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Relationships between radial growth rates and lifespan within North American tree species[1]

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Abstract: We conducted a meta-analysis of tree-ring data to quantify relationships between growth and lifespan in 4 North American tree species: *Tsuga canadensis*, *Quercus alba, Pinus ponderosa,* and *Pseudotsuga menziesii*. Data sets were compiled from across the range of each species and included a total of 14 341 measured time series. For each species we calculated the age at which each tree was sampled and pooled all trees into 50-y bins. Within each of these 50-y bins, we calculated mean ring width and mean basal area increment in 50-y intervals according to cambial age. Thus, ring widths formed during the same time period in the trees' life stage could be compared across trees sampled at increasing ages. In all 4 species the longest-lived trees experienced slower growth rates than trees sampled at relatively young ages. Furthermore, long-lived trees with slow growth rates appear to mix with shorter-lived, fast-growing trees in the same forests. Such a relationship between growth and lifespan within species may be an important component of biodiversity that holds implications for old-growth forest development and long-term management.
Keywords: dendrochronology, growth rate, longevity, old-growth forest.

Résumé : Nous avons effecté une méta-analyse de données de cernes de croissance d'arbres pour évaluer quantitativement les rapports entre la croissance et la durée de vie chez 4 espèces d'arbres d'Amérique du Nord : *Tsuga canadensis*, *Quercus alba*, *Pinus ponderosa* et *Pseudotsuga menziesii*. Les données ont été compilées dans l'ensemble de la distribution de chaque espèce et incluent 14 341 séries temporelles mesurées. Pour chaque espèce, nous avons calculé l'âge auquel chaque arbre a été échantillonné et rassemblé tous les arbres dans des groupes de 50 ans. Dans chacun de ces groupes de 50 ans, nous avons calculé la largeur moyenne des cernes et l'incrément moyen de l'aire basale par intervalles de 50 ans d'âge cambial. Ainsi, les largeurs des cernes formés durant la même période du stade de vie de l'arbre pouvaient être comparées entre les arbres échantillonnés à des âges de plus en plus vieux. Chez les 4 espèces, les arbres ayant les durées de vie les plus longues avaient des taux de croissance plus lents que ceux échantillonnés à des âges relativement jeunes. De plus, les arbres ayant une grande longévité et des taux de croissance lents semblaient se mélanger dans les mêmes forêts avec des arbres ayant une plus courte longévité et une croissance rapide. Un tel rapport entre la croissance et la durée de la vie au sein des espèces peut être une composante importante de la biodiversité ayant des implications pour le développement de forêts anciennes et leur gestion à long terme.
Mots-clés : dendrochronologie, forêt ancienne, longévité, taux de croissance.

Nomenclature: USDA, 2008.

Introduction

The tendency of slow-growing trees to live longer than their faster growing counterparts has been widely and most often informally observed across a range of species and communities. Interspecific differences are relatively well documented: long-lived, late successional species typically grow more slowly, reach sexual maturity later in life, invest more heavily in structural support and defensive compounds, and maintain lower rates of photosynthesis and respiration than shorter-lived, early successional species (Bazzaz, 1979; Loehle, 1988). These trends are also reflected in tree-ring data, which show that long-lived species maintain slower radial growth rates than shorter-lived species on the same sites. For example, the longest-lived broadleaved species in eastern North America (Sperduto *et al.,* 2000; Eastern OLDLIST, 2007), black gum (*Nyssa sylvatica*), produced significantly smaller growth increment widths than the shade-intolerant yellow poplar (*Liriodendron tulipifera*) or loblolly pine (*Pinus taeda*) in Virginia forests (Orwig & Abrams, 1994; Abrams & Black, 2000). Likewise, radial growth rates of the long-lived, late-successional eastern hemlock (*Tsuga canadensis*) were consistently slower than those of the more exploitive and shorter-lived eastern white pine (*Pinus strobus*) (Abrams & Orwig, 1996; Abrams *et al.,* 2000).

