and

deciduous juvenile trees: Carbon gain, hydraulics and nutrient-use efficiencies. *Tree Physiology*, 41, 12–23.

Rao, C. R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology*, 21, 24–43.

Redmond, M. D., Forcella, F., & Barger, N. N. (2012). Declines in pinyon pine cone production associated with regional warming. *Ecosphere*, 3, 1–14. https://doi.org/10.1890/ES12-00306.1

Régnière, J., Saint-Amant, R., & Béchard, A. (2014). *BioSIM 10—User's manual*. Information Report LAU-X-137E.

Reiss, J., Bridle, J. R., Montoya, J. M., & Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, 24, 505–514.

Shannon, C. E. (1948). A mathematical theory of communication. *The Bell System Technical Journal*, 27, 379–423.

Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communication*. University of Illinois Press.

Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180, 923–931. https://doi.org/10.1007/s00442-016-3549-x

Silva Pedro, M., Rammer, W., & Seidl, R. (2016). A disturbance-induced increase in tree species diversity facilitates forest productivity. *Landscape Ecology*, 31, 989–1004.

Simpson, E. H. (1949). Measurement of diversity. *Nature*, 163, 688.

Sousa-Silva, R., Verheyen, K., Ponette, Q., Bay, E., Sioen, G., Titeux, H., Van De Peer, T., Van Meerbeek, K., & Muys, B. (2018). Tree diversity mitigates defoliation after a drought-induced tipping point. *Global Change Biology*, 24, 4304–4315. https://doi.org/10.1111/gcb.14326

Spellerberg, I. F., & Fedor, P. J. (2003). A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. *Global Ecology and Biogeography*, 12, 177–179.

Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., & Zeileis, A. (2008). Conditional variable importance for random forests. *BMC Bioinformatics*, 9, 307.

Sui, D., Wang, Y., Lian, J., Zhang, J., Hu, J., Ouyang, X., Fan, Z., Cao, H., & Ye, W. (2017). Gap distribution patterns in the south subtropical evergreen broad-leaved forest of Dinghushan. *Biodiversity Science*, 25, 382–392.

Svetnik, V., Liaw, A., Tong, C., Culberson, J. C., Sheridan, R. P., & Feuston, B. P. (2003). Random forest: A classification and regression tool for compound classification and QSAR modeling. *Journal of Chemical Information and Computer Sciences*, 43, 1947–1958.

Thompson, I., Mackey, B., McNulty, S., & Mosseler, A. (2009). Forest resilience, biodiversity, and climate change. In *A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems*. Secretariat of the Convention on Biological Diversity. Technical Series, p. 67.

Trugman, A. T., Anderegg, L. D., Wolfe, B. T., Birami, B., Ruehr, N. K., Detto, M., Bartlett, M. K., & Anderegg, W. R. (2019). Climate and plant trait strategies determine tree carbon allocation to leaves and mediate future forest productivity. *Global Change Biology*, 25, 3395–3405.

Tumajer, J., & Lehejček, J. (2019). Boreal tree-rings are influenced by temperature up to two years prior to their formation: A trade-off between growth and reproduction? *Environmental Research Letters*, 14, 124024.

van Lier, O. R., Luther, J. E., White, J. C., Fournier, R. A., & Côté, J.-F. (2022). Effect of scan angle on ALS metrics and area-based predictions of forest attributes for balsam fir dominated stands. *Forestry*, 95, 49–72.

Vergotti, M. J., Fernández-Martínez, M., Kefauver, S. C., Janssens, I. A., & Peñuelas, J. (2019). Weather and trade-offs between growth and reproduction regulate fruit production in European forests. *Agricultural and Forest Meteorology*, 279, 107711.

Wang, W. J., He, H. S., Thompson, F. R., Fraser, J. S., & Dijak, W. D. (2017). Changes in forest biomass and tree species distribution under climate change in the northeastern United States. *Landscape Ecology*, 32, 1399–1413.

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199, 213–227.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33, 125–159.

Wion, A. P., Pearse, I. S., Rodman, K. C., Veblen, T. T., & Redmond, M. D. (2023). Masting is shaped by tree-level attributes and stand structure, more than climate, in a Rocky Mountain conifer species. *Forest Ecology and Management*, 531, 120794.

Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H., Pitman, N. C. A., Poorter, L., Silman, M. R., Vriesendorp, C. F., Webb, C. O., Westoby, M., & Wright, S. J. (2007). Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany*, 99, 1003–1015. https://doi.org/10.1093/aob/mcl066

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., & Diemer, M. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

Zhang, Y., Chen, H. Y. H., & Reich, P. B. (2012). Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *Journal of Ecology*, 100, 742–749. https://doi.org/10.1111/j.1365-2745.2011.01944.x

Zheng, L.-T., Chen, H. Y. H., Biswas, S. R., Bao, D.-F., Fang, X.-C., Abdullah, M., & Yan, E.-R. (2021). Diversity and identity of economics traits determine the extent of tree mixture effects on ecosystem productivity. *Journal of Ecology*, 109, 1898–1908. https://doi.org/10.1111/1365-2745.13614

SUPPORTING INFORMATION

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

Figure S1: Proportion of each component to total forest productivity according to the various diversity indices.

Table S1: Tree functional traits compiled from published sources.

Table S2: Community functional trait structure indices calculation.

Table S3: Description of functional traits used to calculate the community functional trait structure indices.

Table S4: Results of the different clustering analysis.

Table S5: Description of the functional trait structure of communities and diversity indices selected as explicative variables.

Table S6: Morgan's spatial correlation per model and time period.

Table S7: First and second order temporal autocorrelations per model.