

Interactions among trees: A key element in the stabilising effect of species diversity on forest growth

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Abstract

1. There is mounting evidence that species diversity increases the temporal stability of forest growth. This stabilising effect of diversity has mainly been attributed to species differences in their response to fluctuating environmental conditions. Interactions among individuals could also contribute to the stabilising effect of diversity by increasing the mean and reducing the variance of tree growth, however, this has never been directly demonstrated.
2. We used tree-ring width chronologies from temperate and boreal mixed stands of Eastern Canada to identify the role of interactions among individuals in the stabilising effect of diversity on forest growth. Using neighbourhood competition index and a mixed model, we compared the effect of interspecific and intraspecific interactions on the mean and the variance of tree growth.
3. We found that interspecific interactions are less detrimental to tree growth than intraspecific interactions. We also found that interspecific interactions buffer tree response to drought and thereby reduce the variance of tree growth.
4. Our results indicate diversity may increase the mean and reduce the variance of tree growth through interactions among individuals. Thus, we demonstrate interactions among individuals play a role in the stabilising effect of diversity on forest growth, and in doing so, we bring to light other mechanisms of the insurance hypothesis.

KEYWORDS

biodiversity, dendrochronology, ecosystem functioning, forest, insurance hypothesis, stability

1 | INTRODUCTION

Species diversity (hereafter diversity) is a major driver of ecosystems functioning (Cardinale et al., 2012; Hooper et al., 2012). In particular, there is mounting evidence that diversity stabilises forest growth under fluctuating environmental conditions (Aussenac et al., 2017; Hutchison, Gravel, Guichard, & Potvin, 2018; Jucker, Bouriaud, Avacaritei, & Coomes, 2014; Morin, Fahse, Mazancourt, Scherer-Lorenzen, & Bugmann, 2014; Río et al., 2017). However, although significant progress has been made in recent years, our understanding of the mechanisms underlying the diversity–stability relationship in forest ecosystems remains incomplete.

Different theories stand in opposition as regards the link between diversity and stability. On the one hand, the insurance hypothesis predicts that diversity stabilises the productivity of communities (Mazancourt et al., 2013; Yachi & Loreau, 1999) because species differences in their response to fluctuating environmental conditions generate some growth asynchrony, which enables compensations among them and thereby stabilises the community-level productivity. This theory does not account, however, for the way interspecific interactions impact community dynamics. On the other hand, May's (1973) theory and further developments (see the review in Tang and Allesina (2014)) and a test of theory in Jacquet et al. (2016) predict that diversity destabilises community dynamics

because interspecific interactions allow fluctuations to spread in the community and may even amplify them. At the intersection of these theories is the question of how interspecific interactions may impact responses of individuals to fluctuating environmental conditions. Interactions might either exacerbate the response to fluctuating environmental conditions (e.g., if competition for water enhances the effect of droughts) or buffer it (e.g., companion species may prevent the occurrence of frost injuries). In this study, we therefore investigate how interactions among trees influence their response to environmental fluctuations and how this affects the relationship between species diversity and forest growth stability.

Temporal stability (TS; Tilman, 1999) has been commonly used to assess the stabilising effect of diversity in plant communities. TS is measured as the inverse of the coefficient of variation and is therefore given by:

$$TS = \frac{\mu_c}{\sigma_c} \quad (1)$$

where μ_c and σ_c are the mean and the variance of the total growth of a community, respectively. The mean of the total growth of a community may be decomposed as the sum of the mean growth of all its constituent individuals. Similarly, the variance of the total growth of a community may be decomposed as the sum of the growth variances and covariances of all individuals in the community (Aussenac et al., 2017). The TS of a community constituted of n individuals is therefore given by:

$$TS = \frac{\mu_c}{\sigma_c} = \frac{\sum_{i=1}^n \mu_i}{\sum_{i=1}^n \sigma_i + 2 \sum_{i=1}^n \sum_{j>i}^n \text{cov}(g_i, g_j)} \quad (2)$$

where μ_i and σ_i are the mean and the variance of individuals growth, and $\text{cov}(g_i, g_j)$, the growth covariance of individuals i and j . Any factor affecting one of the three components of TS (μ_i , σ_i and $\text{cov}(g_i, g_j)$) may therefore impact the TS of growth at the community level.

