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Intraspecific variability in growth response to environmental fluctuations modulates the stabilizing effect of species diversity on forest growth

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Running title Effect of diversity on forest growth

Summary

1. Differences between species in their response to environmental fluctuations cause asynchronized growth series, suggesting that species diversity may help communities buffer the effects of environmental fluctuations. However, within-species variability of responses may impact the stabilizing effect of growth asynchrony.

2. We used tree ring data to investigate the diversity-stability relationship and its underlying mechanisms within the temperate and boreal mixed woods of Eastern Canada. We worked at the individual tree level to take into account the intraspecific variability of responses to environmental fluctuations.

3. We found that species diversity stabilized growth in forest ecosystems. The asynchrony of species' response to climatic fluctuations and to insect outbreaks explained this effect. We also found that the intraspecific variability of responses to environmental fluctuations was high, making the stabilizing effect of diversity highly variable.

4. *Synthesis*. Our results are consistent with previous studies suggesting that the asynchrony of species' response to environmental fluctuations drives the stabilizing effect of diversity. The intraspecific variability of these responses modulates the stabilizing effect of species diversity. Interactions between individuals, variation in tree size and spatial heterogeneity of environmental conditions could play a critical role in the stabilizing effect of diversity.

Keywords: biodiversity, dendrochronology, growth asynchrony, plant-climate interactions, plant-herbivore interactions, plant-plant interactions, plant population and community dynamics, tree growth

Introduction

Species diversity plays a key role in ecosystem functioning, particularly by stabilizing productivity through time (Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2012; Hooper *et al.* 2012). It has been suggested that species diversity may be critical to ensure ecosystem sustainability in the face of environmental fluctuations. Both theoretical (Yachi & Loreau 1999; de Mazancourt *et al.* 2013; Loreau & de Mazancourt 2013) and grassland experiments (Tilman 1999; Isbell, Polley & Wilsey 2009; Hector *et al.* 2010) suggest that differences in species response to environmental fluctuations is the primary mechanism underlying the stabilizing effect of diversity. As a result, these differences generate asynchronous population dynamics (Loreau 2010), enabling productivity compensations among species and thereby promote the stability of the community-level productivity. Interactions among individuals (i.e. competition and facilitation) may, however, modulate the stabilizing effect of diversity. For instance, it has been shown that competition can amplify the asynchrony of population dynamics by promoting the abundance of species which are better adapted to the growing season climate (Gonzalez & Loreau 2009; Mariotte *et al.* 2013). Although there is mounting evidence of the involvement of these factors in the stabilizing effect of diversity, little is known about their respective contributions.

Unlike grasslands, forests offer several advantages to understanding the mechanisms that control the diversity-stability relationship. First, due to the long life span of trees, population dynamics are much slower in forest communities. As a consequence, forest composition cannot change in response to inter-annual environmental fluctuations. The stabilizing effect of diversity in tree communities would, therefore, mainly rely on the asynchrony of individuals' growth and not on the asynchrony of population dynamics. Second, long records of annual growth are available for individual trees through the use of dendrochronology, providing a longer time perspective on the asynchrony of species response to environmental fluctuations. Finally, unlike grassland communities where individuals are often difficult to define due to the common occurrence of semi-independent parts, trees are easily distinguishable from one another. This feature makes it possible to take into account the variability of individuals' response within species, which may affect the stabilizing effect of diversity. de Mazancourt et al. (2013) has demonstrated analytically, that the stabilizing effect of the asynchrony of species' response to the environment decreases with intraspecific variability of response. This finding is consistent with a study conducted in tree communities (Clark 2010), which demonstrated that species having similar responses to environmental fluctuations may differ in their distributions of individuals' responses. The corollary of this observation is that individuals belonging to species with different (i.e. asynchronous) responses could have similar (i.e. synchronous) responses, which would, therefore, limit the stabilizing effect of the asynchrony of species response. Interactions among individuals and spatial heterogeneity of environmental conditions may be the source of the variability of individuals' response (Cescatti & Piutti 1998; Clark 2010; de Mazancourt *et al.* 2013). As a result, asynchrony of response among species has been shown to be higher between individuals occurring in the same neighbourhoods than within an entire stand (Clark 2010).

Climatic fluctuations (Fritts 1976) and insect outbreaks (Morin *et al.* 2009; Sutton & C. Tardif 2009) are two major drivers of the inter-annual growth variability of trees in North American forests. Since tree species typically respond differently to climatic fluctuations (Rozas, Lamas & García-González 2009; Drobyshev *et al.* 2013), and since insects may be host specific (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013), an increase in tree diversity could help stabilize forest productivity. In the face of insect outbreaks, the stabilizing effect of diversity could not only stem from species differences in their susceptibility to insect attacks, but also from a reduction of herbivory in more diverse forests due to a “host dilution” effect (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013). Some recent studies have investigated the diversity-stability relationship in forest ecosystems in the face of extreme climatic events (Pretzsch 2005; Pretzsch, Schütze & Uhl 2013; Jucker *et al.* 2014) and herbivory (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013). They concluded that diversity has a stabilizing effect on the overall productivity of mixed stands.

We used dendrochronological data (1) to determine whether tree species diversity stabilizes productivity in the temperate and boreal mixed woods of Eastern Canada and (2) to identify the mechanisms underlying the stabilizing effect of diversity. We, therefore, paid particular attention to the intraspecific (i.e. among single trees) variability of responses to annual environmental fluctuations, whatever the mechanisms generating this variability. We conducted our analyses on pairs of individuals occurring in the same neighbourhood so that we worked with individuals that were likely to be interacting together and sharing the same micro-environmental conditions. This approach also enabled us to take into account the variability of individuals’ response to environmental fluctuations while linking measures of stability to growth asynchrony. We first assessed stability as the inverse of the coefficient of variation (mean/variance) of the total growth of pairs of individuals, and compared it between monospecific and mixed pairs. We hypothesized that (**H1**) tree mixture promotes growth stability. We, therefore, expected stability to be higher for pairs of individuals belonging to different species than for pairs of individuals belonging to the same species. Thereafter, we decomposed the effect of diversity on stability into its effect on the mean and the variance of the total growth of pairs of individuals. We hypothesized that (**H2**) diversity stabilizes growth by reducing the variance of the total growth of pairs of individuals, and that, because of a higher growth asynchrony among individuals belonging to different species. We, therefore, expected the variance of the total growth to be lower for pairs of individuals belonging to different species than for pairs of individuals belonging to the same species. We also expected covariance of growth to be lower among individuals belonging to different species than among individuals belonging to the same species. Finally, using multivariate analysis, we identified individuals' response to climatic fluctuations and insect outbreaks. We hypothesized (**H3**) that individuals' response asynchrony to environmental fluctuations drove, at least partially, the stabilizing effect of diversity. We, therefore, expected to obtain significant correlations between environmental variables and growth, indicating that individuals' growth variability stemmed from environmental fluctuations and growth asynchrony stemmed from differences in individuals' response to these fluctuations.

Material and Methods

Data were collected at five 1 ha plots within both temperate and boreal mixed-wood stands in Eastern Canada (Fig. 1). Two boreal mixed-wood stands were sampled on the shores of the Lake Duparquet in Western Quebec, which are found within the balsam fir-white birch bioclimatic domain and at 270-275 m above sea level (a.s.l.). These two stands; D1823 (48.45791; 79.23920) and D1847 (48.50398; 79.32084) were both of fire origins established following fires occurring in 1823 and 1847, respectively (Bergeron 2000). Temperate mixed wood stands were sampled at three locations. The first stand, ABI (48.16253; 79.40121), was located in Abitibi, in the balsam fir-white birch domain at the northern limit of the mixed hardwood forest subzone, 375 m a.s.l. The second stand, BIC (48.33361; 68.81771), was located in the St-Lawrence Lowlands, in the balsam fir-yellow birch domain, approximately at 240 m a.s.l. Finally, the third stand, SUT (45.11280; 72.54129) was located in Eastern Townships, in the sugar maple-basswood domain at an elevation ranging between 645 and 690 m a.s.l. The topography was generally flat at all of the sites, except for SUT, which was on a slope facing north-west. The D1823, D1847 and ABI sites were located in the Clay Belt, a large physiographic region in western Quebec and north-eastern Ontario, characterized by generally thick clay deposits (Veillette 1994). The main soil deposit for the BIC and SUT sites was a glacial till with pockets of organic soil in local depressions.

