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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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Summary

1. Species diversity, and specifically the asynchrony of species response to environmental fluctuations, has been shown to stabilize ecosystem productivity through time, suggesting it may play a critical role in their sustainability in the face of environmental fluctuations. However, the variability of responses within species may impact the stabilizing effect of the asynchrony of species response.

2. Here, 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 level to take into account the intraspecific variability of responses to environmental fluctuations within species.

3. We found that species diversity stabilized growth in forest ecosystems. The asynchrony of species response to climatic fluctuations and to insect outbreaks contributed to 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. However, the intraspecific variability of response appeared to modulate the stabilizing effect of species diversity. Essentially, interactions between individuals and spatial heterogeneity of environmental conditions could play a critical role in the stabilizing effect of diversity.

Key-words: 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 ecosystems 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 ecosystems 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 the asynchrony in species response to environmental fluctuations was the primary mechanism underlying the stabilizing effect of diversity. As a result, it would generate asynchronous population dynamics (Loreau 2010), which would in turn enable productivity compensations among species and thereby promote the stability of the community-level productivity. Interactions among individuals (i.e. competition and facilitation) may 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 understand the mechanisms that control the diversity-stability relationship. First, due to the long life span of trees, population dynamics are much slower in tree 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 species' growth and not on the asynchrony of population dynamics. Interactions among individuals may still modulate the

69 stabilizing effect of diversity, where competition has been previously shown to affect species
70 growth response to fluctuations in climate (Cescatti & Piutti 1998). Second, long records of
71 annual growth are available for forest through the use of dendrochronology, providing a longer
72 time perspective on the asynchrony of species response to environmental fluctuations. Finally,
73 unlike grassland communities where individuals are often difficult to define due to common
74 occurrence of semi- independent parts, trees are easily distinguishable from one and other. This
75 feature allows taking into account the variability of individuals' response within species which
76 may affect the stabilizing effect of diversity. Indeed, de Mazancourt *et al.* (2013) has
77 demonstrated analytically that the stabilizing effect of species asynchrony in their response
78 decreases with intraspecific variability of individuals' response. This finding has been
79 empirically supported by a study conducted in tree communities (Clark 2010) which
80 demonstrated that species having similar responses to environmental fluctuations may differ in
81 their distributions of individuals' responses. The corollary of this observation is that individuals
82 belonging to species with asynchronous responses could have similar (*i.e.* synchronous)
83 responses, which would therefore limit the stabilizing effect of species asynchrony in their
84 response. Interactions among individuals and spatial heterogeneity of environmental conditions
85 may be the source of the variability of individuals' response (Cescatti & Piutti 1998; Clark 2010;
86 de Mazancourt *et al.* 2013). As a result, asynchrony of response among species has been shown
87 to be higher between individuals occurring in the same neighbourhoods than within an entire
88 stand (Clark 2010).

89 Climatic fluctuations (Fritts 1976) and insect outbreaks (Morin *et al.* 2009; Sutton & C. Tardif
90 2009) are the two major drivers of the inter-annual growth variability of trees in North American
91 forests. As tree species typically possess different climatic niches (Rozas, Lamas & García-

González 2009; Drobyshev *et al.* 2013), and as insects are often host specific (Jactel & Brockerhoff 2007), an increase in tree diversity could help stabilize forest productivity. Recently some studies investigated the diversity-stability relationship in forest ecosystems in the face of extreme climatic events (Pretzsch 2005; Pretzsch, Schütze & Uhl 2013) and herbivory (Jactel & Brockerhoff 2007). They highlighted a stabilizing effect of diversity on the overall productivity of mixed stands. Furthermore, tree species asynchrony in their response to climatic fluctuations was found to be the single best predictor of stability of productivity in European forests (Jucker *et al.* 2014).

