ENVIRONMENTAL STUDIES

Functional diversity enhances dryland forest productivity under long-term climate change

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Short-term experimental studies provided evidence that plant diversity increases ecosystem resilience and resistance to drought events, suggesting diversity to serve as a nature-based solution to address climate change. However, it remains unclear whether the effects of diversity are momentary or still hold over the long term in natural forests to ensure that the sustainability of carbon sinks. By analyzing 57 years of inventory data from dryland forests in Canada, we show that productivity of dryland forests decreased at an average rate of 1.3% per decade, in concert with the temporally increasing temperature and decreasing water availability. Increasing functional trait diversity from its minimum (monocultures) to maximum value increased productivity by 13%. Our results demonstrate the potential role of tree functional trait diversity in alleviating climate change impacts on dryland forests. While recognizing that nature-based climate mitigation (e.g., planting trees) can only be partial solutions, their long-term (decadal) efficacy can be improved by enhancing functional trait diversity across the forest community.

INTRODUCTION

Drylands are the largest terrestrial biome, accounting for >41% of the Earth's land surface (*1*). While net primary productivity of forests (hereafter, productivity) is a major component of the global terrestrial carbon cycle (*2*), such functioning in dryland biome is under threat from various types of global change, including climate variability (*3*, *4*), desertification (*5*), and land degradation (*6*, *7*). These impacts can be further exacerbated, as drylands are projected to experience 1.35 times faster warming than the global average (*8*), along with more severe water deficits and atmospheric moisture demand (*9*). Therefore, it is imperative to develop effective strategies to ensure the long-term sustainability of dryland forest functioning under escalating water deficiency (*4*, *10*).

A nature-based solutions approach is increasingly gaining traction in climate policy, which aims to reduce ecosystem vulnerabilities to environmental change through management that takes account of ecosystem functions and resilience (*11*–*13*). Recent frameworks emphasize the critical role of biodiversity–ecosystem functioning (B-EF) relationships for nature-based climate solutions (*11*, *14*). However, whether ecosystem resistance against drought events is enhanced by plant diversity has been hotly debated (*15*–*23*). Experimental studies controlling precipitation have provided strong evidence that more diverse assemblages exhibit greater stability or resistance of ecosystem functioning in response to extreme drought events (pulse driver) (*17*, *24*), and similar patterns were observed at short-term scales in natural systems (*21*, *22*). However, evidence from long-term observation extending to decades is limited. It remains unclear whether the effects of diversity identified by short-term studies are momentary or still hold over long term in complex natural systems, ensuring the long-term sustainability of carbon sinks. This is especially relevant in the case of vulnerable ecosystems, such as drylands, that are experiencing persistently more water stress under global warming (press driver). Synthesizing a large number of direct observations is crucial for generalizing dynamic ecological patterns, which can inform the development of effective nature-based climate solutions (*11*, *14*).

It is postulated that tree diversity may mitigate the negative impacts of climate change if the positive effects of diversity on productivity are persistent throughout or even strengthened by climate change (*18*). While the B-EF relationship in forest ecosystems can depend on spatial variations in environmental contexts (*25*, *26*), whether the temporal changes in climate promote or negate the species complementarity effect, as a consequence of resource partitioning, abiotic facilitation, and biotic feedbacks (*27*, *28*), by altering plant-plant interactions has been an important question (Fig. 1) (*17*, *18*, *29*). By quantifying variations among functional traits within a community, functional trait diversity is expected to represent community processes involving niche partitioning and facilitation (*27*, *30*) and has been shown to promote forest productivity (*26*, *31*). Under environmental changes, dissimilarity in functional response traits is recognized as an important driver for maintaining functions through differential responses of species to environmental perturbations [i.e., response diversity; (*32*)]. However, the effects of tree diversity in mitigating short-term drought events have been contrasting, which could be attributable to combinations and interactions of species with unique traits (identity) (Fig. 2) (*33*–*35*). This provokes a need for partitioning diversity and identity (*36*) effects when examining the climate change-associate B-EF relationship. However, no study has yet determined the community-level functional identity (i.e., the relative abundance of species with certain traits) that may tolerate (or benefit from) a changing climate, despite the importance of species' inherent traits in influencing its capacity to cope with increased temperature and more intense droughts (*37*, *38*).

While a substantial proportion of the global dryland biome is experiencing intensified land degradation and urban expansion (*6*), dryland forests in Canada have remained largely intact. This presents

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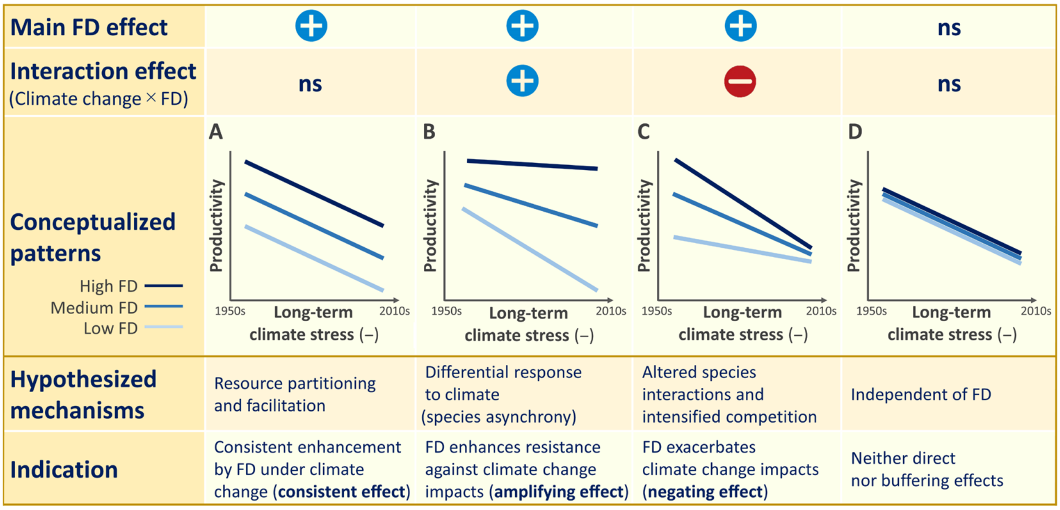


Main FD effect	+	+	+	ns
Interaction effect (Climate change × FD)	ns	+	−	ns
Conceptualized patterns High FD — Medium FD — Low FD —	A	B	C	D
Hypothesized mechanisms	Resource partitioning and facilitation	Differential response to climate (species asynchrony)	Altered species interactions and intensified competition	Independent of FD
Indication	Consistent enhancement by FD under climate change (**consistent effect**)	FD enhances resistance against climate change impacts (**amplifying effect**)	FD exacerbates climate change impacts (**negating effect**)	Neither direct nor buffering effects

Fig. 1. Hypothesized relationships between functional diversity (FD) and forest productivity under the long-term increase in climatic stress. The main effect of FD (intercepts) and divergent responses of productivity to the intensified climate change (slopes) are shown. (**A**) When the main FD effect is present, FD raises productivity consistently across a temporally changing climate such as increased drought stress (the consistently positive effect). (**B**) When the interaction effect ("Climate change × FD") is positive, the FD effect is strengthened by climate change intensification (i.e., high FD communities are more resistant to climate change; the amplified positive effect). (**C**) When the interaction effect is negative, the FD effect is reduced or negated by climate change (i.e., the negative impacts of climate change are exacerbated in high FD communities). (**D**) When both the main and interaction effects are insignificant, there is neither a consistent effect nor an amplifying effect of FD. ns, not significant.