Climate at the sites ranged from boreal continental, characterized by large variability in temperatures between warm and cold seasons, to a moister temperate climate, characterized by warmer temperatures and more precipitation. The monthly average temperature ranged between -16.9°C in January and 17.3°C in July for the D1823 and D1847 sites over the 1953-2013 period. Annual total precipitation was, on average, 866.6 mm. The temperature was similar at the ABI site (-16.6°C; 17.5°C), but annual precipitation was, on average, higher (894.3 mm). The annual average temperature ranged between -13.3°C in January and 17.1°C in July at BIC, and annual precipitation was, on average, 1050.4 mm. Finally, the SUT site was the warmest and the moistest site with temperatures ranging between -11.6°C in January and 16.9°C in July, and annual precipitation of, on average, 1464.8 mm.

All sites were mature forests stands that were undisturbed by logging, with the exception of the BIC site, which was selectively harvested prior to being designated a National Park in 1984. We considered seven species: eastern white cedar (*Thuja occidentalis* L.), white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* L.), yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), and sugar maple (*Acer saccharum* Marshall).

All trees equal or above 10 cm in diameter at breast height (DBH) were measured (Fig. 2) and mapped at each site. Tree positions were used to calculate their relative distance for the neighbourhood analyses. We randomly chose 70 individuals per species and per site in five DBH classes for coring. Sampling intensity across DBH classes was stratified 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 & Smiley 1996; Speer 2010). We removed from the analyses cores with a considerable amount of wood rot making tree ring measurement impossible, yielding a total of 43 to 63 individuals per species and site. The analyses were performed on 2041 cores from 1078 trees (Table 1).

We obtained climate data for each site for the time period 1953-2013 using the BioSIM 10.3 software (Régnière 1996; Régnière & St-Amant 2007). BioSIM is a collection of bioclimatic models and daily weather databases, which can generate climate variables at various temporal resolutions, using a user-supplied list of locations. For each site, BioSIM interpolated data from the eight closest weather stations using inverse distance weighting output, while adjusting for differences in latitude, longitude and elevation between the data and sites. We considered monthly mean temperatures, growth season length (period with daily means above 5°C), total monthly precipitation, total monthly snowfall, and monthly mean drought-code, which reflects water content of the deep compact organic layers (Girardin & Wotton 2009).

We detrended growth series to keep only the variability associated with the annual climatic variability and to remove temporal autocorrelation. Detrending was done by first averaging growth series associated with a single tree to obtain single-tree chronologies. We then standardized these single-tree chronologies using a 32-year cubic smoothing spline with a 50% frequency response (Speer 2010). We pre-whitened the resulting series by autoregressive modelling to remove temporal autocorrelation (Cook 1987) and to obtain detrended individual chronologies. We averaged the detrended individual chronologies using a bi-weight robust mean to obtain detrended master chronologies for each species and site. Transformations were performed using the R package *dplR* (Bunn 2008). Detrended individual and master chronologies were used to analyse the climate-growth relationship, whereas raw individual chronologies were used to investigate individual and species annual growth.

Several insect outbreaks of forest tent caterpillar (*Malacosoma disstria* Hubner.) and spruce budworm (*Choristoneura fumiferana* Clem.) occurred in Eastern Canada during the 1953-2013 period (Morin *et al.* 2009; Sutton & C. Tardif 2009), causing large reductions in tree diameter growth and suggesting that trees responded more to defoliation events rather than to climate during these periods. We ran the analyses for two versions of chronologies, with and without insect outbreaks. To avoid insect-related signals, we removed periods of forest tent caterpillar outbreaks from aspen chronologies, and periods during which spruce budworm outbreaks occurred from white spruce and balsam fir chronologies.

We identified insect outbreaks in a two step procedure. First, we consulted the large-scale aerial surveys of defoliation, carried out by the *Ministère des Forêts de la Faune et des Parcs,* to obtain approximate outbreak dates (Ministère des Forêts 2015). Periods of defoliation attributed to forest tent caterpillar and spruce budworm outbreaks all matched periods of abrupt growth reduction observed in the host species raw master chronologies (obtained by averaging individuals' raw chronologies). For each site, we then identified the exact outbreak dates using pointer years. These are years with particularly narrow or large rings observed in multiple tree ring series in a region (Schweingruber 1996). We identified site-specific pointer years for each species as years for which at least 70% of the trees exhibited a variation in their growth of at least 10% as compared to the previous year. We obtained the exact outbreak dates using the negative and positive pointer years enclosing the periods of defoliation-reduced growth in the raw master chronologies of host species.

Statistical analyses

Temporal stability (*TS*, Tilman 1999) has been commonly used to measure the stabilizing effect of species diversity on the productivity of a community. It is conventionally measured as the inverse of the coefficient of variation (mean/variance) of the total productivity. The effect of diversity on the stability of the total productivity may be decomposed into its effect on the mean and the variance. Furthermore, the variance of the total productivity may be expressed as the sum of the growth variances and covariances of all species in the community. As a consequence, species having asynchronous growth (i.e. low covariance) will decrease the community *TS*. The productivity variance at the community level could be decomposed further as the sum of the growth variances and covariances of all its constituent individuals. Decomposing variance this way allowed for taking into account the variability of individuals' growth (i.e. growth variances), and to link the measures of *TS* to growth asynchrony among individuals (i.e. growth covariances). To facilitate interpretations, we calculated *TS* on the total radial growth of pairs of individuals occurring in the same neighbourhood (defined as an area within 20 m from a focal tree), following the approach of Clark (2010). Proceeding this way enabled us to express the variance of the total growth, and thus *TS*, from a measure of asynchrony (i.e. covariance). *TS* was thus given by:

$$TS = \frac{\mu_{pair}}{\sqrt{\sigma^2{}_{pair}}} \qquad \text{(eqn 1)}$$

where μ_{pair} and $\sigma^2{}_{pair}$ were the mean and the variance of the total growth of a pair of individuals and where

$$\sigma^2{}_{pair} = \sigma^2{}_i + \sigma^2{}_j + 2.cov(i,j) \qquad \text{(eqn 2)}$$

with *i* and *j*, the growth chronologies of two individuals.

We compared the distributions of *TS*, μ_{pair}, $\sigma^2{}_{pair}$, or $cov(i,j)$ obtained for pairs of individuals belonging to the same species to those obtained for pairs of individuals belonging to different species to estimate the effect of species mixture on growth stability, and to understand the mechanisms underlying it. We ran four linear models to disentangle the effect of species mixture from the effect of sites and species based on the following structure:

$$Y = \alpha + MIX + SITE + SP + \varepsilon \qquad \text{(eqn 3)}$$

where *Y* was alternately *TS*, μ_{pair}, $\sigma^2{}_{pair}$, and $cov(i,j)$; *α* - the reference mean; *MIX* - the effect of mixture on the reference mean, indicating whether the measures of *Y* were calculated on trees belonging to the same species or to different species; *SITE* - the effects of sites on the reference mean; *SP* - the effect of species on the reference mean. SP is a factorial effect coded as dummy variables with two categories indicating the presence or the absence of each of the seven species in the pairs of individuals.

We expected that distributions of *TS* values obtained for paired individuals belonging to different species would be higher than those obtained for individuals belonging to the same species, indicating a stabilizing effect of mixture on growth. We also expected that distributions of σ^2_{pair}, and *cov(i,j)* values obtained for paired individuals belonging to different species would be lower than those obtained for individuals belonging to the same species, indicating that growth asynchrony is a driver of the stabilizing effect of mixture. We conducted these analyses on the 1953-2013 period. Since tree neighbourhoods could have been different 60 years prior to sampling, we also conducted these analyses on the 1993-2013 period to ensure the robustness of the results obtained on the 1953-2013 period. In doing so, we assumed changes in tree neighbourhoods to be insignificant during the last 20 years. We performed these analyses both after removing insect outbreak periods from individual chronologies and with insect outbreak periods included.