Here we used dendrochronological data (1) to determine whether tree species diversity stabilized productivity in temperate and boreal mixed woods of Eastern Canada and (2) to better understand the mechanisms underlying the stabilizing effect of diversity. We studied individual chronologies to take into account intraspecific variability of growth responses to environmental fluctuations. We first compared the asynchrony (i.e. levels of correlation) of individuals' growth within and between species. We then assessed the stability of radial increments, measured by the inverse of the coefficient of variation, for groups of individuals growing in the same neighbourhood (interacting together) and analysed differences in stability between monospecific and mixed groups. We hypothesized that (**H1**) diversity promoted stability of growth. We therefore expected the correlations of growth chronologies to be higher within species than between different species. We also expected stability to be higher when measured on the groups of trees belonging to different species than when measured on the groups of trees belonging to the same species. Finally, using multivariate analysis, we identified individuals' response to climatic fluctuations and insect outbreaks. We hypothesized that (**H2**) the asynchrony of response to environmental fluctuations of individuals belonging to different species contributed

115 to the stabilizing effect of diversity. We expected to obtain a significant correlation between
116 environmental factors and growth, which would imply that growth compensations among
117 individuals stemmed from the differences in their responses to environmental fluctuations. Our
118 results are consistent with previous studies suggesting that the asynchrony of species response to
119 environmental fluctuations is a mechanism driving the stabilizing effect of diversity. However,
120 we found that the intraspecific variability of response to environmental fluctuations did
121 modulated the stabilizing effect of the asynchrony of species response.

122

123

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), 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 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. Topography was generally flat at all sites, except for SUT, which laid 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 were 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 season, to a moister temperate climate, characterized by warmer temperatures and more precipitation. 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. Temperature was similar at the ABI site (-16.6°C; 17.5°C), but annual precipitation was on average higher (894.3 mm). 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 undisturbed by logging, for the exception of the BIC site, which was selectively harvested prior to being designated a Canadian 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 and mapped at each site. Mapping trees enabled calculating their relative distance for the neighbourhood analyses. We randomly chose 70 individuals per species 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). Some cores were removed from analyses because of poor dating quality, 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 database, 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 snowfalls, and monthly mean drought-code, which reflects water content of the deep compact organic layers (Girardin & Wotton 2009).

We detrended growth series in order to keep only the variability associated with the annual climatic variability and to remove temporal autocorrelation. This was done by first averaging growth series associated to a single tree to obtain single-tree chronologies. Then we standardized these single-tree chronologies using a 32-year cubic smoothing spline with a 50% frequency response (Speer 2010). We prewhitened the resulting series by autoregressive modelling to remove temporal autocorrelation (Cook 1987) 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 tent caterpillar (*Malacosoma disstria* Hubner.) and spruce budworm (*Choristoneura fumiferana* Clem.) occurred during the 1953-2013 period in Eastern Canada (Morin *et al.* 2009; Sutton & C. Tardif 2009), causing large reductions in tree diameter growth, suggesting that trees responded more to defoliation events rather than to climate during these periods. We thus, ran the analyses for two versions of chronologies, with and without insect outbreaks. To avoid insect-related signals, we removed periods during which forest tent

caterpillar outbreaks occurred from trembling aspen chronologies, and periods during which spruce budworm outbreaks occurred from white spruce and balsam fir chronologies.

We identified insect outbreaks in a two steps 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). Then, for each site, we identified the exact outbreak dates using pointer years: 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 defined the period of lower growth due to insect outbreaks using the negative and positive pointer years enclosing the periods of reduced growth observed in the master chronologies of host species.

Statistical analyses

We compared the asynchrony of individuals' growth within and between species to determine whether tree species diversity stabilized productivity. For that, we built a table of correlation describing the growth correlations between individuals occurring in the same neighbourhoods, both for individuals belonging to the same species and for individuals belonging to different species. Working with individuals rather than with species allowed taking into account intra-species growth variability. We calculated growth correlation both after removing insect outbreak periods from individual chronologies and with insect outbreak periods included. We expected that correlations of individuals' growth between species would be lower than within species, indicating that growth asynchrony is higher between species than within species.