In addition to differences among species, evidence suggests a relationship between growth rates and lifespan within species. Dendrochronologists have long recognized that stunted, slow-growing trees are among the oldest, and for decades they have sought out such individuals for environmental reconstructions. Characteristics such as stem taper, stunted growth, thick lateral branches, a limited crown size or partial dieback, and spiral grain provide often

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much better indicators of old age than a large size (Duvick & Blasing, 1983; Stahle & Chaney, 1994). Over 50 y ago Edmund Schulman (1954) was the first to formally note the linkage between longevity and slow growth, which he observed in conifers occupying harsh sites limited by moisture, temperature, or a combination of both. A growing body of evidence supports Schulman's hypothesis, linking longevity with small stature and consistently low radial growth rates from early in life (Melvin, 2004; Pederson, 2005). Perhaps the most dramatic example quantified to date is that of eastern white cedar (*Thuja occidentalis*), which typically lives approximately 80 y, yet can attain extraordinary ages of more than 1000 y when growing very slowly on cliffs of the Niagara escarpment (Larson, 2001).

In this study we use tree-ring data from the International Tree-Ring Data Bank (ITRDB) and a smaller collection of new tree-ring data to more broadly investigate intraspecific relationships between growth rate and lifespan. Our analysis includes the North American tree species *Tsuga canadensis*, *Quercus alba, Pinus ponderosa,* and *Pseudotsuga menziesii*, allowing us to evaluate deciduous and coniferous species, eastern and western North American species, and early-, mid-, and late-successional species. Within each species, our objectives were to determine whether long-lived and short-lived trees follow different growth trajectories, *i*) across the full data set, which spans a large portion of each species' geographic range, and *ii*) within separate ITRDB collections, sampled at much finer spatial scales. If growth and lifespan relationships do exist, they could have important implications for forest pattern, process, and biodiversity.

Methods

Growth increment data were downloaded from the International Tree Ring Data Bank (http://www.ncdc.noaa.gov/paleo/treering.html) and imported into SAS 9.1 (Carey, North Carolina, USA). Cambial age of each growth increment and tree age at the time of sampling were estimated by counting from the first to the last growth increment in the measurement time series from coring height. Radius was then estimated by summing the growth increments of all previous years, while basal area increment (BAI) was calculated as the difference in approximate tree-ring area between consecutive years. Ages at which trees were sampled were pooled into 50-y classes (trees sampled when they were 1–49 y in age, 50–99 y, 100–149 y, etc.). Within each of these 50-y classes, we calculated mean ring width and mean BAI in 50-y intervals of growth according to cambial age (means during the first 50 y of growth, 50–99 y, 100–149 y, etc.). Thus, ring widths formed during the same ranges of cambial age could be compared across trees sampled at increasing ages. Within each cambial age class, significant differences among trees sampled at increasing ages were detected with ANOVA, using each measurement time series as a replicate. In other words, BAI or ring width was averaged within each cambial age class within each measurement time series prior to the ANOVA analysis. For a different perspective on relationships between growth rates and age at the time of sampling, we plotted mean ring width, estimated total age, and estimated total radius for each measurement time series. Given that the data were parsed into 50-y classes, precise dating of each ring width was not necessary, and we did not verify crossdating for the ITRDB data, though data sets were screened for outliers more than 3 standard deviations from the mean. In most cases, outliers were caused when data did not exactly conform to the ITRDB measurements format, which affected import into SAS 9.1. In the vast majority of cases, these formatting errors were easily corrected.

At a finer scale, we compared growth rates of trees sampled when they were relatively "young" *versus* those sampled when they were relatively "old" within each ITRDB collection. The definition of "young" and "old" trees differed among species (Table I). For example, in *Tsuga canadensis* we considered any tree sampled at an age less than 250 y to be "young" and any tree sampled at an age greater than 350 y to be "old" (Table I). These thresholds were chosen to maximize differences between "young" and "old" groups and still provide adequate sample sizes. Next, *t*-tests assuming unequal variance were conducted between BAI in the "young" and "old" groups within each 50-y cambial age class, using each measurement time series as a replicate. Finally, for each 50-y cambial age class, we subtracted the ITRDB collection average BAI for all "old" trees from the ITRDB collection average BAI of all "young" trees (positive values indicate faster growth of trees sampled when "young"). In total, 12, 21, 12, and 15 ITRDB collections were analyzed for *Tsuga canadensis*, *Quercus alba*, *Pinus ponderosa*, and *Pseudotsuga menziesii*, respectively. However, the sample depth was not constant and occasionally dropped in the oldest cambial age classes. This was due to the fact that in some ITRDB collections no trees were sampled to represent the older age classes. For example, in *Quercus alba* only 17 ITRDB collections had trees that were sampled between 150 and 199 y in age, while all 21 ITRDB collections had trees that were sampled when less than 150 y in age. Consequently, the cambial age class of 150–199 y in age has only 17 comparisons as opposed to the 21 comparisons in all other cambial age classes.

