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Long-term stability of productivity increases with tree diversity in Canadian forests

Xiaxia Ding[a], Peter B. Reich[b,c,d], Masumi Hisano[a,e], and Han Y. H. Chen[a,b,1]

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The temporal stability of forest productivity is a key ecosystem function and an essential service to humanity. Plot-scale tree diversity experiments with observations over 10 to 11 y indicate that tree diversity increases stability under various environmental changes. However, it remains unknown whether these small-scale experimental findings are relevant to the longer-term stability of natural forests. Using 7,500 natural forest plots across much of Canada, monitored over three to four decades on average, we provide strong evidence that higher temporal stability (defined as the mean productivity divided by its SD over time) is consistently associated with greater tree functional, phylogenetic, and taxonomic diversity across all lengths of observations. Specifically, increasing functional diversity from its minimum to maximum values increases stability, mean productivity, and the temporal SD of productivity by 14%, 36%, and 28%, respectively. Our results highlight that the promotion of functionally, phylogenetically, and/or taxonomically diverse forests could enhance the long-term productivity and stability of natural forests.

productivity stability | asynchrony | biodiversity-ecosystem functioning | phylogenetic diversity | functional diversity

Significance

The temporal stability of productivity in natural forests represents a critical service for humanity. Here, a study of the stability of natural forest productivity was conducted using long-term and geographically broad-scale sampling across Canada. This analysis revealed that higher stability is consistently associated with greater functional and phylogenetic diversity in Canada's natural forests across all observation lengths of plots ranging from 12 to 52 y. Our finding highlights that functional and phylogenetic diversity play key roles in the long-term stability of natural forests.

The temporal stability of ecosystem productivity, often defined as the ratio of mean productivity (μ) to its variation in time (SD, σ), is considered an important feature of terrestrial ecosystems that provides a key service to people (1). Given that temporal stability may be related to plant biodiversity (2), there is concern that ongoing biodiversity loss from anthropogenic disturbances could broadly reduce stability (1, 3, 4). Recently, two decadal-length tree diversity experiments have demonstrated that species richness stabilizes the temporal stability of forest productivity (5, 6). However, it remains unclear whether these positive relationships between tree diversity and stability based on short-term, small-scale manipulation experiments can be extended to long-term, large-scale, complex natural forests, which experience major climate and biotic disturbances with cycles of multiple decades. For example, moderate to severe droughts occur only once in several decades (7, 8). Meanwhile, outbreaks of major forest insects, such as spruce budworms [*Choristoneura fumiferana* (Clem.)] and mountain pine beetles (*Dendroctonus ponderosae* Hopkins) in North America, take place every 30 to 40 y (9, 10). Variation in ecological properties, including productivity, can increase with the occurrence of major climate and biotic disturbances (11, 12), weakening relationships between diversity and stability. Longer-term, large-scale data from natural communities could help reveal real-world relationships between diversity and stability and demonstrate the utility of science to policy development (13).

The temporal stability of productivity can increase with diversity through the so-called insurance effect in two ways (14). First, mean productivity can increase with diversity (i.e., "performance-enhancing effect") due to complementarity among species, including resource partitioning, abiotic facilitation and biotic feedbacks, and the positive selection effect (15, 16). Second, the temporal SD of productivity (σ) can decrease with diversity. The σ of a diverse plant community is composed of the components of variance (the summed variances of the productivity of individual species) and covariance (correlation between species). While the variance may increase with diversity, the covariance can decrease as a result of community-wide species asynchrony (thereafter, asynchrony) (17), which can rise from both compensatory dynamics and statistical-averaging (or portfolio effect). Compensatory dynamics can occur when abiotic environmental fluctuations or resource competition harms some species, and their competitors increase in abundance. Statistical averaging results because a community consisting of many independently fluctuating species has a higher probability of being more stable than a community consisting

Author affiliations: [a]Faculty of Natural Resources Management, Lakehead University, Thunder Bay, ON P7B 5E1, Canada; [b]Institute for Global Change Biology, and School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48104; [c]Department of Forest Resources, University of Minnesota, St. Paul, MN 55108; [d]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2747, Australia; and [e]Graduate School of Advanced Science and Engineering, Hiroshima University, Higashihiroshima 739-8511, Japan

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[1]To whom correspondence may be addressed. Email: han.yh.chen@gmail.com.

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of few such species) (18–21). However, how compensatory dynamics and statistical averaging affect stability in natural forests remains unclear.

Additionally, tree species can also respond asynchronously to other trophic organisms, such as specialist insects and pathogens, based on host-plant specificity or high phylogenetic conservatism (22), which may be predicted to some degree based on phylogenetic specificity in the insect- and pathogen-host range (23–25). For example, plant species abundance and their phylogenetic relatedness influence insect and pathogen damage and plant productivity (26, 27). In phylogenetically diverse plant communities, plant productivity can be greater on average due to reductions in biotic damage, while its temporal SD may be smaller due to asynchronous responses of plants to their respective insects and pathogens (23, 28).

Given the above, we hypothesized that diversity would increase mean productivity due to complementarity mechanisms including resource partitioning, abiotic facilitation, and reductions in biotic damage, and increase the temporal SD of productivity but to a lesser extent due to asynchrony offsetting the increased variance scaling to higher productivity (Fig. 1).