We used bootstrapped response functions (Fritts 1976; Guiot 1991) to identify the climatic variables that significantly influenced species growth. In response function analysis, a detrended master chronology of a species (free from insect outbreak signals) was regressed against the principal components obtained on the set of climatic variables. Our rationale to use response functions in this study was twofold. First, we wanted to identify the climatic factors controlling species-specific growth on each site. Second, the response functions were used as a filter to select climatic variables to be introduced in the analysis assessing individuals' response to environmental fluctuations. We ran response functions on site- and species-specific detrended master chronologies and site-specific climate datasets using R package *treeclim* (Zang & Biondi 2015). In these analyses, we used 52 climatic variables of both the year concurrent with and preceding the growth period, starting from June of the year preceding the ring formation and ending with August of the year concurrent with the ring formation. July and August total snowfalls were not used in the response functions since they were null most of the time. Following the same logic, we only considered drought codes for the periods June through August for the year prior to the growing period, and May through August for the current growing season. We also used growing season lengths for the previous and the current years.

We ran redundancy analysis (RDA) to identify individuals' response to environmental fluctuations and to determine whether the asynchrony of response of individuals belonging to different species contributed to the stabilizing effect of diversity. RDA runs a set of independent multivariate regressions, similar to response functions, but then performs a constrained ordination to position the individuals in a multidimensional space of environmental factors (Legendre & Legendre 2012). The distance between individuals in the ordination indicated the asynchrony in their response to environmental fluctuations among them. Our **H3** hypothesis was, therefore, contingent upon obtaining significant RDAs, indicating that environmental fluctuations controlled the variability of individuals' growth. Significant RDAs would, therefore, demonstrate that the asynchrony of individuals' response to environmental fluctuations enabled growth compensations among individuals and thus contributed to the stabilizing effect of species diversity. We ran RDAs on two sets of chronologies, without and with the growth variability caused by insect outbreaks. In the first case, we aimed to consider exclusively the effects of climatic fluctuations on growth. In the second case, we sought to identify tree's response simultaneously to both factors. For these analyses, we added a binary variable indicating the presence of each insect as an additional explanatory variable. The climatic variables used in RDAs were those previously identified in response function analysis. Detrended individual series were considered as response variables, with each annual growth value considered as an observation. RDAs were performed for each site including only years for which all species had growth data for at least 30 individuals. The significance of RDAs was tested with the F-test of the canonical relationships between growth index values and environmental variables. The explained variance values associated with each RDA provided information on the variability of individuals' response to environmental fluctuations. We computed the RDAs with the R package *rdaTest* (Legendre & Durand 2012).

To determine whether diversity had a stabilizing effect through the reduction of herbivory, we studied the relationship between the intensity of the damages caused by insects to host trees and the diversity in the neighbourhood of host trees in a linear regression. We estimated the intensity of insect attacks as the ratio between the mean growth of trees outside insect outbreak periods and their growth during insect outbreaks. We estimated diversity around trees using the Shannon diversity index which measured diversity as a function of species proportion (p_i) in the community. For $i = 1,\ldots,s$ species within a radius (R=20 m) around a tree, the Shannon diversity index H was given by:

$$H = -\sum_{i=1}^{s} p_i ln\,(p_i) \qquad \text{(eqn 4)}$$

where $p_i = ba_i/BA$, with ba_i being the basal area of species i in the neighbourhood and BA being the total basal area in the neighbourhood. We conducted this analysis for trees belonging to the three species susceptible to insect attacks in our sites (*A. balsamea, P. glauca, P. tremuloides*). We expected trees growing in diverse neighbourhoods to be less affected by insect outbreaks.

Results

Models describing *TS*, μ_{pair}, σ^2_{pair}, and *cov(i,j)* as a function of mixture (equation 3) showed the same trends in both the 1953-2013 (Table 2) and 1993-2013 (see Table S1 in Supporting information) periods. *TS* was significantly higher for pairs of individuals belonging to different species than for pairs of individuals belonging to the same species, indicating a stabilizing effect of species mixture (i.e. diversity) on growth (Fig. 3 and Table 2). In contrast, μ_{pair} (Fig. S1), σ^2_{pair} (Fig. S2), and *cov(i,j)* (Fig. S3) were significantly lower for pairs of individuals belonging to different species than for pairs of individuals belonging to the same species, as indicated by the negative and significant parameters associated with the MIX variable in the model (Table 2).

Insect outbreaks amplified the effect of mixture on *TS*, σ^2_{pair}, and *cov(i,j)*. The stabilizing effect of mixture was higher when the signal from insect outbreaks was preserved in the chronologies (MIX = 0.80) as compared to chronologies with no insect outbreak signal (MIX = 0.52; Table 2). The negative effect of mixture on σ^2_{pair} and *cov(i,j)* was stronger when insect outbreaks were preserved in the chronologies (MIX =-0.61, -0.15 respectively) as compared to chronologies without them (MIX = -0.44, -0.10 respectively; Table 2). In contrast, insect outbreaks slightly decreased the negative effect of mixture on μ_{pair} (Table 2).

Response functions showed that the climatic conditions (temperature, precipitation and drought code) of summer months (June to August) of the current growing season were the most influential to growth across species and sites (Table 3). In contrast, we found few significant correlations between species growth and climatic conditions of the autumn of the previous growing season and the early winter (October to February). The northernmost sites (D1823 and D1847) showed a more pronounced global effect of climatic conditions of summer months of the previous growing season on species growth than all of the other sites. We observed some asynchrony between conifers and deciduous species response to climate. For example, on the BIC site, while growth of all deciduous species significantly correlated to current summer drought (i.e. to drought code), this was not the case for balsam fir. Similarly, on the D1823 site, while all conifers growth significantly correlated to current summer drought, the growth of trembling aspen did not.

RDAs showed that the asynchrony of response to environmental fluctuations of individuals' belonging to different species contributed to the stabilizing effect of diversity by enabling growth compensation among individuals (Fig. 4). All RDAs were significant except RDAs performed on chronologies free from insect outbreak signals for the D1823 and D1847 sites (Fig. 4a). However, rather than a lack of correlation between environmental fluctuations and growth, this could be due to the relatively short period on which these RDAs were performed (24 and 29 years for the D1823 and D1847 sites, respectively), after removing the 4 years of forest tent caterpillar outbreak, the 17 years of spruce budworm outbreak, and years for which not all species had growth data for at least 30 individuals. Species-specific ellipses, however, overlapped broadly, despite distinct locations of centroids (i.e. distinct average responses), indicating that species could have close responses to environmental fluctuations. The explained variance for RDAs ranged from 8.6 to 25.6%, indicating that the variability of individuals' response to environmental fluctuations was high.

We found no significant relationship between the intensity of the damages caused by insects to host trees and the diversity in the neighbourhood of host trees (Table 4).

Discussion

Our results showed that diversity stabilized growth in forest ecosystems, supporting the **H1** hypothesis. The stabilizing effect of diversity stemmed from a higher growth asynchrony among individuals belonging to different species, which reduced the variance of the total growth of pairs of individuals, supporting the **H2** hypothesis. The asynchrony of response to environmental fluctuations of trees belonging to different species contributed to the stabilizing effect of diversity, by controlling the growth asynchrony of trees, supporting the **H3** hypothesis. However, the intraspecific variability of response to environmental fluctuations was high, generating a broad overlap of species responses despite differences in their average responses (Fig. 4). This demonstrates the interest of working at the individual-level rather than at the species-level. These results were persistent regardless of whether the forest was temperate or boreal mixed, and in the face of different types of environmental fluctuations (climatic fluctuations and insect outbreaks).

We demonstrated that in forest ecosystems, even when controlling for population dynamics, tree species diversity could stabilize productivity through the asynchrony of responses to climatic fluctuations and insect outbreaks of individuals' belonging to different species. The asynchrony of individuals' response enabled growth compensation among individuals that ultimately produced a stabilizing effect. These results are consistent with previous studies in forest ecosystems (Jucker *et al.* 2014) and grassland communities (Tilman 1999; Isbell, Polley & Wilsey 2009; Hector *et al.* 2010), suggesting that the asynchrony of species response is a mechanism driving the stabilizing effect of diversity.

The stabilizing effect of species mixing was stronger in analyses including both climate and insect outbreak effects, as compared to the analyses operating on chronologies with insect signal removed. We explain that by species differences in their susceptibility to insects and the resulting asynchronized growth series. We speculate that the stabilizing effect of diversity could be further enhanced through (1) a reduction in the outbreak-related mortality both for host and non-host species (both for host and non-host species; Bouchard, Kneeshaw & Bergeron 2005), and (2) the increase in the abundance of the insect natural enemies, limiting herbivory (Cappuccino *et al.* 1998). However, higher neighbourhood diversity did not reduce the insect-induced growth decline of host species during outbreaks, as it has been shown earlier (Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2013). This divergence of results could stem from a difference in the scale of observation. Previous studies were done at the stand level while our study was carried out on a smaller neighbourhood level. Good dispersal abilities of forest tent caterpillar and spruce budworm (Greenbank 1957) could make the induced damage depend on the availability of their host at the stand and regional scales rather than at the neighbourhood scale.