Results

In total we included 460 ITRDB collections containing 14 341 measurement time series in this study (Table I). In all 4 species, mean ring width within each cambial age class generally decreases as the age at which a tree is sampled increases (Figure 1). This is particularly true early in life (the first 50-y age class), when the span in mean ring width is most pronounced, with a consistent range of approximately 1.5 mm in all 4 species (Figure 1). However, highly significant ($P < 0.001$) differences occur for at least the first 200 to 300 y of life (Figure 1). In comparison to mean ring width, mean BAI better separates the growth trajectories of trees sampled at various ages, allowing for the display of 95% confidence intervals (Figure 2). Once again in all species mean growth declines incrementally as the age at time of sampling increases. Overall separation in growth rates is generally most pronounced between 100 and 200 y in cambial age (Figure 2).

As expected, maximum values of total tree radius tend to increase with age at the time of sampling (Figure 3).

However, the mean value of total tree radius eventually plateaus after approximately 200 y, 350 y, 500 y, and 350 y of age in *Tsuga canadensis*, *Quercus alba, Pinus ponderosa*, and *Pseudotsuga menziesii,* respectively (Figure 3). In *Pinus ponderosa*, the mean of total radius even tends to decrease after approximately 550 y. When the full range of data is considered, trees with the largest total radii are not necessarily the oldest. The only exception is *Tsuga canadensis*, in which a rather large tree was sampled at approximately 550 y of age (Figure 3). But for *Quercus alba*, *Pinus ponderosa*, and *Pseudotsuga menziesii* the largest total radii occur primarily between 250 and 350 y, 250 and 500 y, and 150 and 500 y, respectively (Figure 3). Indeed, trees sampled at ages greater than 600 y and even at ages nearing 1000 y are not the larg-

TABLE I. Tree-ring collections downloaded from the International Tree Ring Data Bank. Also shown are criteria for trees sampled when "young" and trees sampled when "old" as used in comparisons of growth rates within ITRDB collections.

Species	Collections	Measurement time series	Growth increments	"Young" group (y)	"Old" group (y)
Pinus ponderosa	179	4872	1 141 890	< 300	> 550
Pseudotsuga menziesii	166	5199	1 393 709	< 350	> 600
Quercus alba	66	2789	521 983	< 200	> 300
Tsuga canadensis	49	1481	347 003	< 250	> 350