Temporal stability (TS, Tilman 1999) estimated as the inverse of the coefficient of variation of the productivity in a community, has been commonly used to measure the stabilizing effect of

species diversity on productivity. However, measuring TS of the overall productivity of mixed stands may not be an appropriate way to estimate the stabilizing effect of diversity, as TS strongly depends on the weight of each species in the overall productivity. Species having unequal proportions in a stand and/or different growth rates may not contribute equally to the overall productivity, which may result in low growth compensations between species and thus in a weak stabilizing effect even for species having asynchronous growth. To address this issue we calculated TS using individual-level radial growth chronologies. More precisely, we averaged single tree raw chronologies for each pair of trees occurring in the same neighbourhood (defined as an area within 20 m from a focal tree) following the approach of Clark (2010), and calculated TS on the resulting chronology. Using individual-level chronologies rather than species-level chronologies eliminated the need to account for differences in species proportions and enabled taking into account individuals' growth variability in the calculation of TS. Averaging individuals' chronologies minimized the effect of the difference in individuals' growth rates on the measure of TS while it maintained the effect of the variability of individuals' growth. Furthermore, focusing on radial growth rather than on measures of productivity such as basal area increment minimized differences in growth rates between individuals due to differences in size.

We compared the distributions of TS 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 TS. To disentangle the effect of species mixture from the effect of sites and species, we built the following linear model using dummy variables:

$$(1) \quad Y = \alpha + MIX + SITE + SP + \varepsilon$$

where Y was TS; α - the reference mean; MIX - the effect of mixture on the reference mean,

indicating whether the measures of TS 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. We performed this analysis both after removing insect outbreak periods from individual chronologies and with insect outbreak periods included. We expected that distributions of TS values obtained for pairwise individuals belonging to the different species would be higher than those obtained for individuals belonging to the same species, indicating a stabilizing effect of mixture on growth.

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 two folds. 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 analysis 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 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.

262 We ran redundancy analysis (RDA) to identify individuals' response to environmental
263 fluctuations and to determine whether the asynchrony of response of individuals belonging to
264 different species contributed to the stabilizing effect of diversity. RDA runs a set of independent
265 multivariate regressions, similar to response functions, but then performs a constrained
266 ordination to position the individuals in a multidimensional space of environmental factors
267 (Legendre & Legendre 2012). The distance between individuals in the ordination indicated the
268 asynchrony in their response to environmental variability among them. Our (**H2**) hypothesis was
269 therefore contingent upon obtaining significant RDAs, indicating that environmental fluctuations
270 controlled the variability of individuals' growth. Significant RDAs would therefore demonstrate
271 that the asynchrony of individuals' response to environmental fluctuations enabled growth
272 compensations among individuals and thus contributed to the stabilizing effect of species
273 diversity. We ran RDAs on two sets of chronologies, without and with the growth variability
274 caused by insect outbreaks. In the first case, we aimed to consider exclusively the effects of
275 climatic fluctuations on growth. In the second case we aimed to identify tree's response
276 simultaneously to both factors. For these analyses we added a binary variable indicating the
277 presence of each insect as additional explanatory variable. The climatic variables used in RDAs
278 were those previously identified in response function analysis. Detrended individual series were
279 considered as response variables, with each annual growth value considered as an observation.
280 RDAs were performed for each site including only years for which all species had growth data
281 for at least 30 individuals. Significance of RDAs was tested with the F-test of the canonical
282 relationships between growth index values and environmental variables. The explained variance
283 values associated with each RDA provided information on the variability of individuals'
284 response to environmental fluctuations. We computed the RDAs with the R package *rdaTest*
285 (Legendre & Durand 2012).

Results

Correlations between individuals' chronologies occurring in the same neighbourhood were generally higher within species than between species (Table 2). However, in some species individuals showed high correlations with those of other species. For instance, the average correlation between white spruce individuals was 0.22 (SD = 0.40), while the average correlation between white spruce and balsam fir was 0.21 (SD = 0.41; on the ABI site, when insect outbreak periods were included in the individual chronologies). Insect outbreaks increased growth asynchrony among species by increasing within-species correlations in host species, reducing the variability of within species correlations for all species, and reducing correlations among trees belonging to species sensitive to different insects (balsam fir/trembling aspen, white spruce/trembling aspen).

TS values (Fig. 2) obtained for pairs of individuals belonging to different species were higher than those obtained for pairs of individuals belonging to the same species, indicating a stabilizing effect of species mixture (i.e. diversity) on growth. Indeed, the parameter associated with the MIX variable in model (1) was positive and significant (Table 3). The stabilizing effect was higher when signal from insect outbreaks was preserved in the chronologies (MIX = 0.80) as compared to chronologies with no insect outbreak signal (MIX = 0.51). Both versions of the model (ran with and without insect outbreaks) had low values of R^2 : 0.16 and 0.17, respectively.