We found a negative effect of diversity on the mean of the total growth of tree pairs. This outcome is contrary to both theoretical predictions and empirical results (Tilman 1999; Yachi & Loreau 1999; Isbell, Polley & Wilsey 2009; Hector *et al.* 2010; de Mazancourt *et al.* 2013; Loreau & de Mazancourt 2013), which have shown that diversity usually increases productivity, in particular through a better resource partitioning between species having different niches. The negative effect of diversity on the mean of the total growth of tree pairs could be an artefact arising due to the fact that we have trees of all sizes (Fig. 2). Radial growth typically initially increases with tree size before decreasing in larger trees. Comparing the total growth of a pair of intermediate-sized firs (growing rapidly) to a pair consisting of a fir and a birch, both of small size (growing slowly), for instance, would lead to the conclusion that diversity has a negative effect on growth, while it would actually be a size effect. The wide range of tree sizes in our data did not allow us to make conclusions on the effect of diversity on the mean of the total growth of tree pairs. Nevertheless, the negative effect of diversity on the mean of the total growth of tree pairs indicates that diversity stabilized growth by reducing the total growth variance, and not because of a positive effect on the total growth mean.

The intraspecific variability of response to environmental fluctuations was high, leading to a highly variable effect of species mixture on *TS* among tree pairs. This variability could stem from interactions among individuals, such as competition and facilitation, and the spatial heterogeneity of environmental conditions (Cescatti & Piutti 1998; Clark 2010; de Mazancourt *et al.* 2013). By modulating individuals' response to environmental fluctuations, these two factors would affect the growth variability of individuals, their growth covariance and, therefore, the variance in the total growth of tree pairs. This outcome is complementary to the findings of Morin et al. (2014) who demonstrated, using virtual experiments based on a forest succession model, that the stabilizing effect of diversity in forest ecosystems was mainly driven by the asynchrony of species response to small disturbances rather than to environmental fluctuations. Finally, given that we worked in mixed stands, most individuals were interacting with trees of several species. Our approach using pairs of individuals did not allow us to conclude on the role of among-tree interactions on the stabilizing effect of diversity, in particular because pairs of individuals may interact with other individuals belonging to different species. This observation does not question the fact that interactions, size and micro-environment could modulate the stabilizing effect of diversity. Our study instead emphasizes the need to further investigate the role of the mechanisms underlying the intra-specific variability of response to environmental fluctuations.

Our work highlights the value of working in forest communities to study the mechanisms driving the diversity-stability relationship. This is especially valuable since it gives us access to the individual-level where growth compensation actually occurs, while eliminating the influence of population dynamics. We showed that diversity increased the stability of growth in forest ecosystems and that the asynchrony of response to environmental fluctuations of individuals' belonging to different species contributed to this stabilizing effect. Mechanisms at the origin of the variability of individuals' response, such as interactions between individuals and spatial heterogeneity of environmental conditions, could, therefore, play a crucial role in the stabilizing effect of diversity.

Author's Contributions

RA, YB, DG and ID conceived the ideas and designed methodology; RA and KP collected the data; RA, CGM and KP analysed the data; RA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

tree-ring data: uploaded online at http://ielab.recherche.usherbrooke.ca

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Table 1: Number of trees cored per species and site. The number of cores are shown in brackets.

Site	A. balsamea	P. glauca	T. occidentalis	A. rubrum	A. saccharum	B. alleghaniensis	P. tremuloides
D1823	48 (84)	47 (94)	52 (98)	-	-	-	54 (107)
D1847	51 (96)	58 (109)	54 (110)	-	-	-	52 (101)
ABI	58 (104)	47 (93)	49 (96)	52 (98)	55 (107)	-	-
BIC	63 (107)	-	-	61 (126)	59 (121)	-	62 (116)
SUT	54 (91)	-	-	-	59 (106)	43 (77)	-

Table 2: Summary of the four linear models describing *TS*, μ_{pair}, σ^2_{pair}, and *cov(i,j)* as a function of mixture, controlling for species and site effects on the 1953-2013 period. α is the mean of *TS* measures calculated on pairs of individuals comprising at least one white cedar on the ABI site. We ran the model both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b).[1] Level of significance: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant (> 0.05). Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloides*).

Reference mean and dummy variables	*TS*				σ^2_{pair}				μ_{pair}				*cov(i,j)*			
	(a) Without insect outbreaks[1]		(b) With insect outbreaks[1]		(a) Without insect outbreaks[1]		(b) With insect outbreaks[1]		(a) Without insect outbreaks[1]		(b) With insect outbreaks[1]		(a) Without insect outbreaks[1]		(b) With insect outbreaks[1]	
α *(reference mean)*	3.044	***	2.847	***	1.154	***	1.293	***	2.750	***	2.692	***	0.201	***	0.244	***
MIX	0.516	***	0.804	***	-0.439	***	-0.606	***	-0.377	***	-0.341	***	-0.105	***	-0.152	***
SITE$_{BIC}$	0.097	***	0.077	**	-0.395	***	-0.364	***	-0.534	***	-0.476	***	-0.105	***	-0.022	***
SITE$_{D1823}$	0.068	*	-0.123	***	-0.370	***	-0.276	***	-0.473	***	-0.477	***	-0.030	***	-0.012	*
SITE$_{D1847}$	0.252	***	0.031	ns	-0.43	***	-0.404	***	-0.533	***	0.570	***	-0.037	***	-0.021	***
SITE$_{SUT}$	-0.495	***	-0.428	***	0.119	***	0.216	***	-0.145	***	-0.055	*	-0.003	ns	0.001	ns
SP$_{Ab}$	-0.063	*	-0.551	***	0.448	***	0.566	***	0.729	***	0.582	***	0.031	***	0.060	***
SP$_{Ar}$	-0.407	***	-0.699	***	0.111	***	0.216	***	-0.032	ns	-0.059	**	0.003	ns	0.026	***
SP$_{As}$	-0.841	***	-1.007	***	0.066	***	0.127	***	-0.347	***	-0.331	***	-0.001	ns	0.014	**
SP$_{Ba}$	-0.317	***	-0.505	***	1.012	***	1.077	***	1.036	***	1.020	***	0.083	***	0.098	***
SP$_{Pg}$	-0.629	***	-0.697	***	0.639	***	0.631	***	0.674	***	0.622	***	0.063	***	0.076	***
SP$_{Pt}$	-0.316	***	-0.736	***	0.477	***	0.722	***	0.853	***	0.844	***	0.042	***	0.079	***
Adjusted R^2	0.173		0.164		0.242		0.257		0.349		0.319		0.071		0.111	
p-value	< 2.2e-16		< 2.2e-16		< 2.2e-16		< 2.2e-16		< 2.2e-16		< 2.2e-16		< 2.2e-16		< 2.2e-16	

Table 3: Site and species-specific climatic variables identified by bootstrapped response function as having a significant correlation with growth: drought code (DC), temperature (T), precipitation (P), snowfall (S), growth season length (GSL). GSL in previous June correspond to the previous year GSL. The sign (+/-) indicates the direction of the correlation. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloides*), To (T. occidentalis).

		previous year							current year							
Site	Sp	jun	jul	aug	sep	oct	nov	dec	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
D1823	Ab														DC-	
	Pg		DC-		DC+									P+	DC-	
	Pt			T-							S+					
	To									T-				T-		T-
D1847	Ab	P+										T+				
	Pg		P+									T+				
	Pt			DC-							S+					
	To			T-	S-				S-					T-		P+
ABI	Ab	GSL-														
	Pg												DC+	T-		T-
	To					P-								T-		P+
	Ar		T-								T+					
	As												T-	S-	DC- P+	DC-
BIC	Ab	GSL-			T- S+											
	Pt										S-			P+	DC-	
	Ar										S-			P+	DC-	
	As													P+	DC-	
SUT	Ab						S-							S+		
	As													DC-		
	Ba					P+						S+				

Table 4: Regressions between the intensity of the damages caused by insects to host trees and the diversity in the host tree neighbourhood. [1] Level of significance: *** < 0.001; ns = not significant (> 0.05). Host species are coded with their initials: Ab (*A. balsamea*), Pg (*P. glauca*), Pt (*P. tremuloides*).