Previous studies in natural forests have reported positive (29–31), negative (32), and nonsignificant (33) relationships between tree species richness and productivity stability. These divergent findings could have arisen for several reasons. First, different lengths of observation (the number of years between the initial and last censuses) can influence the estimation of diversity and stability relationships. For example, diversity experiments have shown that the positive effects of diversity on productivity increase over stand development (34, 35), suggesting an enhanced positive diversity and stability relationship with a longer census duration. Second, species richness per se provides limited information to predict asynchrony and stability (32, 36, 37). Although functional diversity and phylogenetic diversity have been shown to also promote ecosystem stability in experimental systems (38, 39), their roles have been largely ignored in studies in natural forests (32, 40), where environmental fluctuations and natural enemies (which may be more in tune with phylogenetic diversity than taxonomic diversity), such as insect herbivores, prevail and have pivotal influences on forest productivity (9, 23, 41). However, species richness and other taxonomic diversity metrics are usually correlated with functional diversity and phylogenetic diversity, making it difficult to tease apart their separate roles (42). Third, in natural forests, both diversity and stability are likely influenced by climate factors, local site conditions, and stand development, whose effects need to be taken into account (and standardized) when quantifying their relationships between diversity and ecosystem functions (43, 44) (Fig. 1). Therefore, these confounding factors need to be studied and accounted for to achieve the generality of the relationship between diversity and stability in long-term and large-scale natural forests.

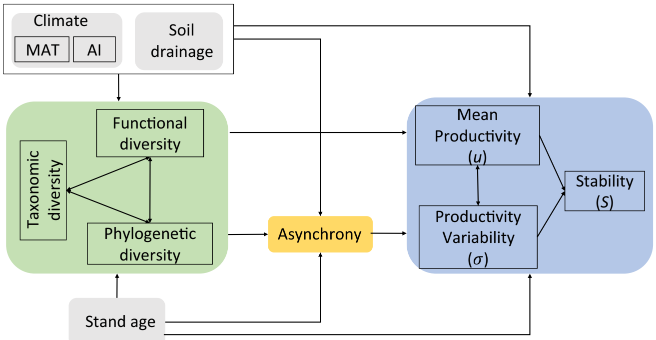

Fig. 1. A priori causal pathways of tree diversity, climate (mean annual temperature, MAT; aridity index, AI), soil drainage, and stand age on asynchrony, mean productivity, temporal SD of productivity, and temporal stability of productivity.

To understand the relationships between temporal stability of productivity and tree diversity, we compiled 65 y (1951–2016) of data collected from 7,498 repeatedly measured unique plots of aboveground live biomass across Canada, whose lengths of observation (the number of years between the first and last census, that is, the census length thereafter) varied from 12 to 52 y (*SI Appendix*, Table S1). We first used linear mixed models to test 1) how stability and its components (μ and σ) were associated with asynchrony and various measures of taxonomic, functional, and phylogenetic diversity, 2) how spatial variations in climate, soil conditions, and stand age affected diversity, stability, and their relationships (Fig. 1), and 3) whether the relationship between diversity and stability changes with the lengths of observations. Finally, we presented the results of structural equation models (SEM) to infer their causal relationships. To produce a meaningful comparison of the dependence of stability on diversity, we employed unified Hill diversity indices (45). Our initial model included Hill taxonomic diversity, functional diversity, and phylogenetic diversity as well as covariates, but the model had large values of variance inflation factor (*SI Appendix*, Table S2). As recommended to reduce collinearity and overfitting (46), we developed two models; one included Hill functional and phylogenetic diversity, and the other included Hill taxonomic diversity. Hill diversity metrics with q = 1 including functional diversity (FDq1), phylogenetic diversity (PDq1), and taxonomic diversity (TDq1) explained greater amounts of variation in our focal measures than their alternatives (q = 0 and 2) (*SI Appendix*, Table S3), hence we focus on them hereafter.

Results

Greater diversity, regardless of the metrics used, resulted in higher productivity (and its variance) and stability. The linear mixed models based on FDq1 and PDq1 explained 42%, 88%, and 75% of the variances of stability, mean productivity, and SD of productivity, respectively (*SI Appendix*, Tables S1 and S4). Stability decreased with FDq1 and PDq1 ($r = -0.23$ and -0.07, respectively) (Fig. 2*A*). Mean productivity increased with FDq1 ($r = 0.20$) (Fig. 2*B*). SD showed positive relationships with FDq1 and PDq1 ($r = 0.35$ and 0.08, respectively, Fig. 2*C*). Similar patterns were found in the models predicted by TDq1 (*SI Appendix*, Fig. S4 and Table S5). The sum effects of FDq1 and PDq1 on stability (sum $r = -0.29$) were slightly greater than that of TDq1 ($r = -0.25$), while they had a slightly smaller effect on mean productivity (sum $r = 0.20$; TDq1 $r = 0.23$), and slightly greater effects on SD (sum $r = 0.43$; TDq1 $r = 0.38$) (*SI Appendix*, Tables S4 and S5).

Asynchrony, which itself is influenced by several aspects of diversity (Figs. 1 and 3), was the dominant predictor of greater stability (standardized coefficient $r = 0.72$ (Fig. 2*A*). Mean productivity increased modestly with asynchrony ($r = 0.05$) (Fig. 2*B*). SD showed a dominant negative association with asynchrony ($r = -0.61$) that was stronger than its relationships with FDq1 and PDq1.

The SEM based on FDq1 and PDq1 conformed well with data and explained 42% of the stability variance and revealed multivariate causal relationships between stability, asynchrony, and diversity while accounting for the effects of covariates (Fig. 3*A*). Stability was positively related to asynchrony (standardized coefficient $r = 0.72$). FDq1 and PDq1 were positively related to stability through their influence on asynchrony, and the positive association between asynchrony and FD was more than three times stronger than between asynchrony and PD (r = 0.30 and 0.08, respectively). In contrast, FDq1 and PDq1 had direct negative relationships with stability (r = −0.23 and −0.08, respectively). As a result, the total effect of FDq1 on stability was 0.07, and that of PDq1 was 0.01. Based on the SEM, stability increased by 14% and 1% with increasing FDq1 and PDq1 from their respective minimums to maximums. The total effect of TDq1 on stability (r = 0.09, *SI Appendix*, Fig. S5) was almost the sum of the effects of FDq1 and PDq1 on stability (r = 0.07 and 0.01, respectively). The simple bivariate plots showed the positive relationships between stability with TDq1, FDq1, and PDq1 at the same order of effect magnitude in SEM (*SI Appendix*, Fig. S3).