an opportunity to assess the explicit impacts of climate change without confounding major anthropogenic factors. Using the networks of 2491 permanent sample plots of dryland biomes in Canada [naturally regenerated, unmanaged; aridity index (AI) < 0.65; (*39*, *40*)], we examined responses of the annual growth rate of aboveground biomass to 57 years of background (non-catastrophic) environmental change in relation to functional trait diversity [hereafter, functional diversity (FD)] and functional identity [community-weighted mean of functional traits (CWM)]. Specifically, we tested the following hypotheses: while biomass growth of dryland forests would decrease over time due to increased water stress, (i) functionally diverse forests would maintain higher levels of productivity than less diverse forests due to niche partitioning regardless of warming and aridification (the consistently positive effect; Fig. 1A); and (ii) functionally diverse forests would experience smaller or no declines in productivity compared to less diverse forests, as a result of divergent species responses to climate change (the amplified positive effect; Fig. 1B). Furthermore, we also predicted that (i) communities with resource-acquisitive traits would grow more with climate warming through higher use of resources (nutrients and water) to achieve rapid acquisition of carbon; and (ii) those with drought-tolerance traits would resist better than resource-conservative or water-demanding traits against decreasing water availability (Fig. 2, B and E) (*41*, *42*). To test these hypotheses, we modeled productivity (i.e., biomass growth rate) as a function of calendar year, representing overall temporal environmental change (*43*). We subsequently explored the relationship between productivity and climate warming and long-term declines in water availability. The response of forest productivity to diversity and environmental change could be confounded by multiple factors in complex natural systems. We addressed this issue by using linear mixed-effects modeling to simultaneously account for covarying endogenous factors including stand age representing recovery from disturbance (i.e., time since fire), environmental controls such as spatial variations in historical climate, soil drainage class, and inherent site quality (*44*).

RESULTS

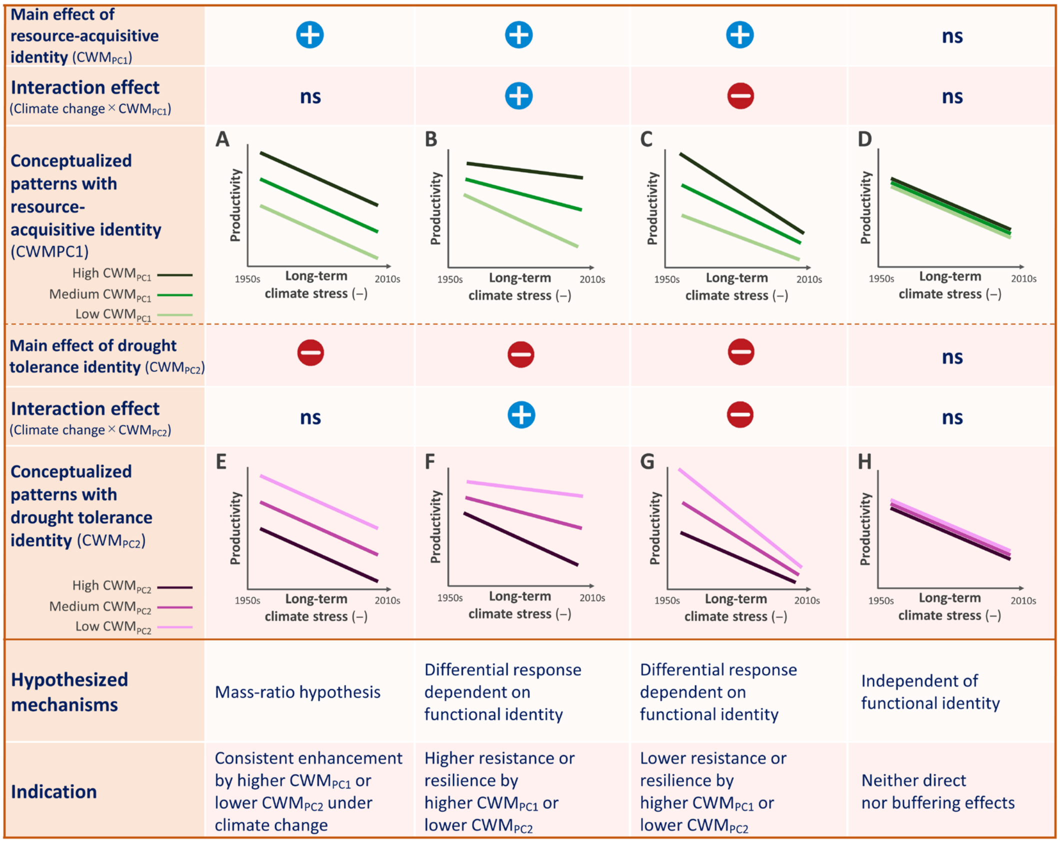
Long-term trends in dryland forest productivity

During the study period (1958 to 2015), the observed values of average productivity were 2.6 ± 0.03 (mean ± 95% confidence interval) Mg ha^{-1} year^{-1}. After accounting for covariates, productivity on average decreased at a rate of 1.3% per decade (Fig. 3A; the model $R^2_{\mathrm{marginal}} = 0.35$ and $R^2_{\mathrm{conditional}} = 0.69$ for Eq. 1). Meanwhile, productivity increased with functional diversity (Fig. 3B). Specifically, increasing functional diversity from its minimum to maximum value increased productivity by 13%.

Productivity was also negatively correlated with drought-tolerant traits ($\mathrm{CWM}_{\mathrm{PC2}}$, "drought tolerance versus moisture-/fertility-demanding" traits; Fig. 4) (Fig. 3D), but it was not associated with resource-acquisitive traits on average ($\mathrm{CWM}_{\mathrm{PC1}}$, higher values representing resource-acquisitive and smaller values signaling conservative traits; Fig. 4) (Fig. 3C). Moreover, the temporal change in productivity was dependent on $\mathrm{CWM}_{\mathrm{PC1}}$ (evident from the statistically significant "Year × $\mathrm{CWM}_{\mathrm{PC1}}$" effect; Fig. 5B). Specifically, productivity in resource-acquisitive forests increased over time, while the rate in resource-conservative forests decreased. Across spatial variations in climate and local site conditions, productivity increased with mean annual temperature, aridity index (higher values are associated with more water availability), and site index, while it decreased with stand age (fig. S1).

Functional dependency in responses to warming and drought

We explored temporal trends of temperature (its anomaly, ATA), water availability [drought intensity (DI) = −1 × standardized precipitation evapotranspiration index (SPEI); likely associated with



Main effect of resource-acquisitive identity ($\mathrm{CWM}_{\mathrm{PC1}}$)	⊕	⊕	⊕	ns
Interaction effect (Climate change × $\mathrm{CWM}_{\mathrm{PC1}}$)	ns	⊕	⊖	ns
Conceptualized patterns with resource-acquisitive identity (CWMPC1) High $\mathrm{CWM}_{\mathrm{PC1}}$ Medium $\mathrm{CWM}_{\mathrm{PC1}}$ Low $\mathrm{CWM}_{\mathrm{PC1}}$	A	B	C	D
Main effect of drought tolerance identity ($\mathrm{CWM}_{\mathrm{PC2}}$)	⊖	⊖	⊖	ns
Interaction effect (Climate change × $\mathrm{CWM}_{\mathrm{PC2}}$)	ns	⊕	⊖	ns
Conceptualized patterns with drought tolerance identity ($\mathrm{CWM}_{\mathrm{PC2}}$) High $\mathrm{CWM}_{\mathrm{PC2}}$ Medium $\mathrm{CWM}_{\mathrm{PC2}}$ Low $\mathrm{CWM}_{\mathrm{PC2}}$	E	F	G	H
Hypothesized mechanisms	Mass-ratio hypothesis	Differential response dependent on functional identity	Differential response dependent on functional identity	Independent of functional identity
Indication	Consistent enhancement by higher $\mathrm{CWM}_{\mathrm{PC1}}$ or lower $\mathrm{CWM}_{\mathrm{PC2}}$ under climate change	Higher resistance or resilience by higher $\mathrm{CWM}_{\mathrm{PC1}}$ or lower $\mathrm{CWM}_{\mathrm{PC2}}$	Lower resistance or resilience by higher $\mathrm{CWM}_{\mathrm{PC1}}$ or lower $\mathrm{CWM}_{\mathrm{PC2}}$	Neither direct nor buffering effects