Empirical studies in forest ecosystems have mainly attributed the stabilising effect of diversity to species differences in their response to fluctuating environmental conditions (Aussenac et al., 2017; Jucker, Bouriaud, et al., 2014; Río et al., 2017), consistent with the insurance hypothesis. Environmental fluctuations increase the variance in growth, but interspecific differences generate growth asynchrony (i.e., low $\text{cov}(g_i, g_j)$) among individuals, which ultimately stabilises growth at the community level. Diversity may also stabilise forest growth by increasing the mean (μ_i) and reducing the variance (σ_i) of tree growth. Indeed, diversity has been found to increase tree mean growth (Chamagne et al., 2017; Chen et al., 2016; Fichtner et al., 2017; Jucker, Bouriaud, et al., 2014; Potvin & Gotelli, 2008), and to reduce the variance of tree growth by buffering tree response to climate fluctuations (Jucker, Bouriaud, et al., 2014; Lebourgeois, Gomez, Pinto, & Me'rian, 2013; Pretzsch, Schütze, & Uhl, 2013). In studies that have examined the stabilising effect of diversity in forest communities, these effects were attributed to favourable interactions among individuals (i.e., reduced competition and facilitation; Jucker, Bouriaud,

et al., 2014; Río et al., 2017; Aussenac et al., 2017)). However, in these studies, interactions were not directly measured. Thus, a direct demonstration of the contribution of interactions to the stabilising effect of diversity is still lacking.

The effects of diversity on the mean and the variance of tree growth reported in previous studies may arise from species complementarity. Complementarity occurs when species exhibit niche partitioning or when interspecific interactions enhance the capture of resources (Cardinale et al., 2007). Species complementarity therefore implies that interspecific interactions are less detrimental to tree growth than intraspecific interactions, consistent with coexistence theory (Chesson, 2000; Ramage et al., 2017). Furthermore, by enhancing the capture of resource by species, or at least by reducing it less than intraspecific interactions, interspecific interactions could make species less sensitive to fluctuations in resource availability (e.g., soil water availability), and thus, more generally, less sensitive to fluctuations in environmental conditions.

We used tree-ring width chronologies from temperate and boreal mixed stands of Eastern Canada to identify the role of interactions among individuals in the stabilising effect of diversity on forest growth. For that, we compared the effect of interspecific and intraspecific interactions on the mean (μ_i) and the variance (σ_i) of tree growth. We assessed interactions among individuals by estimating the net effect of neighbouring trees on the growth of focal trees using the neighbourhood competition index (NCI; Canham, LePage, & Coates, 2004). We used a mixed model to describe tree growth as a function of tree size, summer drought, NCI, the ratio of interspecific NCI over total NCI ($R_{i/t}$) and an interaction between drought and $R_{i/t}$, while accounting for the effects of sites and species. The ratio of interspecific NCI over total NCI indicates the relative importance of interspecific and intraspecific interactions. The higher it is, the more interspecific interactions relative to intraspecific interactions there are. As for the interaction between drought and $R_{i/t}$, it measures the effect of interspecific and intraspecific interactions on tree response to drought. We hypothesised (H1) that interspecific interactions would be less detrimental to tree growth than intraspecific interactions. We therefore expected NCI to have a negative effect on tree growth and $R_{i/t}$ to have a positive effect. We also hypothesised (H2) that interspecific interactions would buffer tree response to drought (thereby reducing the variance of tree growth) while intraspecific interactions would amplify that response (thereby enhancing the variance of tree growth). The lower sensitivity to summer drought of trees surrounded by heterospecific neighbours would arise from species complementarity which would enhance the capture of soil water by those trees and thereby make them less sensitive to fluctuations in soil water availability. We therefore expected total $R_{i/t}$ to dampen the negative effect of drought on tree growth. Validating these hypotheses would indicate that diversity may increase the mean (μ_i) and reduce the variance (σ_i) of tree growth through interactions among individuals, since greater diversity implies less intraspecific interaction relative to interspecific interactions. This would demonstrate that interactions among individuals play a role in the stabilising effect of diversity in forest ecosystems.