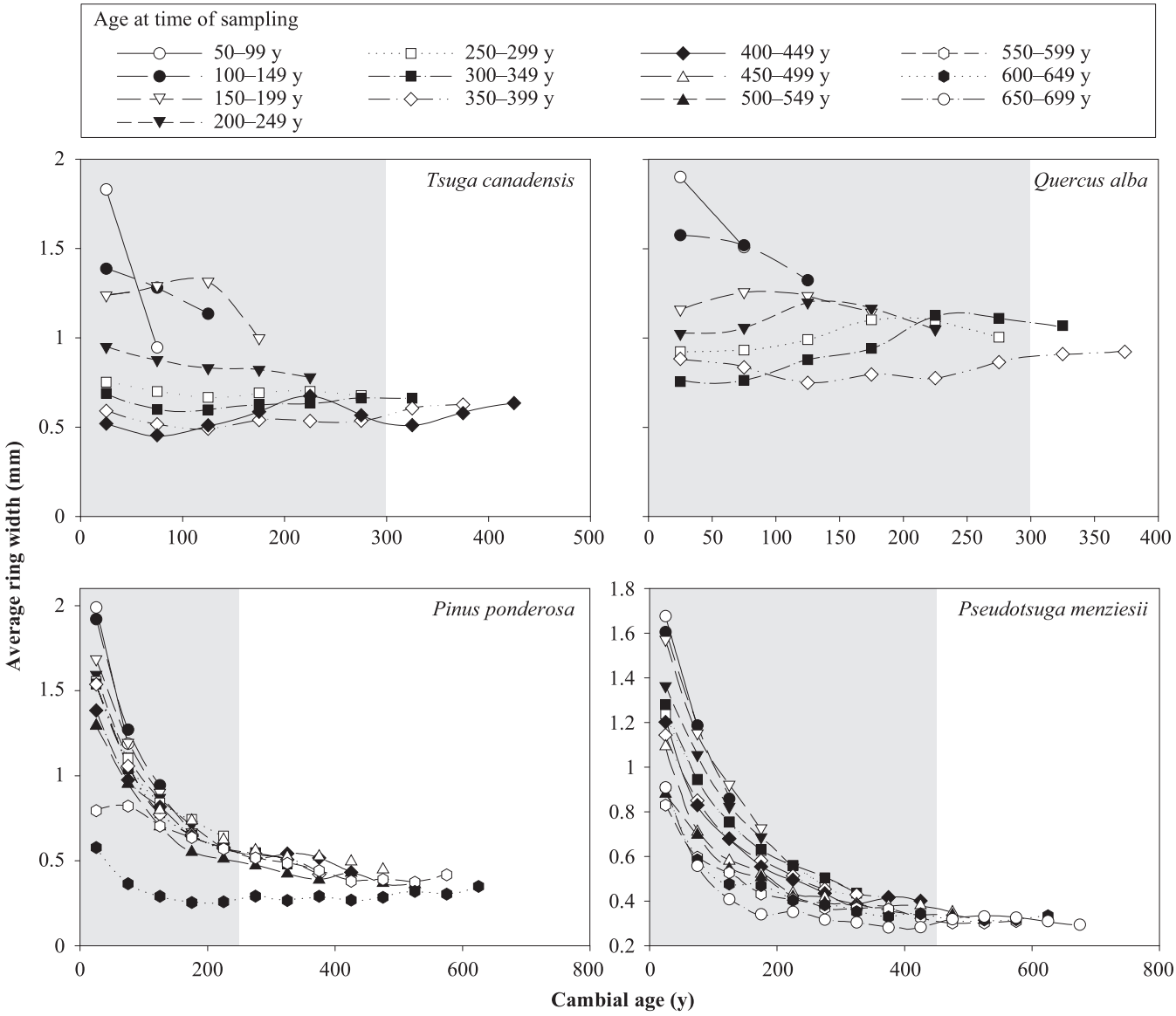

FIGURE 1. Mean annual ring width for trees grouped with respect to the age at which they were sampled. Within each group, mean ring width was calculated across 50-y intervals (cambial age classes) beginning with the first year of recorded growth. Only those groups with more than 5 measurement time series are included. Cambial age classes in which significant ($P < 0.001$) differences in ring width occur are shaded.