Fig. 2. Hypothesized relationships between functional identity [community-weighted mean (CWM)] and forest productivity under the long-term increase in climatic stress. (**A** and **E**) When the main effect of CWM of resource acquisitive ($\mathrm{CWM}_{\mathrm{PC1}}$) or environmental tolerance ($\mathrm{CWM}_{\mathrm{PC2}}$) is present, higher $\mathrm{CWM}_{\mathrm{PC1}}$ or lower $\mathrm{CWM}_{\mathrm{PC2}}$ consistently enhances productivity across a temporally changing climate. (**B** and **F**) When interaction effects ("Climate change × $\mathrm{CWM}_{\mathrm{PC1}}$" or "Climate change × $\mathrm{CWM}_{\mathrm{PC2}}$") are positive, higher $\mathrm{CWM}_{\mathrm{PC1}}$ or higher $\mathrm{CWM}_{\mathrm{PC2}}$ can enhance resistance against climate change (the buffering effect). (**C** and **G**) When the interaction effect is negative, the relatinship between productivity and $\mathrm{CWM}_{\mathrm{PC1}}$ or $\mathrm{CWM}_{\mathrm{PC2}}$ is weakened by climate change (i.e., the negative impacts of climate change are exacerbated in higher CWMPC1 and lower CWMPC2 communities). (**D** and **H**) When both the main and interaction effects are insignificant, there is neither a consistent effect nor a buffering effect of CWM. ns, not significant. See Fig. 4 for the trait distribution in a principal components analysis.

soil water scarcity] over the study period. During the 57 years, temperature (Fig. 6A) and DI (Fig. 6E) increased persistently (but not in parallel; $R^2 = 0.52$ and 0.02 with the calendar year), at the rates of 40 and 19%, respectively.

We then examined how the relationship between productivity and these three climate change drivers was associated with functional identity and diversity. Across our plot networks, we found that productivity decreased with temporal increases in temperature and drought intensity (Fig. 5; the model $R^2_{\mathrm{marginal}} = 0.37$ and $R^2_{\mathrm{conditional}} = 0.72$ for Eq. 2). Our analysis showed that productivity increased consistently with functional diversity across the ranges of warming and drought intensity as indicated by no significant interaction effects of functional diversity and these climate drivers on productivity (Fig. 6, B and F). On average, functionally diverse forests (FD = 0.3, its maximum value) maintained a 12% higher productivity than less diverse forests (FD = 0.0; i.e., monocultures) across the ranges of warming and drought intensity. Notably, the response of productivity to these climate change drivers was dependent on functional identity. Productivity increased with warming in forests with higher $\mathrm{CWM}_{\mathrm{PC1}}$ (higher values associated with higher resource-acquisitive traits) but responded negatively to this driver in forests with lower $\mathrm{CWM}_{\mathrm{PC1}}$ values (associated with resource-conservative traits; Fig. 6C). Forests with lower $\mathrm{CWM}_{\mathrm{PC2}}$ values (associated with greater moisture/fertility requirement) responded negatively to increasing temperature and drought intensity, while those with higher $\mathrm{CWM}_{\mathrm{PC2}}$ (associated with drought tolerance) remained unchanged with these drivers (Fig. 6, D and H).

DISCUSSION

Our analyses showed that dryland forests in Canada suffered from long-term environmental change over the past 57 years, despite the potential benefits of rising CO_2 for tree growth through improved water-use efficiency (*45*, *46*). This corroborates that dryland ecosystems are highly vulnerability to the recent changes in climate (*4*) and highlights contrasting trends with those in other biomes with plentiful rainfall. For example, in humid temperate forests, productivity increases over time along with rising atmospheric CO_2 or climate warming (*47*, *48*). Even in regions experiencing declines in water availability, forest productivity can still exhibit temporal increases if the positive effects of rising CO_2 or warming outweigh the negative impacts of long-term drought (*43*, *49*, *50*). However, in semiarid