TABLE 1 Summary of sites characteristics

	ABI	BIC	D1823	D1847	SUT
Coordinates	48,16253; 79,40121	48,33361; 68,81771	48,45791; 79,23920	48,50398; 79,32084	45,11280; 72,54129
Altitude (m)	375	240	270–275	270–275	645–690
Soil	Thick clay deposits	Glacial till with pockets of organic soil	Thick clay deposits	Thick clay deposits	Glacial till with pockets of organic soil
Annual precipitation (mm)	894.3	1050.4	866.6	866.6	1464.8
Monthly average temperature range (°C)	–16.6 (January) 17.5 (July)	–13.3 (January) 17.1 (July)	–16.9 (January) 17.3 (July)	–16.9 (January) 17.3 (July)	–11.6 (January) 16.9 (July)

2 | MATERIALS AND METHODS

The study was conducted in five one-ha sites within both temperate and boreal mixed-wood stands of Eastern Canada (Supporting Information Figure S1). Two boreal mixed-wood stands (D1823 and D1847) were located in Western Quebec in the balsam fir–white birch bioclimatic domain. The three other sites (ABI, BIC and SUT) were located within temperate mixed-wood stands. One site (ABI) was located at the northern limit of the mixed hardwood forest sub-zone, in the balsam fir–white birch domain. Another site (BIC) was located in St-Lawrence Lowlands, in the balsam fir–yellow birch domain. Finally, the third site (SUT) was located in Eastern Townships, in the sugar maple–basswood domain. The ABI, BIC and SUT sites corresponded to one-ha subplots established within larger sites (of 4, 10.24 and 20 ha, respectively). All sites were mature forest stands undisturbed by logging, with the exception of the BIC site, which had been selectively harvested prior to being designated a national park in 1984. Sites altitudes, coordinates and their climatic and soil characteristics are summarised in Table 1.

All trees equal or >10 cm in diameter at breast height (DBH) were identified, mapped and DBH measured in 2011. Species richness on the study sites ranged from five to 14 species yielding a total of 20 species. Species basal area for each site is presented in Supporting Information Figure S2. We considered six species whose growth were previously shown to be correlated positively to summer precipitation and negatively to summer temperature or summer drought at our study sites (Aussenac et al., 2017): eastern white cedar (*Thuja occidentalis* L.), white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* L.), red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marshall). In 2014, we randomly selected 47–63 individuals per species and site (not all species were present at all sites) in five DBH classes for coring (Table 2). Sampling intensity was stratified across DBH classes to follow the DBH distribution of each species. Two cores were extracted on the opposite sides of the trunk at breast height for each of the selected trees. Cores were measured at 0.01 mm precision, cross-dated and quality checked following standard dendrochronological methods (Stokes, 1996).

We ran our analyses setting the radius (r) within which neighbours could interact with focal trees to either 15 or 20 m (Canham et al., 2004; Coates, Canham, & LePage, 2009). Cores of trees located <15 or 20 m from the site edges were therefore not considered since

TABLE 2 Number of cored trees, trees included in our dataset after having removed those with rotten wood (which prevented cross-dating), and trees used in analyses running with $r = 15$ and 20 m. Species are coded with their initials: Ab (*Abies balsamea*), Ar (*Acer rubrum*), As (*Acer saccharum*), Pg (*Picea glauca*), Pt (*Populus tremuloides*), To (*Thuja occidentalis*)

Site	Species	Cored	Included in dataset	Included in dataset	
				$r = 15$ m	$r = 20$ m
ABI	Ab	60	57	52	50
	Ar	53	50	48	45
	As	55	54	54	54
	Pg	47	47	45	44
	To	50	48	32	24
BIC	Ab	63	62	49	48
	Ar	61	58	50	47
	As	59	52	48	48
	Pt	62	62	52	52
SUT	Ab	55	50	50	50
	As	60	56	56	56
D1823	Ab	51	48	22	16
	Pg	48	46	26	16
	Pt	54	52	30	18
	To	52	52	34	27
D1847	Ab	52	48	15	12
	Pg	58	53	23	20
	Pt	53	49	26	18
	To	54	51	32	26
	Total	1,047	995	744	671

tree size and position information was not available outside the sites, which prevented proper estimation of interactions among individuals for those trees. After having removed cores for which tree rings were impossible to measure due to wood rot, and those from trees located at <15 or 20 m from the site edges, we had at our disposal 744 individuals (for $r = 15$ m) and 671 individuals (for $r = 20$ m; Table 2).

We removed periods of tent caterpillar (*Malacosoma disstria* Hubner.) outbreaks from our analyses to avoid bias in our estimation of climate–growth relationships, following the method of (Aussenac et al., 2017). Indeed, tent caterpillar outbreaks in Eastern Canada

cause large reductions in trembling aspen growth (Sutton & Tardif, 2009), suggesting that trees respond more to defoliation events than to climate during these periods.