	Ab[1]		Pg[1]		Pt[1]	
intercept	2.366	***	2.553	***	3.11	***
slope	- 0.093	ns	- 0.554	ns	0.286	ns
Adjusted R^2	- 0.004		0.024		0	
p-value	0.763		0.07		0.307	

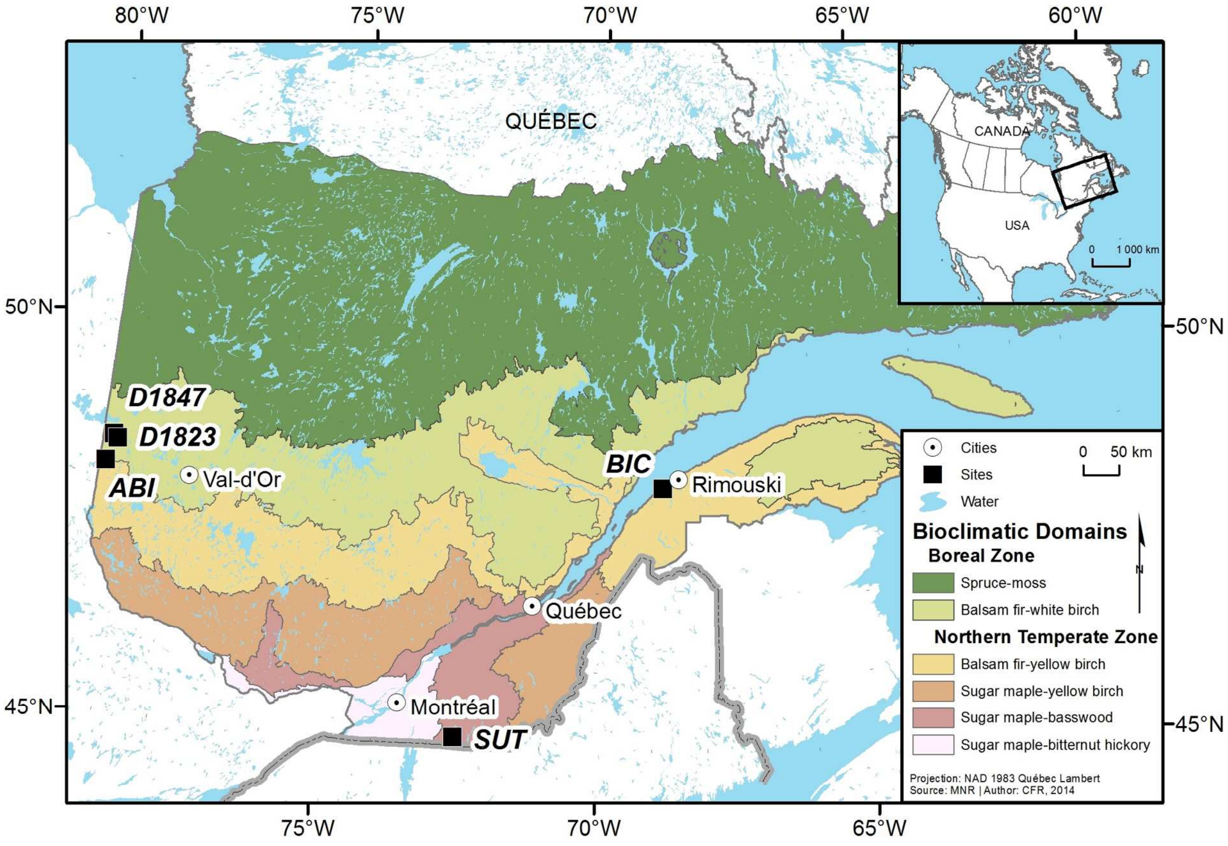


Fig. 1. Study sites and bioclimatic domains of Québec.

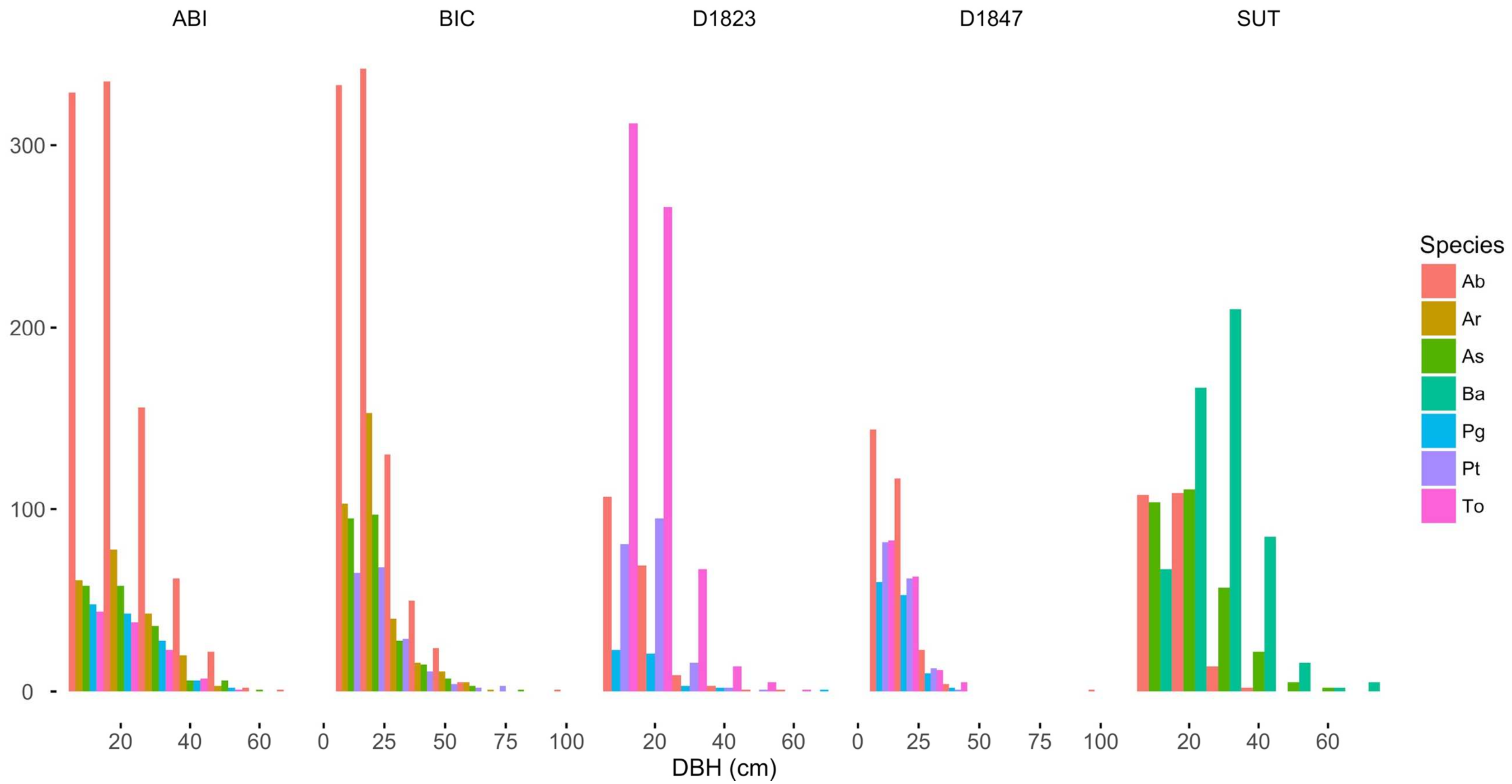


Fig. 2. Species and site-specific distributions of tree diameters at study sites.