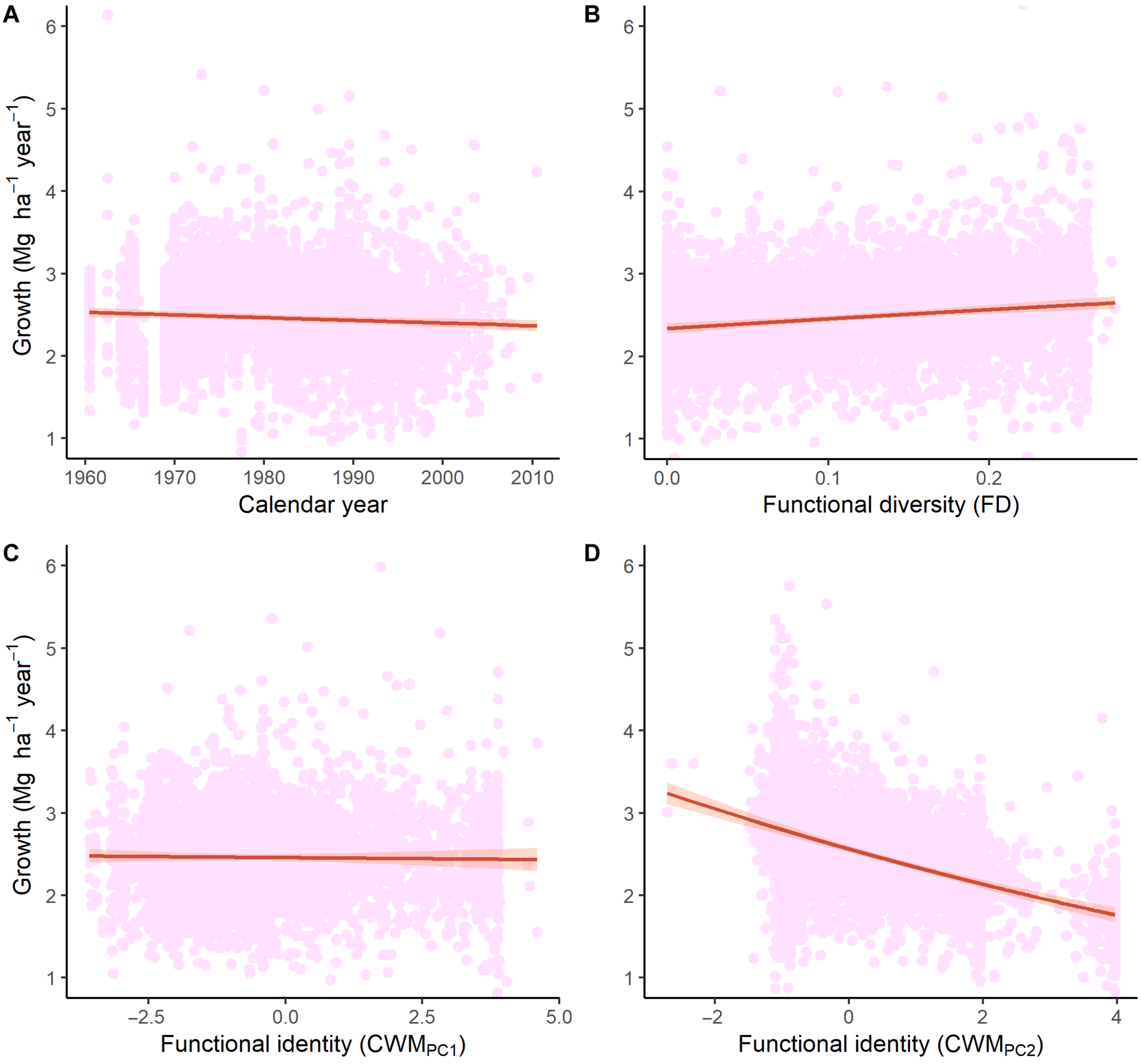


Fig. 3. Fixed effects of calendar year (Year), functional diversity (FD), and functional identity (CWM_{PC1} and CWM_{PC2}). Trends of productivity (biomass growth rate) associated with (**A**) calendar year, (**B**) functional diversity, and (**C** and **D**) functional identity [resource-acquisitive versus resource-conservation strategies (CWM_{PC1}), drought tolerance versus moisture-/fertility-demanding traits (CWM_{PC2})]. Pink dots are the values predicted by partial regressions with each explanatory variable. The red lines are mean values, and shaded areas are 95% confidence intervals fitted by linear mixed-effects modeling. The effects of other fixed variables are shown in fig. S1.

systems, dryland forests are already under substantial water stress. Consequently, any additional reduction in water availability can negate the positive effects of climate change that exacerbate stress (*4*).

By disentangling the relationship between diversity and productivity from its strong dependency on functional identity, our study demonstrates that functional diversity can promote productivity under climatic warming and decreasing water availability. This suggests the remarkable role of resource partitioning (*20*, *27*), reducing intraspecific competition for limited resources (*51*–*53*) through lower neighborhood trait dissimilarity. Meanwhile, facilitation (*28*) such as hydraulic lift by deep-rooting species (*23*) or forest cover created by tall tree species (*54*) could also contribute to the enhancement of forest productivity over time. Field experimental studies reported that plant diversity has a persistent positive effect on biomass production when subject to heat and drought pulses (*15*, *16*, *55*). Our results provide the evidence that tree functional diversity enhances the productivity of dryland forests that have been subject to increases in warming and drought intensification over the past half-century.

Our analysis shows clear patterns in functional identity-associated responses of productivity to warming and drought intensification, in parallel with the persistently positive relationship between functional diversity and productivity. Dryland forests characterized by resource-acquisitive or drought-tolerant traits benefitted or resisted warming and drought, whereas those with conservative or moisture-/fertility-demanding traits suffered. The trends observed here are largely consistent with previous studies of forest inventory, where the productivity of deciduous broadleaf trees having acquisitive traits tends to be favored by elevated CO_2 or climate warming (*37*, *38*, *56*). Moreover, a global study showed that conifers become more susceptible to decreasing water availability with increasing duration of drought, whereas broadleaves are likely to acclimate themselves to aridification (*57*).

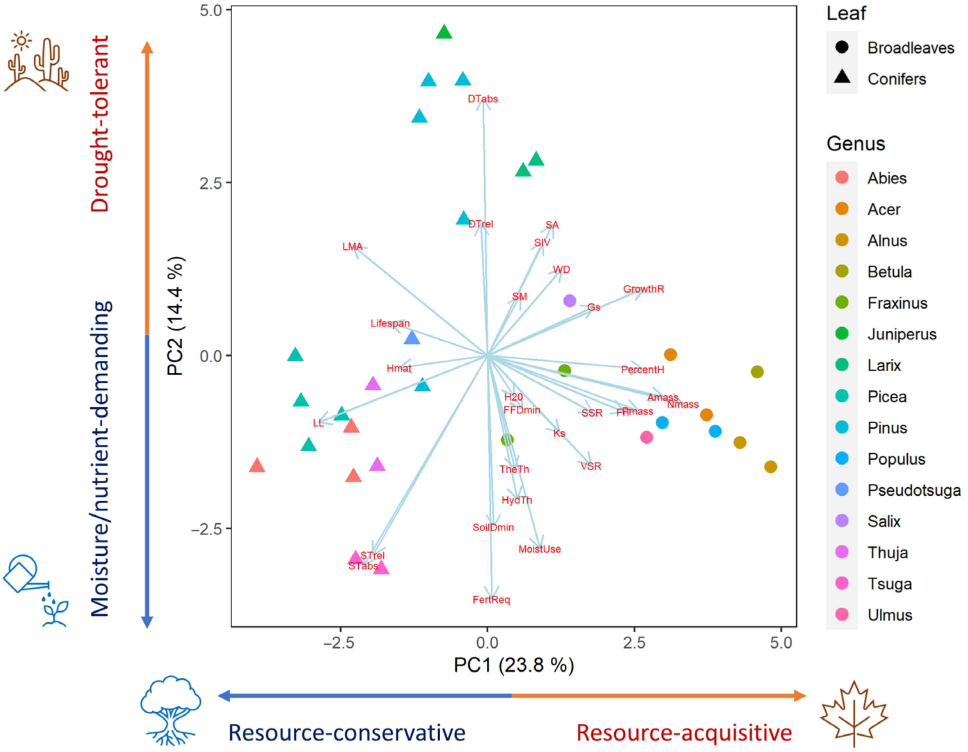


Fig. 4. A result of the principal components analysis showing each tree species and functional trait. The first axis (PC1) represents traits associated with resource-acquisitive (positive PC1) versus resource-conservative strategies (negative PC1), while the second axis (PC2) stands for traits associated with environmental tolerance: drought tolerance (positive PC2) and resource requirements such as moisture and fertility (negative PC2). Nmass, leaf nitrogen content per leaf dry mass; Pmass, leaf phosphorus content per leaf dry mass; Amass, maximum CO_2 assimilation rate per unit dry mass; Ks, sapwood-specific hydraulic conductivity; Gs, stomatal conductance; LMA, leaf mass per area; LL, leaf longevity; WD, wood density; DTabs, absolute drought tolerance; STabs, absolute shade tolerance; HydTh, hydric threshold on the data [based on climate moisture index (CMI)]; TheTh, thermophilic threshold on the data [based on mean annual temperature (MAT)]; GrowthR, relative growth rate; H20, height at 20 years, maximum (meters); Hmat, height, mature (meters); PercentH, percent height 20 years divided by mature (how much % grows when 20; years); Lifespan, tree lifespan; Resprout, resprout ability; DTrel, relative drought tolerance; STrel, relative shade tolerance; FertReq, relative fertility requirement; FiT, relative fire tolerance; FFDmin, frost-free days, minimum; MoistUse, moisture use ability; SoilDmin, root depth (minimum depth of soil required for good growth, centimeters); SA, seed abundance; SM, seed mass (milligrams); SSR, seed spread rate; SIV, seedling vigor; VSR, vegetative spread rate (see also table S3).