The SEMs for stability components, which help explain the response of stability to diversity (Fig. 3), also conformed well to the data and explained 88% and 71% of the variance in μ and σ, respectively (Fig. 4). Specifically, FDq1 had a direct association with μ (r = 0.20, Fig. 4*A*), while σ was directly associated with FDq1 and PDq1 (r = 0.35 and 0.09, respectively, Fig. 4*B*). The greater direct effects of FDq1 and PDq1 on σ than on μ contributed to their direct negative effects on stability (Fig. 3). Meanwhile, μ increased modestly with FDq1 and PDq1 (r = 0.02 and 0.01, respectively), while σ decreased with FDq1 and PDq1 indirectly through asynchrony (r = −0.25 and −0.07, respectively, Figs. 4 and 5). Overall, FDq1 had a greater total effect on μ than PDq1 (r = 0.22 and 0.01, respectively), and σ decreased with FDq1 and PDq1 (r = 0.10 and 0.02, respectively) (Figs. 4 and 5). The two times greater increase in μ than σ via

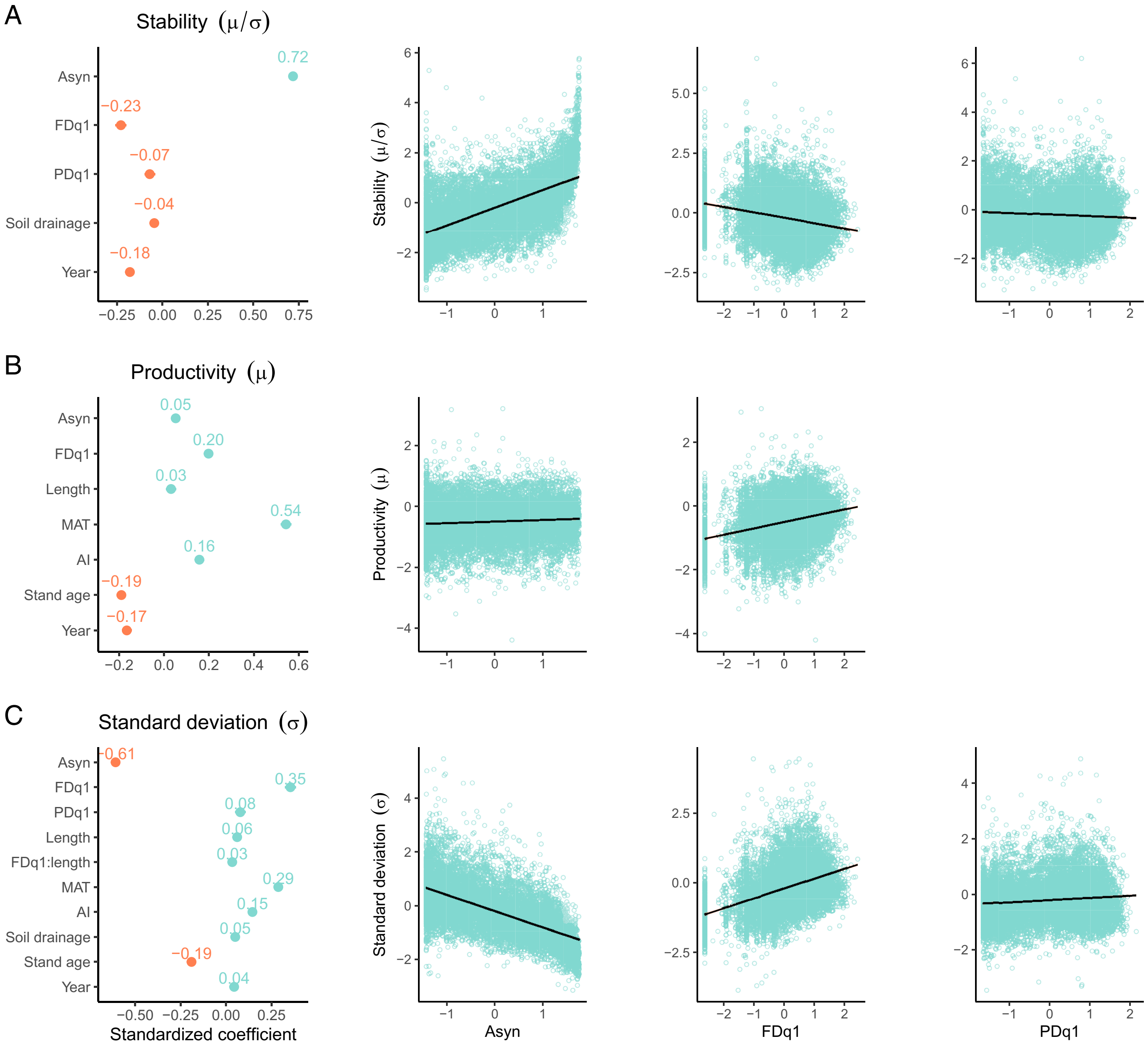

Fig. 2. The relationship between stability, mean productivity, SD, asynchrony, diversity, and covariates. (*A*) Stability. (*B*) Productivity mean. (*C*) The standard deviation of productivity. The scatterplots are the partial relationships between variables. Asyn: the community-level species asynchrony; FDq1: Hill functional diversity at q = 1; PDq1: Hill phylogenetic diversity at q = 1; MAT, AI, and stand age are the long-term averaged mean annual temperature, the long-term averaged aridity index, and the average stand age from the first to last measurement. Soil drainage indicates how rapidly water is removed from soil in relation to supply ranging from 1 (very rapidly drained) to 7 (very poorly drained). Census length (length) is the number of years between the first and last measurement of each sample plot. The year is the middle calendar year of all measurement years of each sample plot; Stability, mean productivity, SD, and stand age were log-transformed. All variables were scaled.