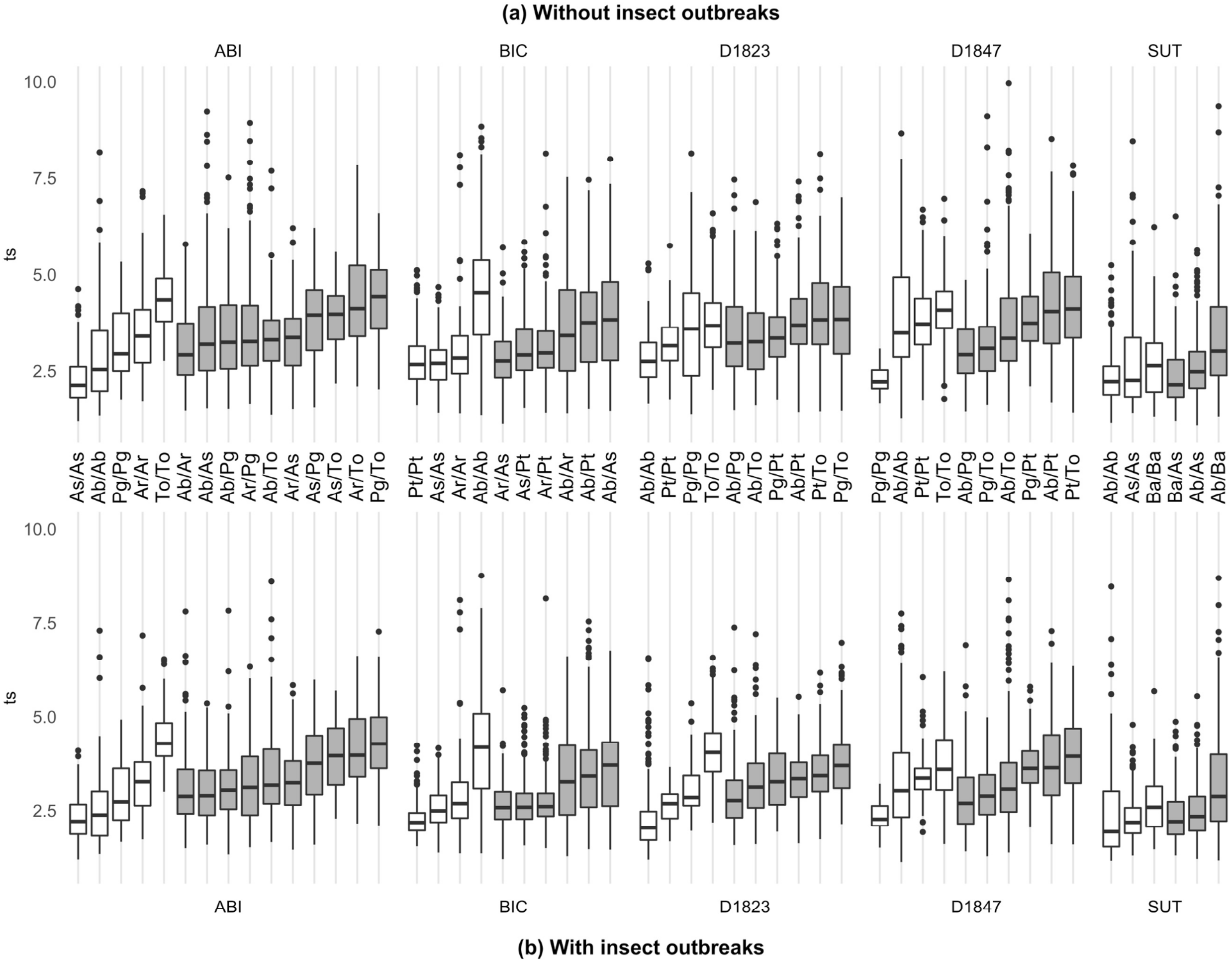


Fig. 3. Site and species-specific distributions of *TS* values measured on paired individuals occurring in the same neighbourhoods. White boxes refer to distributions of *TS* values measured on individuals belonging to the same species, while grey boxes refer to distributions of *TS* values measured on individuals belonging to different species. Distributions were developed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b). Labels indicate to which species the individuals belonged to for each distribution. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloides*), To (*T. occidentalis*).

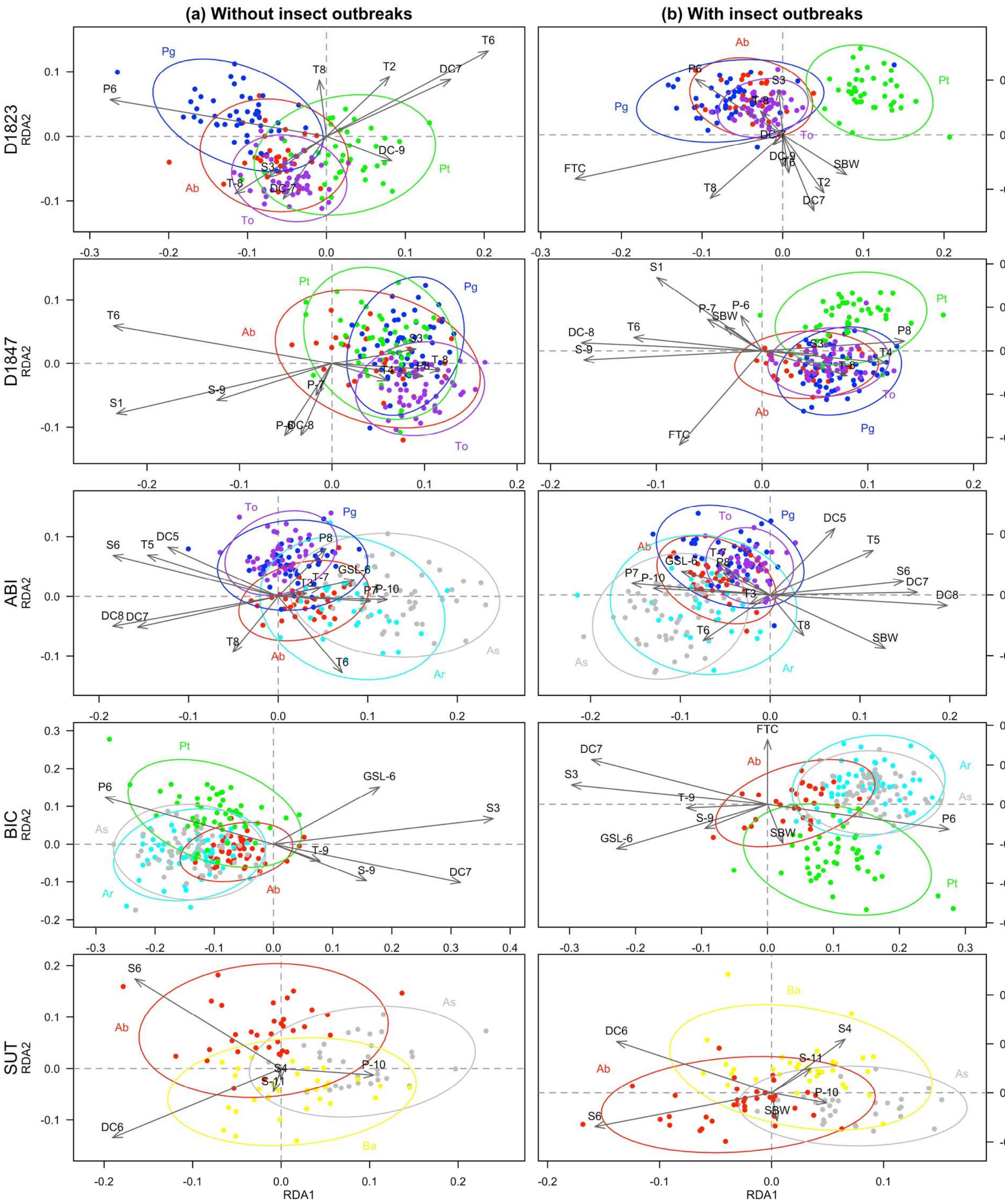


Fig. 4. Site-specific redundancy analysis (RDA) performed with individual standardized chronologies, climatic variables and binary variables indicating the presence of insects. Points

correspond to individual chronologies. Species-specific ellipses containing 95% of species individuals are shown and identified with species initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloides*), To (*T. occidentalis*). Climate variables and binary variables indicating the presence of insects are represented by black arrows: drought code (DC), temperature (T), precipitation (P), snowfall (S), growth season length (GSL), forest tent caterpillar (FTC), spruce budworm (SBW). The numbers following the variables initials indicate the number of the month associated with the variable. Negative values refer to a month of the previous year. RDAs were performed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b).