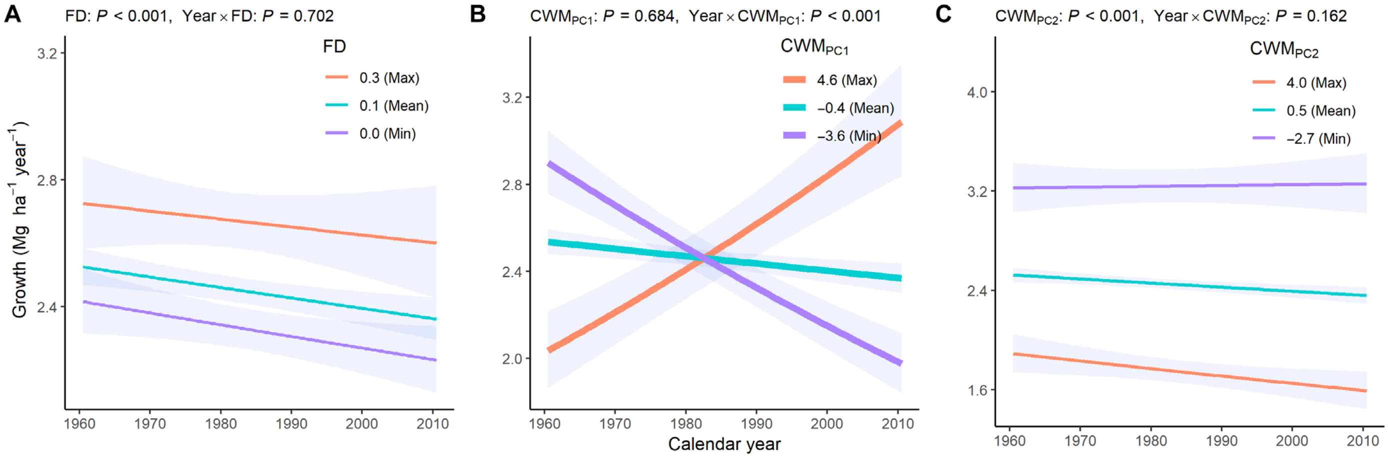


Fig. 5. Responses of productivity to calendar year (representing global environmental change overall) associated with functional identity and diversity. (**A**) Temporal trends in biomass growth with functional diversity (FD). (**B** and **C**) Temporal trends in productivity (biomass growth rate) with functional identity [resource-acquisitive versus resource-conservation strategies (CWM_{PC1}), drought tolerance versus moisture-/fertility-demanding traits (CWM_{PC2})]. The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effects modeling. The FD and CWMs were binned into three levels: their minimum, mean, and maximum values. Line thickness represents the statistical significance of their interaction terms (thick lines, $P < 0.05$; thin lines, $P > 0.05$).

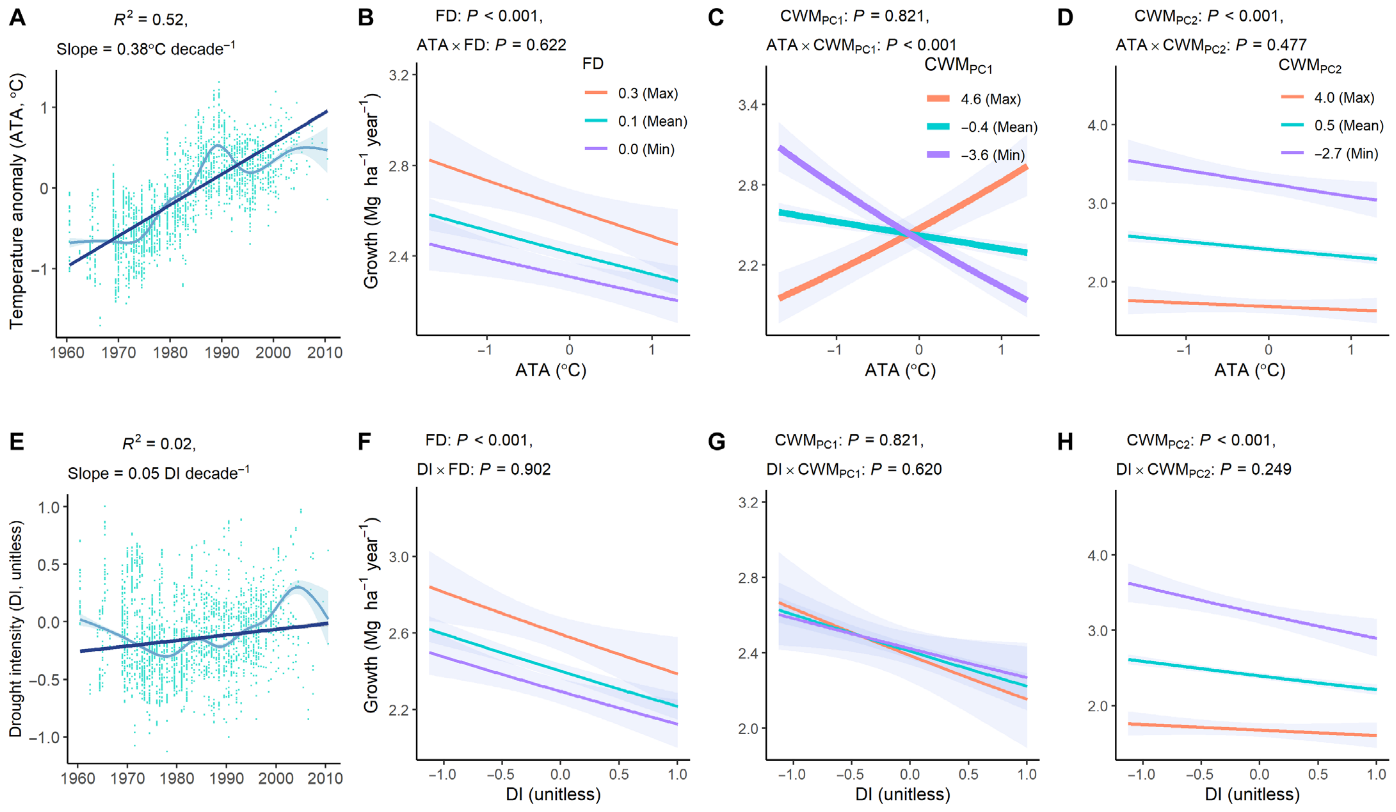


Fig. 6. Temporal trends in climate change drivers and the responses of productivity to each driver. Temporal trends in (**A**) anomaly of annual mean temperature (ATA) and (**E**) drought intensity [DI = −1 × standardized precipitation evapotranspiration index (SPEI)] in surveyed plots. Responses of productivity (biomass growth rate) to ATA and DI associated with functional diversity [FD; (**B** and **F**)], CWM$_{PC1}$ [functional identity associated with resource-acquisitive versus resource-conservation strategies; (**C** and **G**)], and CWM$_{PC2}$ [associated with drought tolerance versus moisture-/fertility-demanding traits; (**D** and **H**)]. The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effects modeling. The FD and CWMs were binned into three levels: their minimum, mean, and maximum values. Line thickness represents the statistical significance of their interaction terms (thick lines, $P < 0.05$; thin lines, $P > 0.05$).

Therefore, the trends observed in this study could be explained by the fact that broadleaf species have higher plasticity in morphological (e.g., leaf area and xylem anatomy) and physiological (e.g., stem hydraulic vulnerability and stomatal conductance) acclimation to changing climate than conifers with conservative traits (*58*, *59*). Such advantageous climate conditions for deciduous broadleaves have led to an increase in their dominance at the expense of conifers in temperate and boreal forests (*41*, *56*).