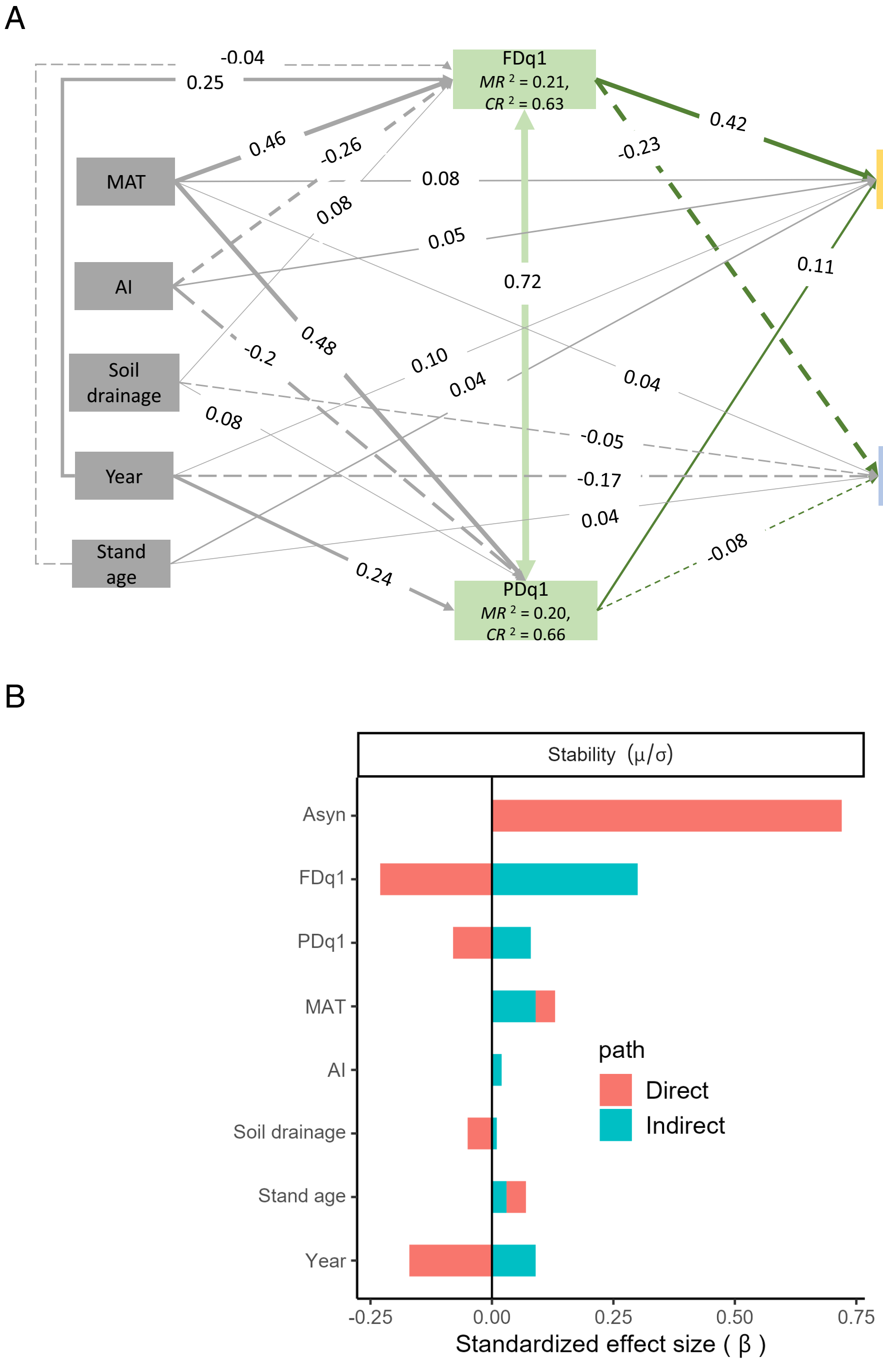

Fig. 3. Structural equation model showing tree diversity, climate, soil conditions, and stand age on the long-term stability of productivity of Canadian forests. (*A*) Path diagram of attributes influencing stability. (*B*) Direct and summed indirect effects. Numbers adjacent to arrows are standardized path coefficients analogous to relative regression weights. Solid and dashed arrows represent positive and negative relationships, respectively. The proportions of marginal and conditional variance explained (MR^2 and CR^2, respectively) appear alongside every response variable. The goodness-of-fit statistics for panel a are Fishers' C = 5.4 and *P* = 0.492, indicating a close model-data fit. All variables are described in Fig. 2.

direct and indirect FDq1 corresponds to the positive relationship between stability and FDq1, which is also consistent with their bivariate relationships (*SI Appendix*, Fig. S3). Increasing the value of FDq1 from minimum to maximum increased 36% and 28% in μ and σ, respectively. Increasing the PDq1 value from minimum to maximum increased μ and σ by 1% and 4%, respectively.

The effects of diversity on stability and its components also had climate-related signatures. Diversity indices were higher in warmer sites (i.e., higher mean annual temperature, MAT) and lower in humid sites (i.e., higher aridity index, AI) (Fig. 3 and *SI Appendix*, Fig. S1). Stability was positively related to MAT and AI when both direct and indirect effects were included (Fig. 3*B*). Meanwhile, μ increased more with MAT and AI than σ did (Fig. 5). Soil drainage class had minor influences on stability, μ and σ (Figs. 3 and 5). Stand age had a positive relationship with stability, corresponding with a stronger negative association with σ than μ (r = 0.07, −0.22, and −0.20, respectively, Figs. 3 and 5). The middle calendar year of the sample plots had a negative relationship with stability due to a greater decrease in μ and a weak increase in σ (r = −0.08, −0.10, 0.01, respectively, Figs. 3 and 5). Stability did not change with census