SUPPORTING INFORMATION

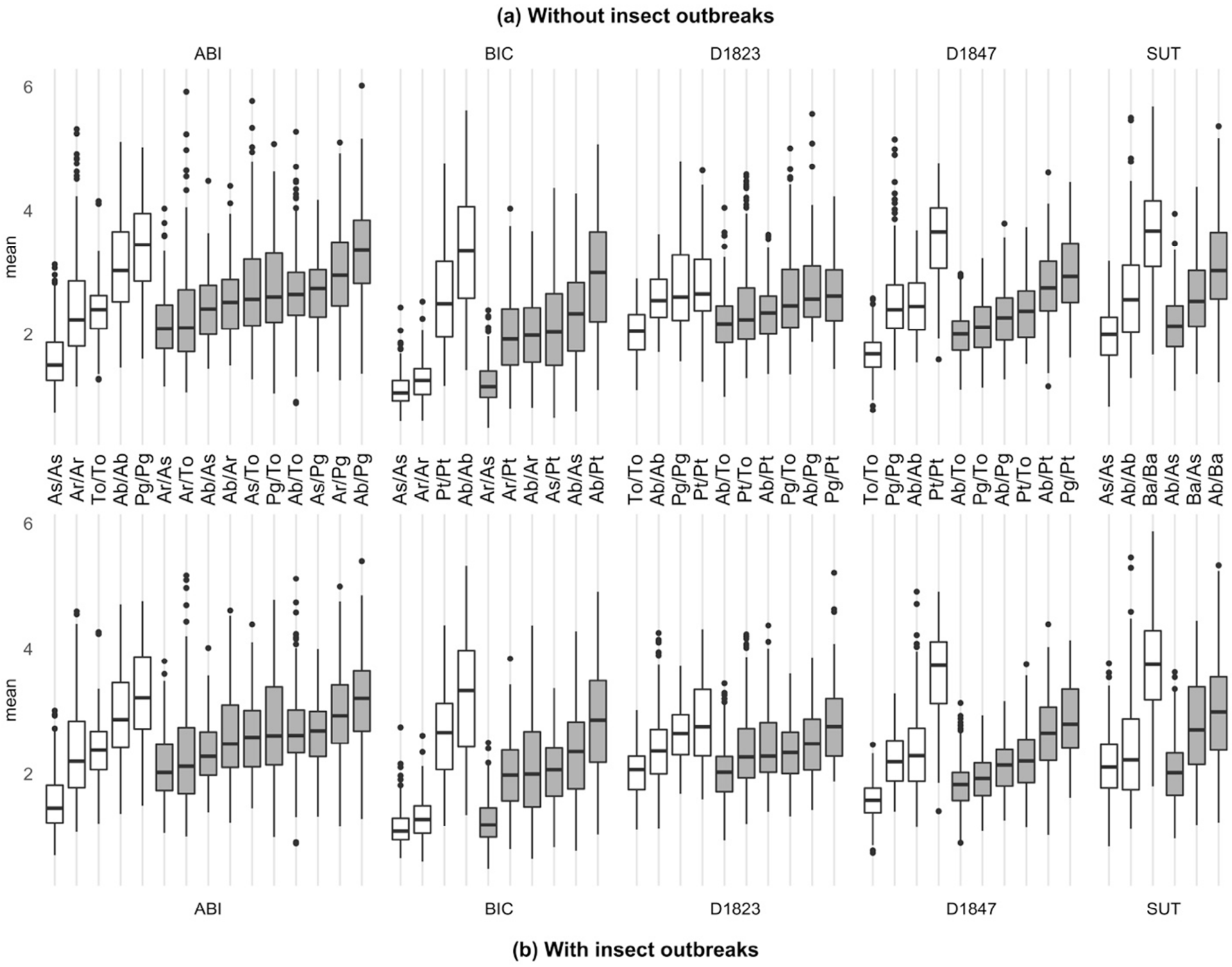
Additional supporting information may be found in the online version of this article:

Table S1: Summary of the four linear models describing *TS*, μ_{pair}, σ^2_{pair}, and *cov(i,j)* as a function of mixture, controlling for species and sites effects over1993-2013.

Figure S1: Site and species-specific distributions of the mean of the total growth of individuals measured on paired individuals occurring in the same neighbourhoods.

Figure S2: Site and species-specific distributions of the variance of the total growth of individuals measured on paired individuals occurring in the same neighbourhoods.

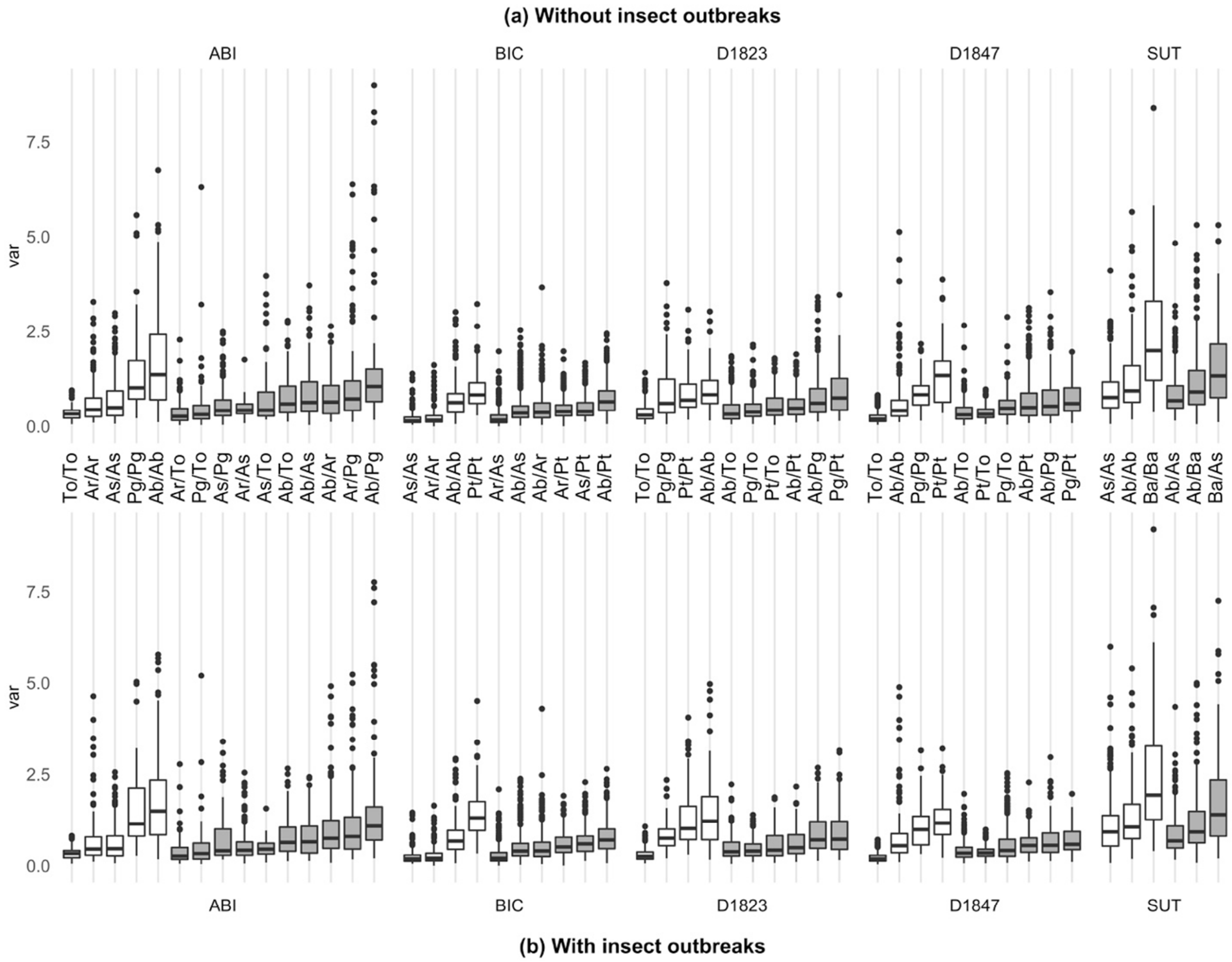
Figure S3: Site and species-specific distributions of covariance among individuals measured on paired individuals occurring in the same neighbourhoods.