In our study, drought-tolerant forests were overall less productive than drought-intolerant (or moisture-/fertility-demanding) forests. However, despite their lower mean productivity, drought-tolerant forests would remain steady under long-term warming and drying. This provides insights into the functional shifts of Canadian boreal forests toward higher drought tolerance under long-term climate change (*41*).

We demonstrate the functional dependency of long-term trends in forest functioning by explicitly partitioning the effects of functional diversity and identity (species complementarity versus dominance effect). This empirically suggests the potential role of biodiversity in alleviating climate change impacts (*15*, *18*) in natural systems. Our results raise concerns about the future health of functionally monotonic forests under increasing frequency and/or severity of heat and drought stress in drylands because an increase in drought vulnerability of tree growth can compound the consequence of previously identified higher risks of mortality (*60*). Our finding reveals that transitioning forests from monospecific to functionally diverse mixed woods by planting or inducing regeneration of species with distinctive traits or prioritizing the conservation of such mixed forests would be effective in coping with the impacts of climate change. In addition, our study shows the critical role of functional identity in maintaining and improving the long-term functioning of natural forests. Our study suggests that forest management or planting schemes designed to promote productivity or CO_2 absorption rate (*13*) should favor resource-acquisitive or fast-growing species (e.g., broadleaves) that can best tolerate or even benefit from warming. On the other hand, if management seeks to enhance long-term resistance or stability of the functioning of dryland forests (*4*), then increasing the relative abundance of drought-tolerant (conservative or slow-growing) species should be prioritized under chronic moisture deficit. Therefore, we suggest that future nature-based climate solutions for carbon sequestration potential (e.g., planting trees and assisted natural regeneration) should consider multi-faceted aspects of functional components for the long-term sustainability of forest functioning in the face of escalating climate change.

MATERIALS AND METHODS

Study area and forest inventory data

To examine the temporal changes in biomass growth, we used an extensive network of permanent sampling plots (PSPs) established by the provincial governments of British Columbia (BC), Alberta (AB), Saskatchewan (SK), and Manitoba (MB) in Canada between the 1950s and 1980s [geographically and temporally extending and refining our previous plot network; (*50*)]. We selected plots from the network according to the following criteria: (i) PSPs with AI < 0.65 (*39*, *40*); (ii) unmanaged PSPs without major human disturbances, defined by the data providers; (iii) PSPs with known stand age; (iv) PSPs with all trees tagged and their diameter at breast height (DBH) repeatedly measured (see table S1 for variations in census intervals); (v) PSPs with ≥30 trees and plot size at least 200 m^2 to represent the stand and tree community; and (vi) PSPs with known coordinates properly recorded. Each province set different tree size criteria for monitoring [DBH thresholds = 4.0 cm (BC), 7.2 cm (SK), and 9.1 cm (AB) and no threshold in MB]. We hence excluded trees with DBH < 9.1 cm to avoid the biased estimation of biomass from the different sampling efforts (see Supplementary Text S1 and fig. S2 for more inspection). We defined trees that reached 9.1-cm DBH between two consecutive censuses as recruitments. A total of 2491 plots (229.6 ha; 49°01′N to 60°00′N, 95°52′W to 129°06′W) were selected for our analyses, with 293,217 trees measured during the monitoring period of 1958 to 2015. The average monitoring period was 31 years with 4.1 census times. The mean annual temperature and precipitation in the area varied between −3.0° and 8.5°C and between 337.7 and 649.7 mm (1958 to 2015), respectively, covering "semiarid" (AI = 0.2 to 0.5; 673 plots) and "dry subhumid" (AI = 0.5 to 0.65; 1818 plots) forests (*40*) across boreal and temperate zones.

Annual aboveground biomass growth

Plot-level aboveground biomass was calculated by summing the biomass of all trees in each plot for each measurement. The aboveground biomass of individual trees was estimated on the basis of allometric equations specific to each tree species of Canada (for the stem, bark, leaves, and branches, respectively) (*61*, *62*). To estimate biomass for rarely occurring species (plot-level mean relative abundance ≤ 0.35%; listed in table S2), for which allometric equations were unavailable, we used the regionally appropriate equations of angiosperm and gymnosperm produced by pooling these species into "angiosperm" and "gymnosperm" groups (*61*, *62*), respectively. As a measure of plot-level productivity, we then calculated the growth rate of annual aboveground biomass (ΔAGB_{GI}, Mg ha^{-1} $year^{-1}$) as the sum of yearly biomass gain by the growth of surviving trees and ingrowth by previously unidentified recruitment trees between two successive surveys divided by census length in years (*43*).

Functional diversity and composition

We focused on the following three important functional metrics in determining the capacity of forest growth to the climate change drivers.

Functional diversity (FD)

Functional diversity quantifies the variations among functional traits (*63*) of individual stems within a stand, which is linked to niche partitioning in resource use and shown to be related to higher forest productivity (*26*, *31*). We calculated functional dispersion, which accounts for species abundance and the distance of species to the center of multi-trait functional space, using the FD package (*63*).

Functional identity (CWM)

Functional traits of tree species can directly link to forest productivity since a greater abundance of species with beneficial traits can increase the mean trait value of the community to ensure functioning over time based on the mass-ratio hypothesis (*36*). We calculated the community-weighted mean of trait values (hereafter CWM) as functional identity, defined as the average value of a particular trait within a community by weighting the values of each taxon based on their relative abundance of basal area. The CWM thus takes account of the most dominant species in a community to reflect the impacts of environmental fluctuations and their consequences on ecosystem functioning (*64*).

To calculate the plot-level FD, we used 33 key functional traits associated with growth and competitive strategies, as well as environmental tolerance capacities based on literature (*64*–*67*): For example, leaf nitrogen content per leaf dry mass (N_{mass}), leaf phosphorus content per leaf dry mass (P_{mass}), maximum CO_2 assimilation rate per unit dry mass (A_{mass}), stomatal conductance (G_s), leaf mass per area (LMA), tree and leaf life span (Lifespan and LL, respectively), shade tolerance (ST), drought tolerance (DT), fertility requirement (FertReq), minimum depth of soil required for growth (SoilDmin), and moisture use-ability (MoistUse) (all the 33 traits are listed in table S3). Trait values were extracted from the TRY database (www.try-db.org), the PLANTS database (https://plants.usda.gov/home), and other published sources (table S3). Although the majority of trait data (25 of 33 traits) were fully obtained for all species, some traits were not (e.g., 93% of species for three traits and 43 to 80% for five traits; see details in table S3). Similar to previous studies (*68*), we hence imputed the missing trait values by specified evolutionary models (*69*). We first generated phylogenetic information (an evolutionary "tree") with the V.PhyloMaker package (*70*) and then phylogenetically reconstructed the species-level trait data using the Rphylopars package (*69*). We used the Rphylopars approach because it is suggested to impute trait values most accurately among other comparable methods when missing data < 60% (applicable to our case) by preserving the response-trait slope (*71*). Because most of the traits here were categorized as not only functional effective traits but also functional response traits (see table S3), FD was expected to represent certain aspects of response diversity (*32*).