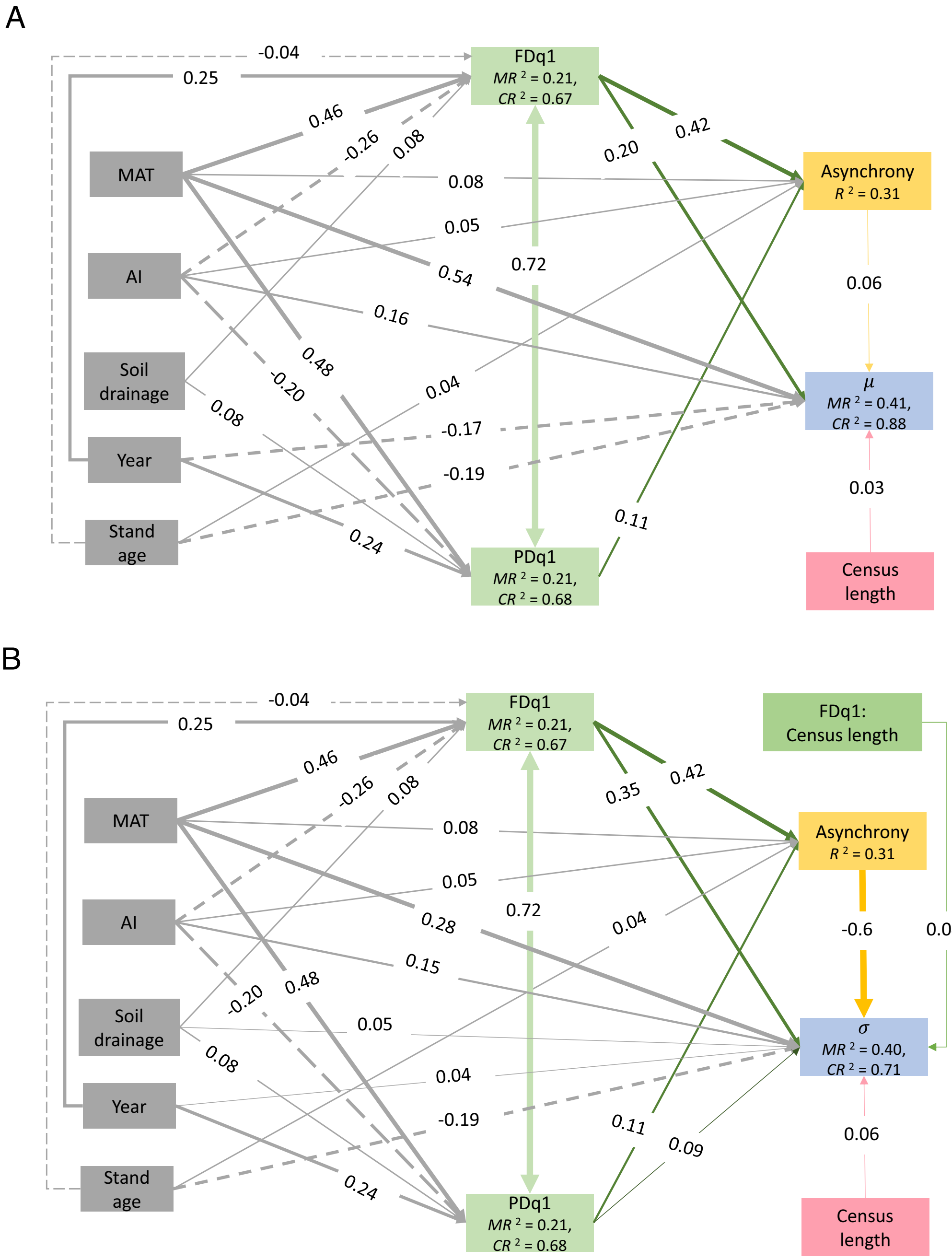

Fig. 4. Structural equation model showing tree diversity, climate and soil conditions, and stand age on mean productivity (μ) and productivity SD (σ) in Canadian forests. (*A*) Path diagram of attributes influencing μ. (*B*) Path diagram of attributes influencing σ. Numbers adjacent to arrows are standardized path coefficients analogous to relative regression weights. Solid and dashed arrows represent positive and negative relationships, respectively. The proportions of marginal and conditional variance explained (MR^2 and CR^2, respectively) appear alongside every response variable. The goodness-of-fit statistics for panels *A* and *B* are Fishers' C = 18.2 and *P* = 0.196, indicating a close model-data fit. All variables are described in Fig. 2.

length. However, μ and σ were greater for plots with longer census lengths (Figs. 3 and 5).

Discussion

Our analyses indicate that species asynchrony served as the dominant mechanism underlying the positive relationship between diversity and the long-term stability of our studied natural forests. This finding extends those previously reported in short-term experimental and observational studies (3, 4, 6, 39, 47) to long-term (as long as 65 y) observations in the large-scale natural forests in Canada.

We found that functional diversity served as a strong predictor for stability. This finding is in agreement with the theoretical expectation that functionally diverse communities have a high probability of containing species that occupy different ecological niches, showing different preferences for internal or external factors, leading to asynchronous responses between species and resulting in more stable community productivity (18). Our finding of a stronger effect of functional diversity than phylogenetic diversity on stability differs from those of some prior studies of experimental grasslands (39) and natural forests (32). One of the possible reasons for the difference in their relative importance could be how they were quantified. Previous studies quantified functional

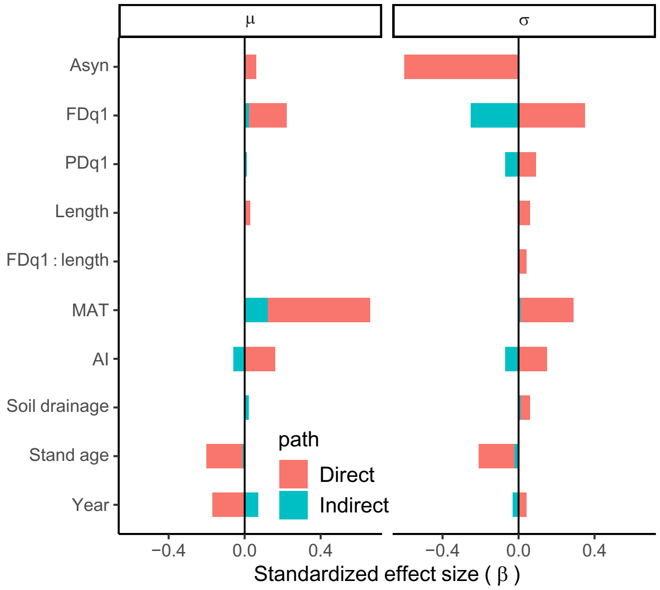

Fig. 5. The bar plot of summarized direct and indirect paths by predictors on mean productivity (μ) and productivity SD (σ) in the structural equation models in Fig. 4. All variables are described in Fig. 2.