(a) Without insect outbreaks

(b) With insect outbreaks

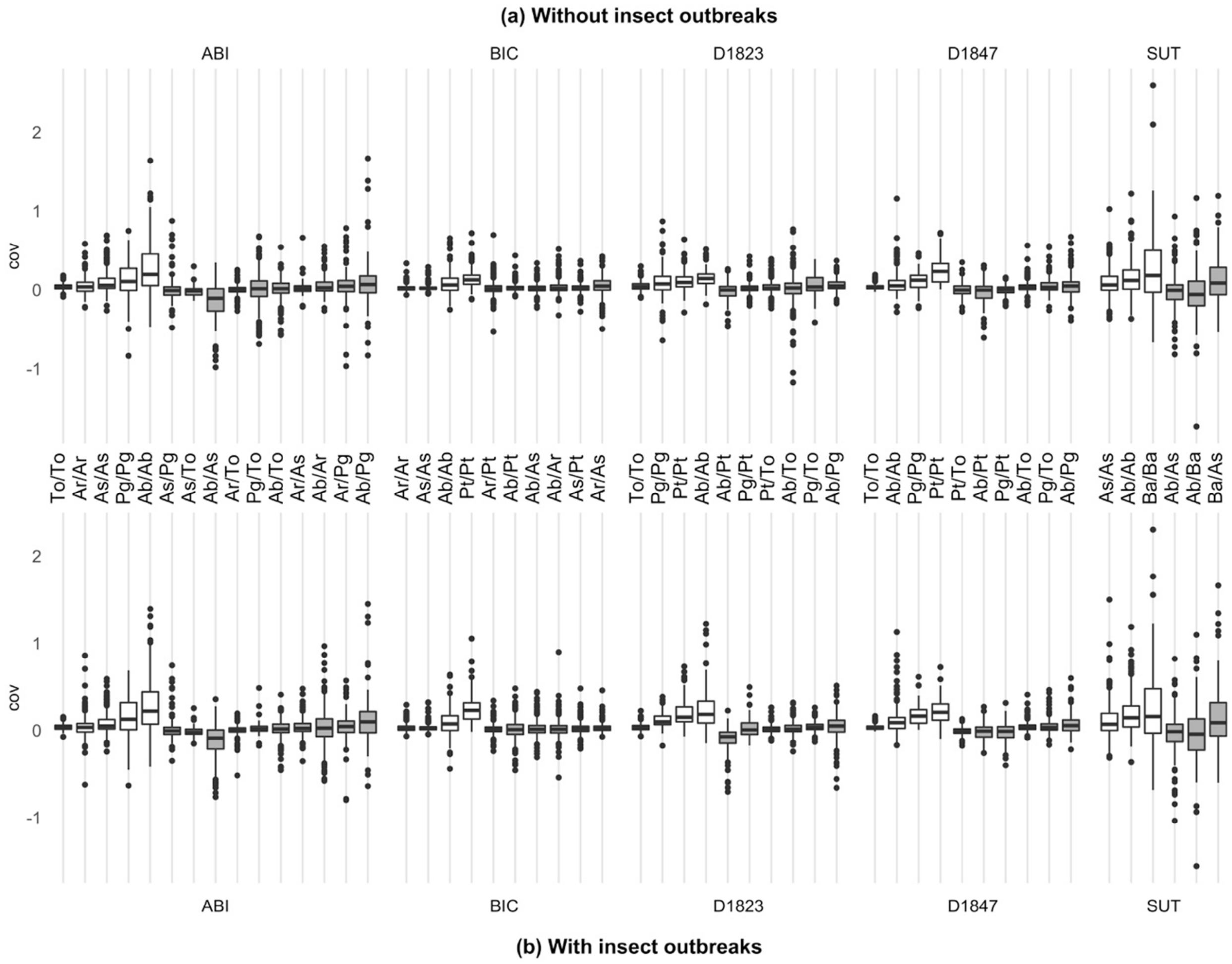
Figure S1: Site and species-specific distributions of the mean of the total growth of individuals measured on paired individuals occurring in the same neighbourhoods. White boxes refer to distributions of mean values measured on individuals belonging to the same species, while grey boxes refer to distributions of mean values measured on individuals belonging to different species. Distributions were developed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b). Labels indicate to which species the individuals belonged to for each distribution. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloïdes*), To (*T. occidentalis*).



(a) Without insect outbreaks

(b) With insect outbreaks

Figure S2: Site and species-specific distributions of the variance of the total growth of individuals measured on paired individuals occurring in the same neighbourhoods. White boxes refer to distributions of variance values measured on individuals belonging to the same species, while grey boxes refer to distributions of variance values measured on individuals belonging to different species. Distributions were developed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b). Labels indicate to which species the individuals belonged to for each distribution. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloïdes*), To (*T. occidentalis*).


(a) Without insect outbreaks

(b) With insect outbreaks

Figure S3: Site and species-specific distributions of covariance among individuals measured on paired individuals occurring in the same neighbourhoods. White boxes refer to distributions of covariance values measured on individuals belonging to the same species, while grey boxes refer to distributions of covariance values measured on individuals belonging to different species. Distributions were developed both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b). Labels indicate to which species the individuals belonged to for each distribution. Species are coded with their initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloïdes*), To (*T. occidentalis*).

Table S1: Summary of the four linear models describing *TS* , *μ_pair* , *σ2_pair* , and *cov(i,j)* as a function of mixture, control 2013. α is the mean of TS measures calculated on pairs of individuals comprising at least one white cedar on the ABI site. W outbreak periods from individual chronologies (a) and with insect outbreak periods included (b).1 Level of significance: *** significant (> 0.05). Species are coded with their initials: Ab (A. balsamea), Ar (A. rubrum), As (A. saccharum), Ba (B. alleg

Reference mean and dummy variables	TS		σ^2_pair		μ_pair	
	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]	(a) Without insect outbreaks[1]	(b) Wit outbr
α (reference mean)	4.1307 ***	3.96455 ***	0.61869 ***	0.72716 ***	2.72099 ***	2.66006
MIX	0.67945 ***	0.92854 ***	-0.27206 ***	-0.38138 ***	-0.2992 ***	-0.2699
SITE_{BIC}	-0.28062 ***	-0.09825 ***	-0.11645 ***	-0.15939 ***	-0.4904 ***	-0.457
$\text{SITE}_{\text{D1823}}$	-0.35978 ***	-0.61309 ***	-0.16308 ***	-0.10603 ***	-0.7298 ***	-0.6501
$\text{SITE}_{\text{D1847}}$	-0.56521 ***	-0.59463 ***	-0.15693 ***	-0.13804 ***	-0.8401 ***	-0.7688
SITE_{SUT}	-1.0954 ***	-1.02153 ***	0.2452 ***	0.22064 ***	-0.0866 ***	-0.0745
SP_{Ab}	0.07923 *	-0.03242 ns	0.33244 ***	0.35632 ***	0.96641 ***	0.97932
SP_{Ar}	-0.58197 ***	-0.80077 ***	0.11192 ***	0.1718 ***	-0.1161 ***	-0.1033
SP_{As}	-0.92654 ***	-1.12228 ***	-0.08069 ***	-0.03683 *	-0.6734 ***	-0.6615
SP_{Ba}	-0.32704 ***	-0.5458 ***	0.36233 ***	0.43724 ***	0.53982 ***	0.5318
SP_{Pg}	-0.92133 ***	-0.92827 ***	0.41353 ***	0.43516 ***	0.45047 ***	0.48738
SP_{Pt}	-0.48819 ***	-1.54905 ***	0.38561 ***	0.65657 ***	0.90557 ***	0.67205
Adjusted R^2	0.1797	0.2858	0.189	0.2344	0.4034	0.3
p-value	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2

ling for species and sites effects over 1993-
e ran the model both after removing insect
< 0.001; ** < 0.01; * < 0.05; ns = not
ghaniensis), Pg (P. glauca), Pt (P. tremuloides).

	cov(i,j)	
h insect eaks[1]	(a) Without insect outbreaks[1]	(b) With insect outbreaks[1]
***	0.09975 ***	0.13824 ***
***	-0.0561 ***	-0.0914 ***
***	0.00121 ns	-0.0051 ns
***	0.00053 ns	0.00886 **
***	-0.001 ns	0.00591 ns
**	0.02144 ***	0.01353 ***
***	0.02854 ***	0.03577 ***
***	0.00504 ns	0.01972 ***
***	-0.0168 ***	-0.0066 *
***	-0.0025 ns	0.01975 ***
***	0.0354 ***	0.04168 ***
***	0.04136 ***	0.07861 ***
983	0.07276	0.1334
e-16	< 2.2e-16	< 2.2e-16