Before calculating CWMs, we performed a principal components analysis using the values of 29 of the 33 traits (excluding all the categorical traits; table S3) to obtain a functional spectrum (*65*) of the tree species (Fig. 4). The first axis [principal component 1 (PC1)] explained 23.8% of the variation, which was associated with N_{mass}, P_{mass}, A_{mass}, G_s, LL, Lifespan, LMA, etc. The second axis (PC2) explained 14.4% of the variation, and it was correlated with DT, FertReq, MoistUse, SoilDmin, LMA, and WD (Fig. 4). We used these values of PC1 and PC2 to calculate their CWMs (CWM_{PC1} and CWM_{PC2}, respectively). CWM_{PC1} represented resource-acquisitive higher CWM_{PC1} represented resource-acquisitive traits, characterized by fast-growing through high use of resources (carbon, nutrients, and water) to achieve rapid acquisition of carbon, while lower CWM_{PC1} represented resource-conservative traits, which involves slow returns through considerable savings, reduced respiratory and resource uptake rates, thereby enhancing survival (*65*, *67*, *72*). On the other hand, CWM_{PC2} encompassed environmental tolerance versus moisture-/fertility-demanding traits (*64*, *66*).

Global environmental change drivers

Overall environmental change

Following previous studies (*43*), we used the middle calendar year (Year) to represent the effects of global environmental change overall on biomass growth. The middle calendar year was calculated as the mean of two consecutive censuses.

Climate warming and long-term drought

Using the data of monthly mean temperature and mean precipitation and potential evapotranspiration acquired by BioSIM (*73*), subsequently, we calculated the anomaly of annual mean temperature (ATA; degrees Celsius; defined as a deviation from their long-term means between 1958 and 2015) and the annual SPEI (unitless) of the growing season (see the definition below) using the SPEI package in R (*74*). SPEI accounts for both precipitation and potential evapotranspiration to determine drought (likely associated with soil moisture availability), and it standardizes the value by its log-logistic probability distribution (*74*), allowing the relative comparison of water requirements on a spatiotemporal scale. To facilitate the interpretation of the results, we used the negated metric of SPEI, defined as drought intensity (DI) = −1 × SPEI (greater values of DI indicate drier conditions). The growing season in the study area was defined as the period between May and October (corresponding to the frost-free season in the region; see Supplementary Text S2 for alternative considerations).

Spatial variations in climate

We calculated the long-term average (between 1958 and 2015) of the AI ($\mathrm{AI_{ave}}$) and mean annual temperature ($\mathrm{MAT_{ave}}$, °C) as environmental controls of forest growth and diversity. Monthly mean temperature, precipitation (PPT; centimeters), and potential evapotranspiration (PET; centimeters) were obtained by BioSIM software version 11 (*73*) for each plot to calculate annual AI (annual PPT divided by annual PET) (*40*). BioSIM generates plot-level climates based on the simulation using daily observations and monthly historical statistics from the sampled points (latitude/longitude), being adjusted by differences in elevation (*73*).

Site quality

In forest ecosystems, plot-level growth and diversity could be dependent on local site quality. The site quality of each plot was calculated as the site index, which was estimated using species-specific growth curves and represented the total height (meters) of the dominant trees at a stand age of 100 years (*75*). *Pinus contorta* was the dominant tree species for 874 of the 3036 plots. Site indices of plots dominated by other species were standardized by converting them to that of *P. contorta* using a published site index conversion equation for tree species in western Canada (*75*). Alternative to the site index, we also considered soil drainage class [from "1" ("rapidly drained") to "7" ("poorly drained")] to control for the site condition (Supplementary Text S3). The choice of these variables did not influence the results of the subsequent analysis (fig. S5).

Stand age

We used stand age (SA; representing time since catastrophic disturbances) to account for the effects of the history of natural disturbances and forest development processes on biomass growth (*76*). We calculated the middle age between two successive measurements. Stand age represents changes in stand structural attributes such as stem density and stand basal area associated with forest succession. Stand ages in PSP data were available in the PSP datasets provided by the provincial governments. Ages were based on either known fire history or coring dominant trees in the plot or outside plots. With coring used, the average age of the oldest species was assigned as stand age or time since the last stand-replacing disturbance.

Statistical analysis

To test whether the temporal change in biomass growth is dependent on functional diversity and identity, we constructed the following linear mixed-effects model to factor out the confounding effects of biotic and abiotic covariates:

$$
\begin{gathered}
\ln(\Delta \mathrm{AGB_{GI}})_{ij} = (\mathrm{Intercept}) + (\mathrm{Year})_j + \ln(\mathrm{FD})_{ij} + (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{CWM_{PC2}})_{ij} + (\mathrm{Year})_j \times \ln(\mathrm{FD})_{ij} + \\
(\mathrm{Year})_j \times (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{Year})_j \times (\mathrm{CWM_{PC2}})_{ij} + (\mathrm{MAT_{ave}})_i + \\
(\mathrm{AI_{ave}})_i + (\mathrm{SI})_i + \ln(\mathrm{SA})_{ij} + (\mathrm{MAT_{ave}})_i \times (\mathrm{Year})_j + \\
(\mathrm{MAT_{ave}})_i \times \ln(\mathrm{FD})_{ij} + (\mathrm{MAT_{ave}})_i \times (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{MAT_{ave}})_i \times (\mathrm{CWM_{PC2}})_{ij} + \\
(\mathrm{AI_{ave}})_i \times (\mathrm{Year})_j + (\mathrm{AI_{ave}})_i \times \ln(\mathrm{FD})_{ij} + (\mathrm{AI_{ave}})_i \times (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{AI_{ave}})_i \times (\mathrm{CWM_{PC2}})_{ij} + \\
(\mathrm{SI})_i \times (\mathrm{Year})_j + (\mathrm{SI})_i \times \ln(\mathrm{FD})_{ij} + (\mathrm{SI})_i \times (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{SI})_i \times (\mathrm{CWM_{PC2}})_{ij} + \ln(\mathrm{SA})_{ij} \times (\mathrm{Year})_j + \\
\ln(\mathrm{SA})_{ij} \times \ln(\mathrm{FD})_{ij} + \ln(\mathrm{SA})_{ij} \times (\mathrm{CWM_{PC1}})_{ij} + \ln(\mathrm{SA})_{ij} \times (\mathrm{CWM_{PC2}})_{ij} + (1 \mid \mathrm{Plot\ ID})
\end{gathered}
\tag{1}
$$

where *i* and *j* were the *i*th plot at *j*th census, respectively. $\Delta\mathrm{AGB_{GI}}$ was the annual aboveground biomass growth. $\mathrm{MAT_{ave}}$ and $\mathrm{AI_{ave}}$ were the long-term averages of mean annual temperature and AI, SI was site index, SA was stand age, Year was the calendar year representing the long-term environmental change overall, and FD was functional diversity quantified as functional dispersion. For calendar year and stand age, we used their middle values calculated as the average of the two consecutive censuses. We included a random plot identity effect (Plot ID, accounting for site-specific disturbance history and other unknown factors). We used the model accounting for all of these predictors because it had the lowest Akaike information criterion (AIC) value. $\Delta\mathrm{AGB_{GI}}$ was transformed by a natural logarithmic, which minimized the deviation of the model residuals from normality. SI, SA, and FD were also log-transformed to improve the model fitness based on AIC and visual inspections of their distributions. All the explanatory variables were centered and scaled (mean = 0, SD = 1) before analysis to allow coefficient comparison. The maximum variance inflation factor (VIF) was 2.5. We performed the linear mixed-effects modeling using the lme4 package with the restricted maximum likelihood estimation (*77*).