We used the BioSIM 10.3 software (Régnière & St-Amant, 2007) to generate site-specific annual series of mean Canadian Drought Code (DC) calculated over the June to August period. The DC is calculated from daily maximum temperature, 24-hr precipitation and dates of snow cover to estimate the daily rate of soil drying (Lawson & Armitage, 2008). It reflects the water content of deep compact organic layers. For each site, BioSIM interpolated data from the eight closest weather stations using inverse distance weighting, while adjusting for differences in latitude, longitude and elevation between the weather stations and the sites.

2.1 | Statistical analyses

We estimated interactions among individuals by measuring the net effect of neighbouring trees on the growth of focal trees as a function of the size (DBH) of the neighbours, and as an inverse function of the distance between the focal trees and their neighbours. For that, we used the neighbourhood competition index (NCI; Canham et al., 2004). For $j = 1, \dots, n$ neighbours within a radius ($r = 15$ or 20 m) around a focal tree i , the NCI is given by:

$$NCI_i = \sum_{j=1}^n \frac{DBH_j^\gamma}{distance_{ij}^\delta} \tag{3}$$

where δ and γ are parameters to estimate. We also calculated the interspecific NCI ($NCI_{i,inter}$) considering only neighbours belonging to a species different from the one of the focal tree. However, $NCI_{i,inter}$ was not included in our model on its own but rather as part of the $R_{i/t}$ ratio ($R_{i/t}$ being the ratio of interspecific NCI over total NCI, i.e., $NCI_{i,inter}/NCI_i$). The focal trees were the cored individuals. We calculated NCI_i and $NCI_{i,inter}$ using a single DBH value for each neighbour, the one measured in 2011, since past DBH could be reconstructed only for focal trees, that is, cored trees. We therefore limited the time window of our analyses to the 1991–2013 period to ensure that tree size and position measured in 2011 (used to estimate NCI_i and $NCI_{i,inter}$) reflected the growing conditions of focal trees.

Using a mixed model, we measured the effect of interactions among individuals on tree growth and on tree response to drought to identify the role of interactions among individuals in the stabilising effect of diversity on forest growth. The model describes tree annual basal area increment (BAI) as a function of tree size (DBH), summer drought (DC), NCI, the ratio of interspecific NCI over total NCI ($R_{i/t}$) and an interaction between DC and $R_{i/t}$. We considered species identity (sp) and sites (si) as crossed random effects. We log-transformed BAI to obtain normally distributed residuals. The model was defined as follows:

$$\log(\widehat{BAI}_{sp,si}) = (\alpha_0 + a_{sp} + a_{si}) + (\beta_1 + b_{1,sp} + b_{1,si}) DBH + (\beta_2 + b_{2,sp} + b_{2,si}) DC + (\beta_3 + b_{3,si}) NCI + \beta_4 R_{i/t} + \beta_5 (DC \cdot R_{i/t}) \tag{4}$$

$$\log(BAI_{sp,si}) \sim \mathcal{N}(\log(\widehat{BAI}_{sp,si}), \sigma^2) \tag{5}$$

$$a_{sp,si} \text{ and } b_{sp,si} \sim \mathcal{MVN}(0, \Sigma) \tag{6}$$

where DBH, DC, NCI and $R_{i/t}$ are the fixed effects; a_{sp} and a_{si} are random intercepts accounting for the effect of species and sites on the population intercept; $b_{1,sp}$ and $b_{1,si}$ are random slopes accounting for the effect of species and sites on the size–growth relationship; $b_{2,sp}$ and $b_{2,si}$ are random slopes accounting for the effect of species and sites on tree response to drought; and $b_{3,si}$ is a random slope accounting for the effect of sites on tree response to NCI. We standardised all variables in order to compare parameter estimates. The observations $\log(BAI_{sp,si})$ were assumed to follow a normal distribution \mathcal{N} with mean $\log(\widehat{BAI}_{sp,si})$ and variance σ^2 (Equation 5), and the random parameters were assumed to follow a multivariate normal distribution (\mathcal{MVN}) centred on 0 and with Σ the matrix containing the variances and covariances between the random effects (Equation 6).

Based on our **H1** hypothesis, we expected that β_3 would be negative, indicating increasing competition for resources in crowded neighbourhoods. We also expected that β_4 would be positive, indicating that interspecific interactions are less detrimental to growth than intraspecific interactions, and therefore that diversity may increase tree growth through interactions among individuals. Consistent with our **H2** hypothesis, we also expected that β_5 would be positive. That would indicate that interspecific interactions buffer tree response to drought while intraspecific interactions amplify that response, and therefore that diversity may reduce the variance of tree growth through interactions among individuals.