diversity as the sum of dissimilarity in the trait space of pairwise species and phylogenetic diversity as the mean pairwise distance, while we employed the unified Hill functional, phylogenetic, and taxonomic diversity, which allows a comparison of their relative importance at the same dimension (48, 49). However, similar to previous studies (50), higher functional diversity was associated with higher phylogenetic diversity in our dataset ($r = 0.72$, Fig. 3), suggesting that the effects of functional diversity estimated in our statistical models accounted in part for those from phylogenetic diversity (and vice versa). This view was supported by the strong phylogenetic signals in leaf structure and leaf habitat traits (*SI Appendix*, Fig. S8). Our findings imply that the strategies for forest restoration, conservation, and plantations should encourage forests with higher diversity by combining species with different functional traits related to tree growth, reproduction, and survival and including species with wide phylogenetic distances so that they can better cope with drought events and outbreaks of insects and pathogens.

We found that diversity increased mean productivity and, to a lesser extent, productivity SD, resulting in an increase in stability. Numerous studies have reported higher mean productivity in diverse ecosystems (34, 51, 52). The positive diversity-productivity relationship is usually a result of positive selection effects and much more so by complementarity effects of niche partitioning and facilitation related to functional and phylogenetic diversity (15, 16). Higher diversity is associated with higher mean productivity due to increased utilization and retention of aboveground and belowground resources, positive plant–soil interactions with respect to soil fertility, and reductions in biotic damage (15, 43, 53–55). As expected and previously demonstrated in short-term studies of natural grasslands and forest plantations (6, 47), we found that higher diversity was associated with higher asynchrony, resulting in a lesser increase in long-term SD than mean productivity in natural forests. The greater decrease in SD through asynchrony related to functional and phylogenetic diversity could be attributed to the asynchronous responses of different tree species to temporal environmental fluctuations (17) and their respective insects and pathogens (23, 28).

Additionally, by decomposing species asynchrony into compensatory and statistical averaging effects following a method described previously (20), we found that the compensatory dynamics had twice as large an effect on stability as the statistical averaging ($r = 0.60$ and 0.34, respectively) by increasing mean productivity and decreasing SD (*SI Appendix*, Fig. S6). However, the compensatory effect was only weakly associated with functional diversity ($r = 0.05$), while the statistical averaging effect was more positively associated with both functional and phylogenetic diversity ($r = 0.59$ and 0.21, respectively) (*SI Appendix*, Fig. S6). In contrast to the low importance of compensatory dynamics found in a 10-y-old tree diversity experiment (6), our study of 65 y of observations found a strong compensatory effect on stability, probably because trees invest in long-lasting structures and need a long time to show dynamic changes. Our result of the weak association between the compensatory effect and diversity might be attributed to the finding that tree compositional shifts (i.e., alteration of dominant species or species with specific responses to certain types of disturbances along succession) overwhelmed the effect of diversity in our long-term study (56) since succession could play a dominant role in the compensatory effects on stability (21). Meanwhile, our result of the strong positive association between statistical averaging effects and functional and phylogenetic diversity is consistent with the expectation that statistical averaging effects depict the fact that aggregated productivity varies less in more diverse communities (21, 57). Our findings provide evidence supporting the theoretic expectation that compensatory dynamics, which are less sensitive to species diversity, play a strong role in ecosystem stability in heterogeneous environments (18), such as in the natural forests we studied. Nevertheless, similar to a previous grassland study (20), statistical averaging contributed more to the relationship between diversity and stability than did compensatory dynamics.

Our finding that higher temperatures promoted diversity and mean productivity is consistent with previous studies (43, 58). Furthermore, higher temperatures promote stability through diversity and asynchrony, as suggested previously (59). However, decreasing aridity (an increasing aridity index, indicating higher moisture) decreased functional and phylogenetic diversity. This is related to the less diverse plots with overlapping traits distributed in the wet western region of Canada, as demonstrated in this present study (*SI Appendix*, Fig. S1) and a previous study (43). Furthermore, older stands are associated with higher stability but low mean productivity, consistent with previous studies (33, 60).

In our study, stability did not change significantly with census length while both mean productivity and productivity SD increased, as expected (11, 12, 34, 35). Moreover, there were no significant interaction effects of census length and functional, phylogenetic, or taxonomic diversity on stability (Fig. 2 and *SI Appendix*, Fig. S4), indicating a consistent relationship between diversity and stability over the census lengths from 12 to 52 y in our studied forests. Our finding of a strong positive relationship between long-term stability and tree diversity of natural forests generalizes the results of short-term experimental and observational studies to long-term temporal, large spatial real-world Canadian natural forests, which had experienced various major climate and biotic disturbances during the study period from 1951 to 2016 (8–10). Collectively, our results together with previous findings demonstrate that biodiversity acts as a strong force in stabilizing the productivity of various ecosystems under a wide range of abiotic and biotic environments.