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 4). 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 more pronounced global effect of climatic conditions of summer months of the previous growing season on species growth than all 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. 3). Indeed, all RDAs were significant except RDAs performed on chronologies free from insect outbreak signals for the D1823 and D1847 sites (Fig. 3a). 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, indicating that species could have close responses to environmental fluctuations. Values of explained variance for RDAs ranged from 8.6 to 25.6%, indicating that the variability of individuals' response to environmental fluctuations was high.

Discussion

Our results showed that diversity stabilized growth in forest ecosystems, supporting **H1** hypothesis. We found that the asynchrony of response to environmental fluctuations of trees belonging to different species was contributing to this effect, supporting **H2** hypothesis. We nonetheless found that the variability of individuals' response to environmental fluctuations was high, even though species responses were closely similar (Fig. 3), which demonstrates the interest of working at the individual-level rather than at the species-level. These results were persistent regardless if 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 in the absence of 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. This was due to the fact that the insect species we considered were host specific (spruce budworm influencing balsam fir and white spruce growth, and forest tent caterpillar influencing trembling aspen growth). Tree species being affected at different time, their growth asynchrony increased which amplified the stabilizing effect of diversity. This stabilizing effect of diversity due to species differences in

their sensitivity to insects could be even stronger as outbreak-related mortality tend to decrease (both for host and non-host species) with the pre-outbreak abundance of host species (Bouchard, Kneeshaw & Bergeron 2005).

We showed that the variability of individuals' response was high. Interactions between individuals and spatial heterogeneity of environmental conditions could influence variability by modulating individuals' response to environmental fluctuations (Cescatti & Piutti 1998; Clark 2010; de Mazancourt *et al.* 2013). As a result, effect of species diversity on productivity metrics may be more difficult to assess. This outcome is complementary with 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. The high variability of individuals' response explained the high variability of growth correlations among individuals we observed within and between species, and thereby explain the low R^2 values associated to both versions of model (1). The highly variable growth correlations suggested that some individuals could have synchronous growth even if they belonged to species having asynchronous growth on average, which would make the effect of tree species mixture on TS highly variable. This outcome was consistent with Clark's (2010) observations who found similarly high intraspecific variability.

Our work highlights the value of working in forest communities to study the mechanisms driving the diversity-stability relationship. This is especially valuable as it gives us access to the individual-level where growth compensation actually occurs, while it eliminates 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'

375 belonging to different species contributed to this stabilizing effect. Mechanisms at the origin of
376 the variability of individuals' response, such as interactions between individuals and spatial
377 heterogeneity of environmental conditions, could therefore play a crucial role in the stabilizing
378 effect of diversity.

379

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391 Data accessibility

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

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

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site	A. balsamea	P. glauca	T. occidentalis	A. rubrum	A. saccharum	B. alleghaniensis	P. tremuloïdes
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)	-

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Table 2: Average radial growth correlations between individuals occurring in the same neighbourhoods. Standard deviations are shown in brackets. Row names and columns names correspond to species initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloïdes*), To (*T. occidentalis*). Values in diagonals correspond to correlations between individuals belonging to the same species, other values correspond to correlations between individuals belonging to different species. Correlations were calculated both after removing insect outbreak periods from individual chronologies (a) and with insect outbreak periods included (b).