Neighbourhood competition index being a nonlinear function, its parameters (γ and δ) could not be estimated using traditional optimisation methods for linear mixed models. We bypassed this difficulty by developing an iterative optimisation method. The following steps were repeated for all possible combinations of γ and δ , with γ and δ values ranging from 0 to 20 in increments of 0.01 (the 0–20 interval broadly covers the earlier reported γ and δ values for boreal and temperate forests (Canham et al., 2004; Thorpe, Astrup, Trowbridge, & Coates, 2010):

1. We calculated a NCI for each tree using a combination of γ and δ values.
2. We used the *lmer* function from the R package *lme4* to fit an instance of our model using the NCI values calculated above. The *lmer* function returned the likelihood and the parameter estimates of this instance.

We thus obtained a likelihood value and parameter estimates for all possible combinations of γ and δ . γ and δ estimates were those values of γ and δ maximising the model likelihood (Supporting Information Figure S3). The parameter estimates were those parameter values associated with the γ and δ estimates. This procedure has the advantage of using well-documented optimisation functions and of being simple to set up.

We computed the credible intervals of the mixed model parameters using the 2.5% and 97.5% quantiles of their posterior distribution. Parameters were significant at the 10%, 5% or 1% level, if 90%, 95% or 99% of their posterior distribution were larger or smaller than 0, respectively. We obtained the posterior distributions of the parameters using the *sim* function from the R package *arm*. The *sim* function generated posterior distributions from the joint posterior distribution of the model parameters, using noninformative prior distributions, that is, it simulated values for each parameter while accounting for the correlation among parameters. We computed the marginal and conditional R^2 (R_m^2 and R_c^2 respectively; Nakagawa & Schielzeth, 2013; Johnson, 2014), which describe the proportion of variance explained by the fixed effects alone, and the proportion of variance explained by both the fixed and random effects, respectively. R_m^2 and R_c^2 were calculated with the *r.squaredGLMM* function from the R package *MuMIn*.

3 | RESULTS

Both versions of the model (considering $r = 15$ or 20 m) yielded the same results. We found that tree size, summer drought and interactions among individuals all significantly affected tree growth (Table 3 and Supporting Information Table S1). Here, parameter estimates are directly comparable because variables were standardised. Tree size had the strongest positive effect while NCI had the strongest negative effect. The effect of drought was slightly stronger than the one of $R_{i/t}$, but drought had a negative effect on tree growth while $R_{i/t}$ had a positive effect. We also found that $R_{i/t}$ affected tree growth response to drought as evidenced by the significant interactions between $R_{i/t}$ and DC. Because β_5 was positive, $R_{i/t}$ buffered the negative effect of drought on tree growth.

Random effects explained about 63%–65% of the random variation in both model versions (Table 4 and Supporting Information Table S2). The species effect explained about 38%–40% of it, while

TABLE 3 Summary of the fixed effects of the model (for $r = 20$ m). Variables associated with the fixed effects are shown in brackets. The 2.5% and 97.5% quantiles of the posterior distributions were used to define the 95% credible interval of fixed effects. The 50% quantiles indicate the parameter estimates. Parameters were significant at the 10% (*), 5% (**), or 1% (***) level, if 90%, 95% or 99% of their posterior distribution were larger or smaller than 0, respectively. Our optimisation resulted in the following parameter estimates for NCI: $\gamma = 2.32$ and $\delta = 1.37$. The model $R_m^2 = 0.34$ and $R_c^2 = 0.63$

	2.5%	50%	97.5%
α_0	6.072	6.392***	6.709
β_1 (DBH)	0.442	0.534***	0.630
β_2 (DC)	-0.127	-0.058*	-0.009
β_3 (NCI)	-0.239	-0.134**	-0.025
β_4 ($R_{i/t}$)	0.038	0.049***	0.061
β_5 (DC. $R_{i/t}$)	0.025	0.034***	0.045

the site effect explained 22%–26%. The standard deviations of the random slopes ($b_{1-2,sp,si}$) indicated that the size–growth relationship as well as the response to summer drought were variable across species and modulated by site conditions. Besides, the standard deviation of the random slopes ($b_{3,si}$) indicated that site conditions also modulated tree response to NCI.