Human activities have led to the loss of biodiversity and ecosystem functioning and services that are vital for human existence and well-being (61). Two short-term tree diversity experiments have shown that a greater number of tree species leads to greater temporal stability of productivity (5, 6), but the results from natural forests are mixed (29–33). Several reasons could explain the previously divergent findings. First, species evenness plays an important role in ecosystem functioning (34, 62). The lack of positive diversity effects in previous studies could be attributed to the fact that most studies in natural forests used only species richness to represent diversity. Our analysis shows that species richness (i.e., Hill number with q = 0) is not as effective as Shannon diversity (Hill number with q = 1) in predicting stability (*SI Appendix*, Table S3). This is consistent with the idea that both richness and evenness promote higher productivity and/or stability (34, 62), because Shannon diversity incorporates both richness and evenness, in contrast to the richness metric alone. Second, the magnitude (or range) of diversity can influence the outcome as we show that stability increases continuously with increasing diversity. A limited range of diversity such as comparing monocultures versus two species mixtures would likely find statistically insignificant results, in particular, combined with limited sample sizes. Third, the strength of the diversity and stability relationships is theoretically expected to increase with environmental heterogeneity and the variation of stand development stages and disturbances (18), and thus the lack of a positive relationship could result from sampling stands with limited variations in the environment, disturbances, and stand ages.

Our results show that when climate factors, soil conditions, and stand age were statistically controlled, the temporal stability of productivity was persistently positively associated with functional, phylogenetic, and taxonomic diversity at all census lengths observed at a large geographic scale for Canadian natural forests, many of which have experienced major droughts (7) and moderate to severe defoliation due to various kinds of tree species-specific insects (9). Specifically, we found strong evidence that higher long-term stability was greater in functionally and phylogenetically diverse forests due to a greater increase in mean productivity than the SD of productivity operating through species asynchrony, attributable to both compensatory dynamics and statistical averaging. Our findings highlight the importance of both functional and phylogenetic diversity in stabilizing long-term productivity in natural forest ecosystems.

Materials and Methods

Study Area and Available Data. To examine the long-term stability of productivity, we used a network of permanent sampling plots (PSPs) established by the provincial governments of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Nova Scotia, and Newfoundland and Labrador since 1940s. We selected PSPs using the following criteria: i) unmanaged, with known stand age; ii) have all trees marked with their diameter at breast height (DBH) > 9 cm; iii) have ≥ three censuses of repeated measurements; iv) plot size ≥400 m^2; and v) have at least 20 trees with DBH ≥9 cm on average between the first and last measurement. Following these criteria, a total of 7,498 unique permanent sampling plots (PSP) with 29,430 observations between 1951 and 2016 were selected (*SI Appendix*, Fig. S1). Since the provinces used different DBH thresholds for measurement, we standardized all plots by accounting for only trees with the largest threshold used (Saskatchewan), DBH ≥ 9 cm. The selected plots have an average plot size of 528 m^2, ranging from 400 m^2 to 2023 m^2. Mean annual temperature and aridity index (the ratio of precipitation to potential evapotranspiration) varied from −4.3 °C to 9.7 °C and from 0.3 to 6.6, respectively. The total measurement length, i.e., the number of years between the first and last census, ranged from 12 to 52 y, and the mean length was 36.1 y. The number of censuses ranged from 3 to 8, and the mean was 4. Individual intercensus intervals varied between 1 and 32 y, and the mean was 9.3 y (*SI Appendix*, Table S1).

For each plot, we calculated the temporal stability of productivity as μ/σ, where μ is the mean value of the annual increase in aboveground biomass over each census interval (Mg ha^{-1} yr^{-1}), including the growth of surviving trees and recruitments over repeated measures (60) and σ as their temporal SD across census intervals (3). The aboveground live biomass (Mg ha^{-1}) was the sum of biomass from stem, bark, leaves, and branches derived from the application of species-specific allometric equations in Canada and was standardized by plot size per hectare (63).

Hill Number of Phylogenetic Diversity, Functional Diversity, and Taxonomic Diversity. We employed the unified diversity indices, including Hill functional, phylogenetic, and taxonomic diversity, to enable a meaningful and complementary comparison of their relative importance on temporal stability (45), using the "*HillR*" package (64). We prepared the community data of the relative basal area of each tree species for each plot at each census, functional traits, and the phylogenetic tree of the 84 species that appeared in our study. We obtained eight functional traits related to species growth and reproduction for each tree species from the TRY database (65). These traits are leaf nitrogen content per leaf dry mass (Nmass), leaf phosphorus content per leaf dry mass (Pmass), specific leaf area (SLA), wood density (WD), shade tolerance (ST) (class 1 to 5), drought tolerance (DT) (class 1 to 5), leaf habit (Habit) (deciduous = 1 versus evergreen = 0), and phylogenetic group (angiosperm = 1, gymnosperm = 0), which is identical to using leaf structure (broadleaf = 1 versus conifer = 0) (66). Because our traits data included both continuous and category variables, the Gower's distance was used to calculate functional diversity. We obtained the phylogenetic tree via the "*phylo.maker*" function from the "*PhyloMaker*" package (67). Hill taxonomic diversity (TD) at q = 0 is simply species richness, for q = 1, it is the (exponential) Shannon entropy, and for q = 2, it is the inverse Simpson index. Functional diversity (FD) quantifies the effective total number of equally distinct functional groups, and phylogenetic diversity (PD) quantifies the effective total branch length (45). The Hill diversity metrics of q = 1 and 2 are influenced by the dominant species that are not biased due to the sample size and are sufficiently accurate in estimating diversity without the need for rarefaction (68). Because Hill taxonomic, phylogenetic, and functional diversity varied temporally over censuses within each plot, we used their average values, respectively, similar to previous studies (3).

Asynchrony, Compensatory Dynamics, and Statistical Averaging. Asynchrony was calculated at the community level and defined as 1-synchrony. Synchrony was calculated as $\frac{\sigma_{x_T}^2}{\left(\sum_i \sigma_{x_i}\right)^2}$, the ratio between the variance of the aggregated community productivity and the summed variances of the productivity of individual species (17). We calculated the synchrony index using the package "*codyn*" (69) and selected the metric of "Loreau," which was not sensitive to variable species richness across communities. This community-wide species asynchrony is standardized between 0 (perfect synchrony, that is, for monocultures) and 1 (perfect asynchrony).