512

(a) Without insect outbreaks

(b) With insect outbreaks

		Ab	Pg	Pt	To			Ab	Pg	Pt	To
D1823	Ab	0.23 (0.44)				D1823	Ab	0.47 (0.32)			
	Pg	0.09 (0.41)	0.45 (0.29)				Pg	0.2 (0.34)	0.41 (0.26)		
	Pt	-0.04 (0.4)	0.18 (0.32)	0.31 (0.35)			Pt	-0.24 (0.29)	0.03 (0.29)	0.47 (0.23)	
	To	0.2 (0.36)	0.3 (0.29)	0.13 (0.35)	0.33 (0.32)		To	0.12 (0.33)	0.25 (0.26)	0.09 (0.28)	0.28 (0.29)
D1847	Ab	0.24 (0.45)				D1847	Ab	0.36 (0.38)			
	Pg	0.2 (0.45)	0.53 (0.3)				Pg	0.29 (0.37)	0.51 (0.28)		
	Pt	0 (0.35)	-0.05 (0.35)	0.24 (0.31)			Pt	-0.04 (0.32)	-0.07 (0.28)	0.37 (0.24)	
	To	0.28 (0.37)	0.25 (0.39)	-0.02 (0.35)	0.39 (0.29)		To	0.33 (0.32)	0.28 (0.35)	-0.05 (0.28)	0.41 (0.25)
ABI	Ab	0.45 (0.4)				ABI	Ab	0.48 (0.35)			
	Ar	0.04 (0.47)	0.16 (0.39)				Ar	0.07 (0.44)	0.15 (0.38)		
	As	-0.27 (0.47)	0.2 (0.41)	0.42 (0.34)			As	-0.25 (0.41)	0.18 (0.4)	0.4 (0.32)	
	Pg	0.16 (0.42)	0.13 (0.35)	-0.02 (0.44)	0.15 (0.45)		Pg	0.21 (0.41)	0.12 (0.32)	0 (0.41)	0.22 (0.4)
	To	0.07 (0.39)	0.03 (0.36)	-0.03 (0.3)	0.12 (0.33)		To	0.07 (0.35)	0.04 (0.33)	-0.04 (0.28)	0.12 (0.29)
					0.25 (0.28)						0.25 (0.26)
BIC	Ab	0.25 (0.39)				BIC	Ab	0.29 (0.39)			
	Ar	0.14 (0.39)	0.21 (0.34)				Ar	0.11 (0.39)	0.22 (0.33)		
	As	0.19 (0.36)	0.24 (0.35)	0.26 (0.32)			As	0.11 (0.36)	0.24 (0.33)	0.27 (0.3)	
	Pt	0.2 (0.32)	0.15 (0.29)	0.13 (0.32)	0.34 (0.27)		Pt	0.03 (0.29)	0.07 (0.26)	0.1 (0.25)	0.46 (0.23)
SUT	Ab	0.35 (0.4)				SUT	Ab	0.43 (0.36)			
	As	-0.02 (0.4)	0.24 (0.37)				As	-0.05 (0.41)	0.24 (0.35)		
	Ba	-0.07 (0.44)	0.2 (0.43)	0.23 (0.38)			Ba	-0.06 (0.46)	0.17 (0.41)	0.2 (0.39)	

Table 3: Summary of the linear model of temporal stability (TS) as a function of mixture, controlling for species composition. 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. tremuloïdes*).

Reference mean and dummy variables	(a) Without insect outbreaks ¹		(b) With insect outbreaks ¹	
α (reference mean)	3.04444	***	2.84786	***
MIX	0.51658	***	0.80483	***
SITE _{BIC}	0.09760	***	0.07760	**
SITE _{D1823}	0.06859	*	-0.12307	***
SITE _{D1847}	0.25295	***	0.03145	ns
SITE _{SUT}	-0.49506	***	-0.42845	***
SP _{Ab}	-0.06347	*	-0.55131	***
SP _{Ar}	-0.40765	***	-0.69920	***
SP _{As}	-0.84191	***	-1.00762	***
SP _{Ba}	-0.31777	***	-0.50529	***
SP _{Pg}	-0.62928	***	-0.69799	***
SP _{Pt}	-0.31697	***	-0.73663	***
Adjusted R ²	0.1734		0.1644	
p-value	< 2.2e-16		< 2.2e-16	

Table 4: 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*).