4 | DISCUSSION

Our results show that interspecific interactions are less detrimental to growth than intraspecific interactions, supporting the **H1** hypothesis. Furthermore, we found that interspecific interactions buffer tree response to drought while intraspecific interactions amplify that response, supporting the **H2** hypothesis. These outcomes indicate that diversity may increase the mean and reduce the variance of tree growth through interactions among individuals, since higher diversity implies reduced intraspecific interactions relative to interspecific interactions. Thus, our results demonstrate that interactions among individuals play a role in the stabilising effect of diversity in forest ecosystems. Our findings are consistent with previous studies showing that diversity had a positive effect on tree growth (Chamagne et al., 2017; Chen et al., 2016; Fichtner et al., 2017; Jucker, Bouriaud, et al., 2014; Potvin & Gotelli, 2008), and reduced the variance of tree growth by buffering tree response to climate fluctuations (Jucker, Bouriaud, et al., 2014; Lebourgeois et al., 2013; Pretzsch et al., 2013). The fact that neighbourhood interactions (NCI) have a stronger effect on tree growth than drought in both versions of our model is also consistent with previous findings showing tree growth is more strongly affected by competition than by climate (Zhang, Huang, & He, 2015). However, our results also show these two factors interact to affect tree growth.

Species and site effects explained almost two thirds of the random variation of the model by affecting the size–growth relationship and the response to summer drought and to NCI. Thus, species and site conditions may ultimately impact the stabilising effect of diversity. The species effect is likely to arise from the differences among species in their intrinsic growth rates and in their tolerance

TABLE 4 Standard deviation (SD) of the model random effects and residuals, and their associated percentage of the total random variation (for $r = 20$ m). Variables associated with the random effects are shown in brackets

	SD	%
a_{sp}	0.432	25.71
$b_{1,sp}$ (DBH)	0.111	6.61
$b_{2,sp}$ (DC)	0.096	5.71
a_{si}	0.192	11.43
$b_{1,si}$ (DBH)	0.076	4.52
$b_{2,si}$ (DC)	0.029	1.73
$b_{3,si}$ (NCI)	0.148	8.81
Residuals	0.596	35.48

to drought events. As for the site effect, it may be due to climate, soil fertility and soil water supply, which may control both tree growth and tree response to drought. Site conditions could also impact the stabilising effect of diversity by modulating interactions among individuals. For instance, favourable interactions among trees (i.e., reduced competition and facilitation) have been found to be more frequent as site conditions become harsher (Paquette & Messier, 2011), as predicted by the stress gradient hypothesis (Bertness & Callaway, 1994). Here, our results do not support this hypothesis as we do not observe a reduced response to NCI at sites in the harshest climatic conditions (Supporting Information Table S3 and S4). However, our experiment was not designed to interpret site-related effects but rather to test our hypotheses across a wide range of conditions. Thus, many covariates varying with climate harshness (e.g., species richness and edaphic conditions) may prevent the detection of the stress gradient hypothesis.

Although our results demonstrate that interactions among individuals play a role in the stabilising effect of diversity on forest growth, they do not mean, however, that this role is necessarily stabilising. Indeed, previous studies have shown that diversity does not always buffer species response to drought nor does it always increase tree growth (Forrester et al., 2016; Grossiord et al., 2014). The effect of diversity on species response to drought depends on site conditions and species combinations. Thus, in some cases, interactions among heterospecific individuals might have a destabilising effect on forest growth.

Our results, albeit fully empirical, also suggest an extension of the diversity–stability theory. On the one hand, neglecting the effect of ecological interactions, the insurance hypothesis (Mazancourt et al., 2013; Yachi & Loreau, 1999) predicts that species differences in their response to fluctuating environmental conditions stabilise the productivity of communities. On the other hand, May's theory considers that interspecific interactions are destabilising for community dynamics (May, 1973). Here, at the crossroads between these conflicting theories (McCann, 2000), we do find that interspecific interactions may stabilise productivity at the community level by buffering individual response to fluctuating environmental conditions. This finding adds another mechanism to the insurance hypothesis, while it also refutes May's prediction (although his theory does not consider explicitly fluctuating environments). Further theoretical analyses of the diversity–stability relationship should consequently consider fluctuations in environmental conditions, as well as the diversity dependence of the response to these fluctuations.

Our study also goes one step further than previous studies of the insurance effect with trees, with a mechanistic analysis of the drivers of growth variance. Furthermore, most studies consider diversity directly, for instance, by computing species richness, while here we consider the effect of the ratio of inter- to intraspecific interactions on individual growth. In doing so, we are able to directly assess predictions arising from the coexistence theory which requires stronger intraspecific competition relative to interspecific competition to maintain species richness

(Chesson, 2000; Ramage et al., 2017). The major limitation, however, remains, as in other studies of the insurance hypothesis with trees, that our analyses only consider one demographic process: individual growth. Considering the other demographic processes (i.e., recruitment and mortality) might bring to light other mechanisms underlying the diversity–stability relationship. Additionally, the links between demographic processes could add complexity to previously described mechanisms, in particular, by producing feedbacks. For instance, the often reported growth–mortality trade-off might modulate the stabilising mechanisms based on growth. Further studies accounting for the full life cycle of trees and measurements of demography are required.