Subsequently, we examined how warming, changes in water availability, and atmospheric aridification affected biomass growth by replacing the calendar year in Eq. 1 with these climate change drivers

$$
\begin{gathered}
\ln(\Delta \mathrm{AGB_{GI}})_{ij} = (\mathrm{Intercept}) + (\mathrm{ATA})_{ij} + (\mathrm{DI})_{ij} + \ln(\mathrm{FD})_{ij} + (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{CWM_{PC2}})_{ij} + \\
(\mathrm{ATA})_{ij} \times \ln(\mathrm{FD})_{ij} + (\mathrm{ATA})_{ij} \times (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{ATA})_{ij} \times (\mathrm{CWM_{PC2}})_{ij} + \\
(\mathrm{DI})_{ij} \times \ln(\mathrm{FD})_{ij} + (\mathrm{DI})_{ij} \times (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{DI})_{ij} \times (\mathrm{CWM_{PC2}})_{ij} + \\
(\mathrm{MAT_{ave}})_i + (\mathrm{AI_{ave}})_i + (\mathrm{SI})_i + \ln(\mathrm{SA})_{ij} + (\mathrm{MAT_{ave}})_i \times (\mathrm{ATA})_{ij} + \\
(\mathrm{MAT_{ave}})_i \times (\mathrm{DI})_{ij} + (\mathrm{MAT_{ave}})_i \times \ln(\mathrm{FD})_{ij} + (\mathrm{MAT_{ave}})_i \times (\mathrm{CWM_{PC1}})_{ij} + \\
(\mathrm{MAT_{ave}})_i \times (\mathrm{CWM_{PC2}})_{ij} + (\mathrm{AI_{ave}})_i \times (\mathrm{ATA})_{ij} + (\mathrm{AI_{ave}})_i \times (\mathrm{DI})_{ij} + \\
(\mathrm{AI_{ave}})_i \times \ln(\mathrm{FD})_{ij} + (\mathrm{AI_{ave}})_i \times (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{AI_{ave}})_i \times (\mathrm{CWM_{PC2}})_{ij} + \\
(\mathrm{SI})_i \times (\mathrm{ATA})_{ij} + (\mathrm{SI})_i \times (\mathrm{DI})_{ij} + (\mathrm{SI})_i \times \ln(\mathrm{FD})_{ij} + \\
(\mathrm{SI})_i \times (\mathrm{CWM_{PC1}})_{ij} + (\mathrm{SI})_i \times (\mathrm{CWM_{PC2}})_{ij} + \ln(\mathrm{SA})_{ij} \times (\mathrm{ATA})_{ij} + \ln(\mathrm{SA})_{ij} \times (\mathrm{DI})_{ij} + \\
\ln(\mathrm{SA})_{ij} \times \ln(\mathrm{FD})_{ij} + \ln(\mathrm{SA})_{ij} \times (\mathrm{CWM_{PC1}})_{ij} + \ln(\mathrm{SA})_{ij} \times (\mathrm{CWM_{PC2}})_{ij} + (1 \mid \mathrm{PlotID})
\end{gathered}
\tag{2}
$$

where ATA was the anomaly of annual mean temperature and DI was drought intensity.

Assessing multicollinearity

ATA and DI were assumed to increase with time simultaneously. Although the correlation between ATA and DI was relatively weak ($r = 0.11$) and the maximum VIF for Eq. 2 was 2.5, we took a proactive approach to address potential collinearity issues in our linear mixed-effects modeling. To inspect potential issues of collinearity (*78*), we conducted (i) penalized parameter estimates by ridge regression, which is less sensitive to multicollinearity by shrinking the regression coefficients toward zero (Supplementary Text S4.1) (*78*) and (ii) sequential regression by prioritizing either climate change driver to regress the detrended residuals with others (Supplementary Text S4.2). These alternative analyses produced qualitatively similar results (fig. S4), which confirmed that collinearity among the climate variables was not an issue in our modeling framework.

Robustness of the analysis

To further assess the reliability of our approach, we performed additional substitute analyses: (i) modeling with subsets of plots randomly sampled 1000 times to investigate the variability and any biases that may arise from sampling different subsets of the data (Supplementary Text S4.3) and (ii) modeling with stricter plot selection criteria (continuously monitored for ≥20 years; 1535 plots; Supplementary Text S4.4) to confirm our results with a core set of data most likely to capture the long-term trends (*43*). These methods produced qualitatively similar outcomes (fig. S5), which supports the robustness of our main analysis.

Potential effects of unobserved covariates

Our observational approach is designed to capture the correlation between diversity and productivity in natural systems. We therefore aimed to interpret the estimated effect as a causal relationship (B➔EF) by accounting for multiple observable covariates and the random plot identity effect. However, in complex ecological systems in nature, it is challenging to measure all potential confounding variables that may be associated with both diversity and productivity. Overlooking unmeasurable yet significant confounders can obscure or mimic the causal relationship between diversity and productivity (*79*). To inspect whether unobserved and unaccounted confounders could have caused false coefficient estimates of the main effects of diversity metrics, we used (i) "fixed effects panel data regression," which is a common approach to infer causal relationships in the fields outside of ecology, and (ii) a "lagged dependent variable design." These methods were recently applied by Dee *et al.* (*79*) to the framework of the B-EF studies (Supplementary text S4.5). As these two approaches both yielded qualitatively similar coefficient estimates (but not for species richness; fig. S6), influences of unobservable confounders to the main diversity effects were negligible, and biomass growth was not necessarily determined by its own lagged endogenous processes (Supplementary Text S4.5).

Inspecting spatial autocorrelation

Last, we inspected the spatial dependence of the model residuals in Eqs. 1 and 2 by applying Moran's I test in the spdep package (*80*). We found no autocorrelation [$P = 0.432$ for each model; based on the great circle distances (*80*) of the plot coordinates]. For the interpretation of all the analyses, we focused not only on the statistical significance (P values or 95% confidence intervals) but also on their effect sizes (*81*).

Supplementary Materials

This PDF file includes:

Supplementary Texts S1 to S4
Figs. S1 to S6
Tables S1 to S3
References

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Acknowledgments: We are grateful to E. B. Searle for assistance with the PSP data compilation. We also appreciate K. Yu for advice in obtaining environmental variables, X. Ding for insights into the PSP data inspection, and K. Uchida for comments on the earlier draft. We thank the provincial governments of British Columbia, Alberta, Saskatchewan, and Manitoba for providing the PSP data for our analysis and the TRY initiative for providing the plant traits database (www.try-db.org). **Funding:** The study was supported by the Japan Society for the Promotion of Science (JSPS) KAKENHI (the Grant-in-Aid for JSPS Fellows: grant number 20 J00178), the Natural Sciences and Engineering Research Council of Canada (STPGP 506284), and ETH Zürich (the Grant for Young Researchers' Exchange Programme between Japan and Switzerland: JP-EG_06_042021). X.C. acknowledges the support from NSFC Excellent Young Scientists Fund (overseas) and the Scientific Research Startup Fund Project of Zhejiang A&F University (2024LFR019). M.H. appreciates M. Soga for support throughout the program of the JSPS Research Fellowship. **Author contributions:** Conceptualization: M.H. and H.Y.H.C. Methodology: M.H., H.Y.H.C., and X.C. Data curation: M.H. and H.Y.H.C. Resources: M.H., H.Y.H.C., and J.G. Investigation: M.H. Formal analysis: M.H. Visualization: M.H. and X.C. Validation: M.H. Supervision: H.Y.H.C., J.G., and X.C. Project administration: H.Y.H.C. Funding acquisition: M.H., H.Y.H.C., and X.C. Writing—original draft: M.H. Writing—review and editing: M.H., X.C., J.G., and H.Y.H.C. All authors contributed to the discussion and interpretation of data and revisions and approved the final version of the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data and R codes needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials and figshare (https://doi.org/10.6084/m9.figshare.25367542.v1).

Submitted 8 December 2023
Accepted 20 March 2024
Published 24 April 2024
10.1126/sciadv.adn4152