Site	Sp	previous year								current year							
		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+						
BIC	As													T-	S-	DC-P+	DC-
	Ab	GSL-			T- S+												
	Pt										S-				P+	DC-	
	Ar										S-				P+	DC-	
SUT	As														P+	DC-	
	Ba					P+						S+					

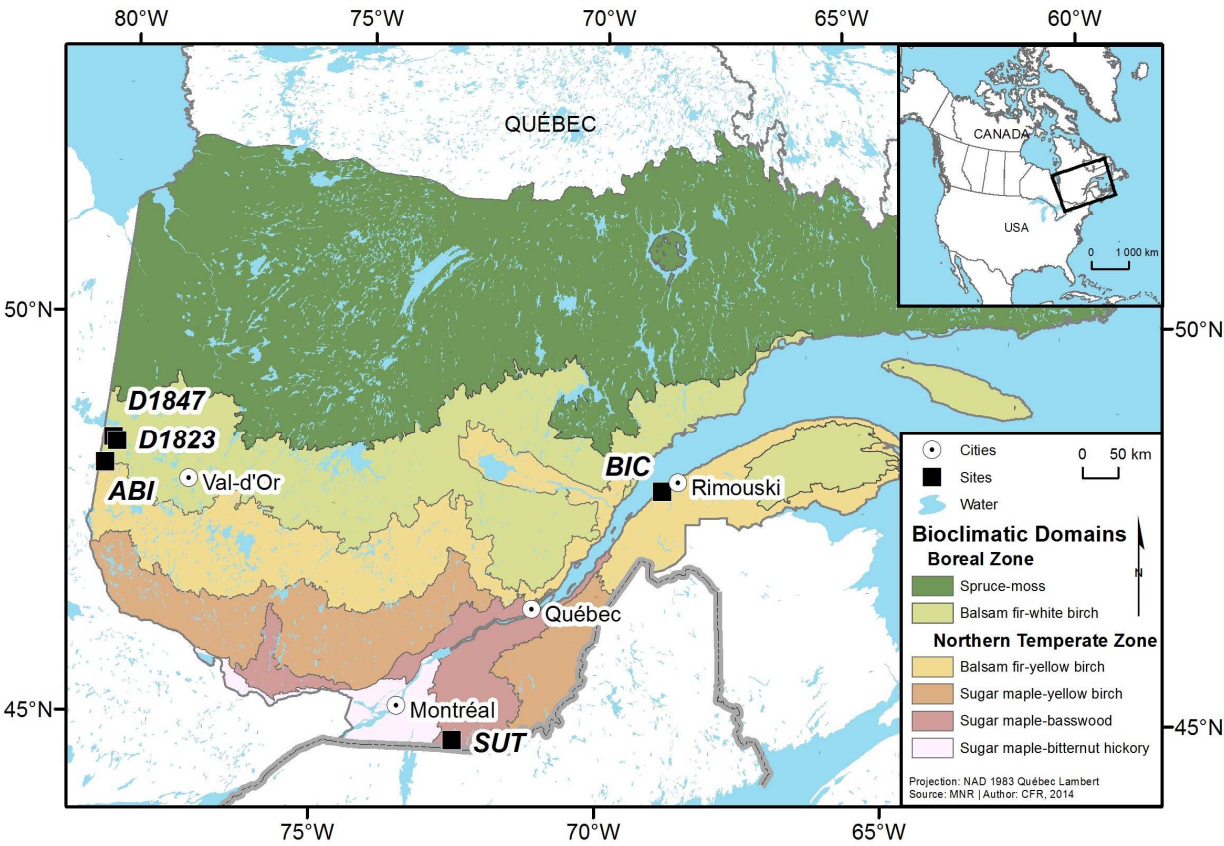


Fig. 1. Study sites and bioclimatic domains of Québec.