Our study helps better understand the mechanisms underlying the diversity–stability relationship in forest ecosystems. We provide a framework for understanding how interactions can play a role in the stabilising effect of diversity on forest growth. We show that interspecific interactions are less detrimental to tree growth than intraspecific interactions and that they buffer tree response to climate fluctuations thereby stabilising forest growth. To our knowledge, these mechanisms had never been demonstrated directly as part of the diversity–stability relationship, neither theoretically nor empirically. Further studies are needed to determine whether our conclusions hold across a range of climates and forest types.

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AUTHORS' CONTRIBUTIONS

R.A., Y.B., D.G. and I.D. conceived the ideas and designed methodology; R.A. collected the data; R.A. and D.G. analysed the data; R.A. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.t536h7s>, (Aussenac, Bergeron, Gravel, & Drobyshev, 2018).

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REFERENCES

- Aussenac, R., Bergeron, Y., Ghotsa Mekontchou, C., Gravel, D., Pilch, K., & Drobyshev, I. (2017). Intraspecific variability in growth response to environmental fluctuations modulates the stabilizing effect of species diversity on forest growth. *Journal of Ecology*, 105(4), 1010–1020. <https://doi.org/10.1111/1365-2745.12728>
- Aussenac, R., Bergeron, Y., Gravel, D., & Drobyshev, I. (2018). Data from: Interactions among trees: a key element in the stabilising effect of species diversity on forest growth. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.t536h7s>
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology and Evolution*, 9(5), 191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
- Canham, C. D., LePage, P. T., & Coates, K. D. (2004). A neighborhood analysis of canopy tree competition: Effects of shading versus crowding. *Canadian Journal of Forest Research*, 34(4), 778–787. <https://doi.org/10.1139/x03-232>
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ... Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59. <https://doi.org/10.1038/nature11148>
- Cardinale, B. J., Wright, J. P., Cadotte, M. W., Carroll, I. T., Hector, A., Srivastava, D. S., ... Weis, J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, 104(46), 18123–18128. <https://doi.org/10.1073/pnas.0709069104>
- Chamagne, J., Tanadini, M., Frank, D., Matula, R., Paine, C., Philipson, C. D., ... Hector, A. (2017). Forest diversity promotes individual tree growth in central European forest stands. *Journal of Applied Ecology*, 54(1), 71–79. <https://doi.org/10.1111/1365-2664.12783>
- Chen, Y., Wright, S. J., Muller-Landau, H. C., Hubbell, S. P., Wang, Y., & Yu, S. (2016). Positive effects of neighborhood complementarity on tree growth in a neotropical forest. *Ecology*, 97(3), 776–785. <https://doi.org/10.1890/15-0625.1>
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31(1), 343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>
- Coates, K. D., Canham, C. D., & LePage, P. T. (2009). Above-versus below-ground competitive effects and responses of a guild of temperate tree species. *Journal of Ecology*, 97(1), 118–130. <https://doi.org/10.1111/j.1365-2745.2008.01458.x>
- Fichtner, A., Härdtle, W., Li, Y., Bruelheide, H., Kunz, M., & Oheimb, G. (2017). From competition to facilitation: How tree species respond to neighbourhood diversity. *Ecology Letters*, 20(7), 892–900. <https://doi.org/10.1111/ele.12786>
- Forrester, D. I., Bonal, D., Dawud, S., Gessler, A., Granier, A., Pollastrini, M., & Grossiord, C. (2016). Drought responses by individual tree species are not often correlated with tree species diversity in European forests. *Journal of Applied Ecology*, 53(6), 1725–1734. <https://doi.org/10.1111/1365-2664.12745>
- Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Checko, E., ... Gessler, A. (2014). Tree diversity does not always improve resistance of forest ecosystems to drought. *Proceedings of the National Academy of Sciences*, 111(41), 14812–14815. <https://doi.org/10.1073/pnas.1411970111>
- Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L., ... O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486(7401), 105. <https://doi.org/10.1038/nature11118>
- Hutchison, C., Gravel, D., Guichard, F., & Potvin, C. (2018). Effect of diversity on growth, mortality, and loss of resilience to extreme climate events in a tropical planted forest experiment. *Scientific Reports*, 8(1), 15443. <https://doi.org/10.1038/s41598-018-33670-x>
- Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P., & Gravel, D. (2016). No complexity–stability relationship in empirical ecosystems. *Nature Communications*, 7, 12573. <https://doi.org/10.1038/ncomms12573>
- Johnson, P. C. (2014). Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. *Methods in Ecology and Evolution*, 5(9), 944–946. <https://doi.org/10.1111/2041-210X.12225>
- Jucker, T., Bouriaud, O., Avacaritei, D., & Coomes, D. A. (2014). Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. *Ecology Letters*, 17(12), 1560–1569. <https://doi.org/10.1111/ele.12382>
- Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., & Coomes, D. A. (2014). Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests. *Journal of Ecology*, 102(5), 1202–1213. <https://doi.org/10.1111/1365-2745.12276>
- Lawson, B. D., & Armitage, O. (2008). *Weather guide for the Canadian forest fire danger rating system*. Edmonton, AB: Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre.
- Lebourgeois, F., Gomez, N., Pinto, P., & Mérian, P. (2013). Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *Forest Ecology and Management*, 303, 61–71. <https://doi.org/10.1016/j.foreco.2013.04.003>
- May, R. M. (1973). *Stability and complexity in model ecosystems*. Princeton, NJ: Princeton University Press.
- Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., Luca, E., Grace, J. B., ... Loreau, M. (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters*, 16(5), 617–625. <https://doi.org/10.1111/ele.12088>
- McCann, K. S. (2000). The diversity–stability debate. *Nature*, 405(6783), 228. <https://doi.org/10.1038/35012234>
- Morin, X., Fahse, L., Mazancourt, C., Scherer-Lorenzen, M., & Bugmann, H. (2014). Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. *Ecology Letters*, 17(12), 1526–1535. <https://doi.org/10.1111/ele.12357>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining r^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Paquette, A., & Messier, C. (2011). The effect of biodiversity on tree productivity: From temperate to boreal forests. *Global Ecology and Biogeography*, 20(1), 170–180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x>
- Potvin, C., & Gotelli, N. J. (2008). Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecology Letters*, 11(3), 217–223. <https://doi.org/10.1111/j.1461-0248.2007.01148.x>
- Pretzsch, H., Schütze, G., & Uhl, E. (2013). Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. *Plant Biology*, 15(3), 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>
- Ramage, B. S., Johnson, D. J., Gonzalez-Akre, E., McShea, W. J., Anderson-Teixeira, K. J., Bourg, N. A., & Clay, K. (2017). Sapling growth rates reveal conspecific negative density dependence in a temperate forest. *Ecology and Evolution*, 7(19), 7661–7671. <https://doi.org/10.1002/ece3.3298>
- Régnière, J., & St-Amant, R. (2007). Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. *International Journal of Biometeorology*, 51(5), 415–430. <https://doi.org/10.1007/s00484-006-0078-z>
- Río, M., Pretzsch, H., Ruiz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., ... Annighöfer, A. (2017). Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*–*Fagus sylvatica* mixtures across Europe. *Journal of Ecology*, 105(4), 1032–1043.
- Stokes, M. A. (1996). *An introduction to tree-ring dating*. Tucson, AZ: University of Arizona Press.

- Sutton, A., & Tardif, J. (2009). Forest tent caterpillar outbreaks dynamics from Manitoba to New Brunswick. In S. Gauthier, M.-A. Vaillancourt, A. Leduc, L. De Grandpre', D. Kneeshaw, H. Morin, ... Y. Bergeron (Eds.), *Ecosystem management in the boreal forest* (pp. 183–200). Quebec City, QC: Presse de l'Universite' du Quebec.
- Tang, S., & Allesina, S. (2014). Reactivity and stability of large ecosystems. *Frontiers in Ecology and Evolution*, 2, 21.
- Thorpe, H. C., Astrup, R., Trowbridge, A., & Coates, K. D. (2010). Competition and tree crowns: A neighborhood analysis of three boreal tree species. *Forest Ecology and Management*, 259(8), 1586–1596. <https://doi.org/10.1016/j.foreco.2010.01.035>
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles. *Ecology*, 80(5), 1455–1474.
- Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences*, 96(4), 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>
- Zhang, J., Huang, S., & He, F. (2015). Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy*

of Sciences, 112(13), 4009–4014. <https://doi.org/10.1073/pnas.1420844112>

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