Compensatory dynamics is the reduction in productivity of some species being compensated by other species. It is determined by the negative species covariance and measured as the summed SD of individual species productivity divided by the SD of the community productivity, $\frac{\sqrt{\sum_i \sigma_i^2}}{\sigma_{comm}}$ (20). Values above 1, reflecting compensatory dynamics, correspond to great community stability. Statistical averaging, or the portfolio effect, assumes that species within communities are independent, and the scaled variance decreases with species richness (1/species richness) (57). It was measured as $\frac{\sum_i \sigma_i}{\sqrt{\sum_i \sigma_i^2}}$ (20).

Climate Factors, Local Soil Conditions, Stand Age, and Middle Calendar Year. Similar to the previous study (70), we used plot spatial locations to derive plot climate and soil condition. We extracted the mean annual temperature (MAT, °C) from the WorldClim dataset (71) and the aridity index (AI) from CGIAR Consortium (72) (https://cgiarcsi.community/) for each plot location between 1951 and 2016 for each plot as proxies for the site-specific local historical climate. We obtained the soil drainage level (increasing soil water availability from 1 to 7) from SoilGrids to represent the local soil characteristics (73, 74). Stand age for each plot was determined based on the last recorded stand-replacing fire or by coring at least three dominant/codominant trees of each species inside or outside the plot when the plots were established. The average ring counts of the oldest tree samples provided a conservative estimate of the time since stand establishment (75). During the long-term sampling, we estimated stand age and year as the middle age and middle year between the first and last census, respectively, to account for the temporal difference among plots.

Statistical Analysis. We used linear mixed models to examine the effects of Hill taxonomic, functional, and phylogenetic diversity and covariates (MAT, AI and soil drainage, stand age) as hypothesized (Fig. 1). Our full models for stability, μ and σ included the interaction effects of census length and its interaction effect with diversity. We included the number of censuses as a random variable to minimize the influence of random sampling efforts. To prevent overfitting (46), we obtained the most parsimonious model based on Akaike's information criterion (AIC) with the "*dredge*" function using the package "*MuMIn*" (76) (*SI Appendix*, Table S2). To minimize collinearity (46), taxonomic diversity with modeled separately from functional and phylogenetic diversity (*SI Appendix*, Table S2). Among alternatives (q = 0, 1, and 2), we found that diversity variables at q = 1 were the best to predict stability, μ and σ, based on AIC (*SI Appendix*, Table S3). To facilitate comparisons among predictors and models, we scaled all variables, that is, minus their respective means and divided by their SD, prior to analysis.

Similar to previous studies (77), we tested the spatial autocorrelation of residuals using Moran's *I* test and found significant effects of spatial autocorrelation for mean productivity (μ), Hill functional and phylogenetic diversity models. Subsequently, similar to previous studies (77), we calculated the spatial distance at which such spatial effect decreased to nonsignificant for those models. We found that a distance of 0.3 km was the most appropriate and generated an identification for each group of plots (GroupID) as the random factor in the models mentioned above (*SI Appendix*, Tables S4 and S5).

To confirm the robustness of our results, we incorporated the temporal variability of the climate variables and plot size. Specifically, using the method described previously (78), we derived the anomalies of annual mean temperature and climate moisture index for all years from the first to last census for each plot. We then calculated the SD of temperature anomaly (sdATA) and climate moisture anomaly (sdACMIA) to present the temporal climate variabilities. The inclusion of these climate variabilities and plot size as covariates in our models did not change the effects of Hill diversity on stability (*SI Appendix*, Table S6). Moreover, asynchrony did not show a strict Gaussian distribution (*SI Appendix*, Fig. S2), although the normality assumption was met for all component models based on model residuals (*SI Appendix*, Fig. S9). Therefore, we alternatively applied glmmTMB and the Tweedie family (79) to test the relationship between asynchrony and Hill diversity variables and found similar results to the linear model (*SI Appendix*, Tables S4 and S7).

The coefficient plot showed the relative importance of predictors of stability and its components. The regression plot showed the relationships between predictors and stability as well as its components after accounting for the effects of climate, soil drainage, and stand age. We also employed structural equation modeling (SEM) to show a full view of the direct and indirect paths involved in the component models. We started from the full model based on the prior path diagram (Fig. 1) and eliminated the variables that did not contribute substantial information. SEMs that achieved a good fit were selected based on the recommended evaluation parameters, the chi-square test ($P > 0.05$ for a satisfactory fit) (80). The lower Akaike information criterion (AIC) was used to select SEM alternatives. We used the "*PiecewiseSEM*" package for our structural equation model analyses (81). The taxonomic diversity SEM explained a similar magnitude of variation in stability (*SI Appendix*, Fig. S5). Furthermore, similar to previous studies (44), we also assessed bivariate relationships between different diversities and stability (μ and σ) (*SI Appendix*, Fig. S3). Because functional and phylogenetic diversity were correlated (*SI Appendix*, Fig. S7), we investigated phylogenetic signals within functional traits, following previous studies (82) (*SI Appendix*, Fig. S8).

We calculated the range change as the difference between the maximum value of predictor times standardized effect size and the minimum value of predictor times standardized effect size, following the method described previously (83). The percentage change was calculated as the range change divided by the unscaled mean value of each response variable, such as stability, μ and σ.

To address the mechanisms associated with species asynchrony in the diversity-stability relationship (21), we examined the relationship between stability (also its components) and compensatory and statistical averaging effects, following the method described previously (20). Furthermore, we examined how compensatory and statistical averaging effects were related to Hill functional and phylogenetic diversity. All statistical analyses were performed in R 4.3.2 (84).

Data, Materials, and Software Availability. Computer codes and data have been deposited in Github (https://github.com/XiaxiaDing1025/Temporal-stability_diversity_XXD.git) (85).

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