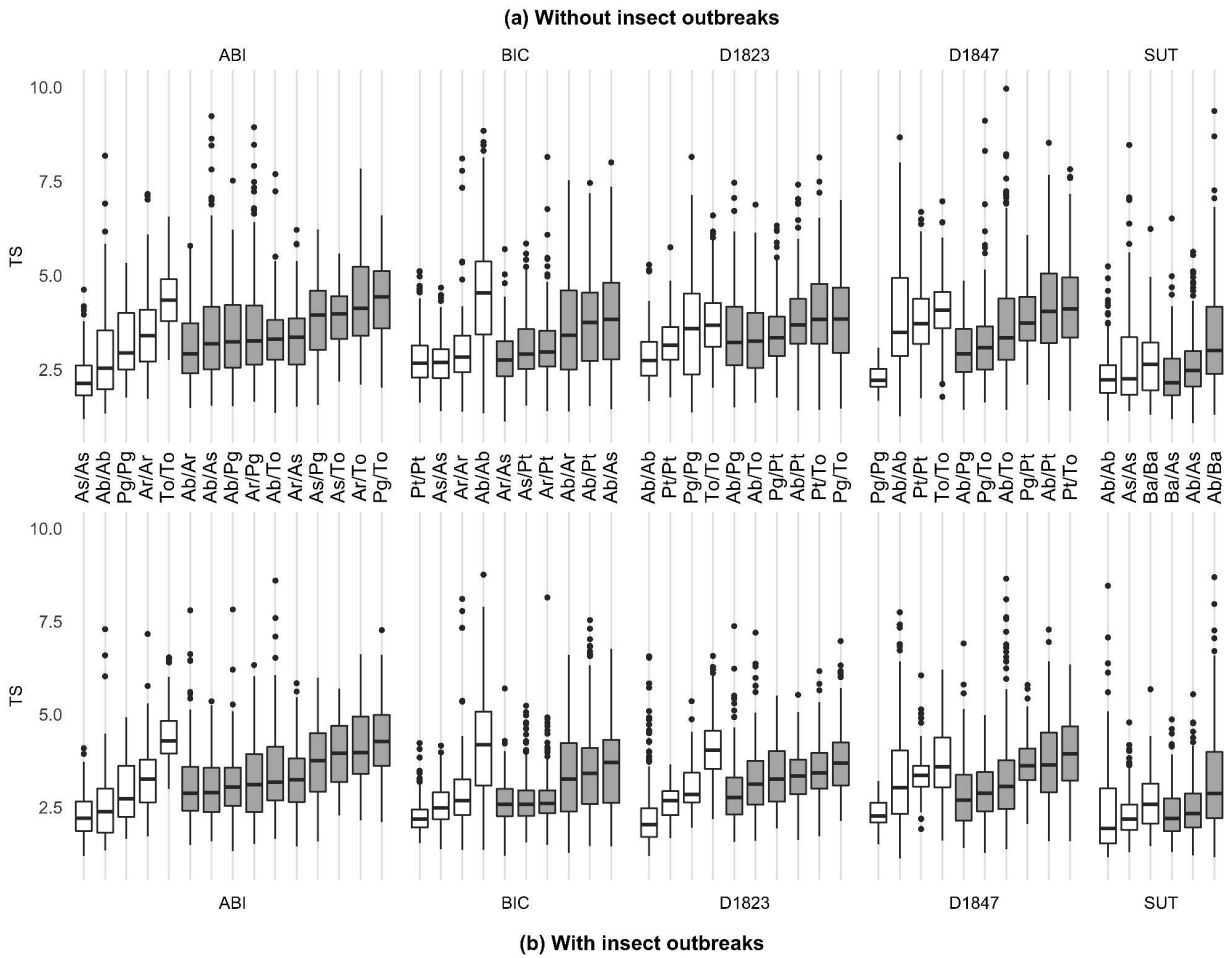


Fig. 2. Site and species-specific distributions of TS values measured on pairwise individuals occurring in the same neighbourhoods. White boxes refer to distributions of TS values measured on individuals belonging to the same species, while grey boxes refer to distributions of TS values measured on individuals 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 belonged the individuals 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*).

547



548 **Fig. 3.** Site-specific redundancy analysis (RDA) performed with individual standardized
549 chronologies, climatic variables and binary variables indicating the presence of insects. Points
550 correspond to individual chronologies. Species-specific ellipses containing 95% of species
551 individuals are shown and identified with species initials: Ab (*A. balsamea*), Ar (*A. rubrum*), As
552 (*A. saccharum*), Ba (*B. alleghaniensis*), Pg (*P. glauca*), Pt (*P. tremuloïdes*), To (*T. occidentalis*).
553 Climate variables and binary variables indicating the presence of insects are represented by black
554 arrows: drought code (DC), temperature (T), precipitation (P), snowfall (S), growth season
555 length (GSL), forest tent caterpillar (FTC), spruce budworm (SBW). The numbers following the
556 variables initials indicate the number of the month associated to the variable. Negative values
557 refer to a month of the previous year. RDAs were performed both after removing insect outbreak
558 periods from individual chronologies (a) and with insect outbreak periods included (b).
559