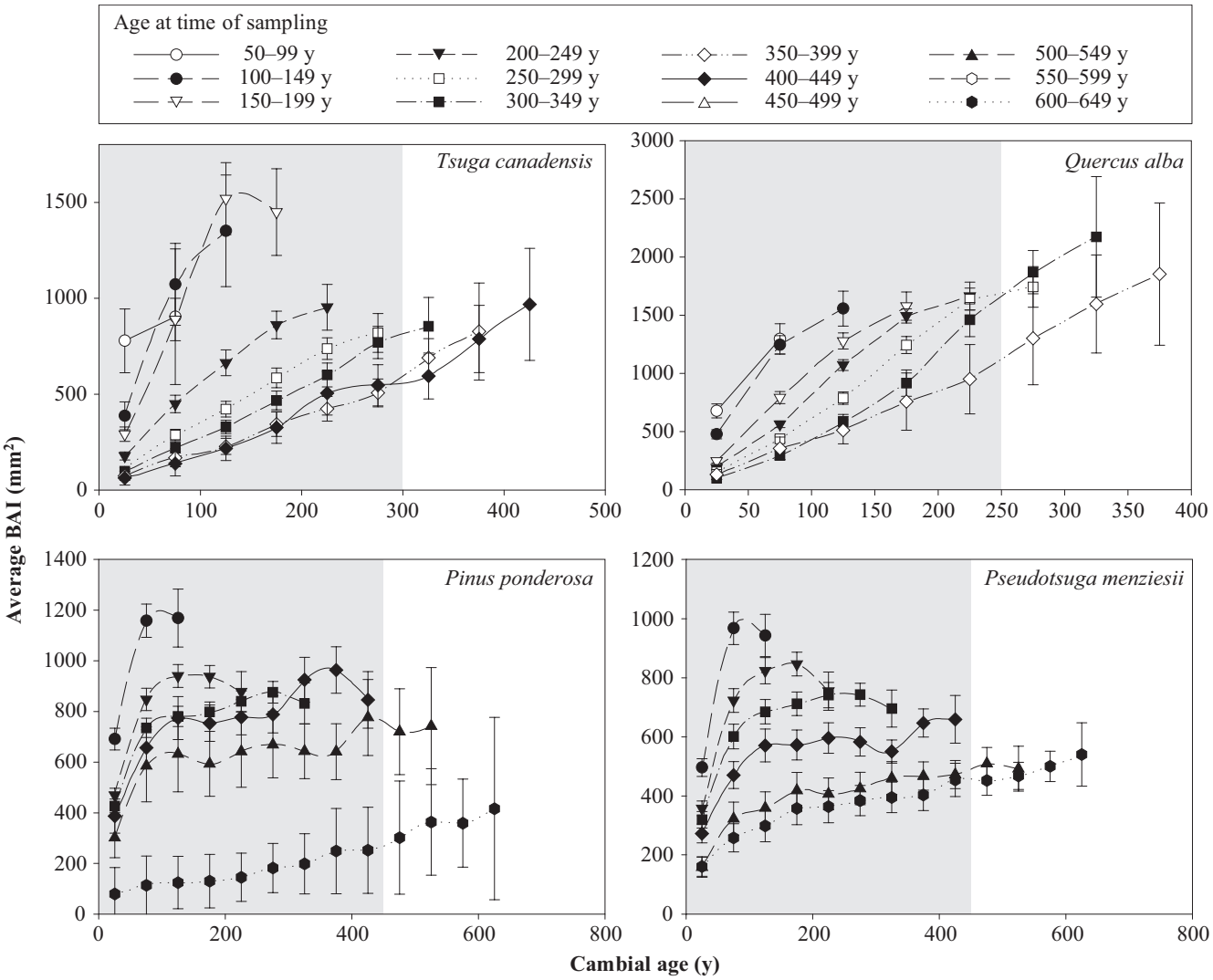

FIGURE 2. Mean annual basal area increment (BAI) for trees grouped with respect to the age at which they were sampled. Within each group, mean BAI and 95% confidence intervals were calculated across 50-y intervals (cambial age classes) beginning with the first year of recorded growth. For clarity, only alternate classes are shown for *Pinus ponderosa* and *Pseudotsuga menziesii*. Cambial age classes in which significant ($P < 0.001$) differences in BAI occur are shaded.

est in *Pinus ponderosa* and *Pseudotsuga menziesii*. Also, minimum values for total radius tend to increase with age in all species, such that the smallest trees only occur in trees sampled when quite young, suggesting lower size limits for a given age class (Figure 3).

T-tests show significant differences between the mean BAI of trees sampled when "young" and trees sampled when "old" within ITRDB collections (Table I; Figure 4). Positive values indicate that trees sampled when "young" have a higher mean BAI for the given cambial age class. In *Tsuga canadensis* all significant differences are positive, indicating that trees in the "old" group grow more slowly than their "young" counterparts within ITRDB collections. An even stronger trend is evident for *Quercus alba*, in which every difference between "young" and "old" groups is positive (Figure 4). With the exception of one ITRDB collection in the first 4 cambial age classes and 2 ITRDB collections in the last cambial age class, "old" trees had lower growth rates relative to "young" trees within *Pinus ponderosa* collections (Figure 4). Although many *Pseudotsuga menziesii* ITRDB collections have minimal differences between "young" and "old" classes, all significant differences are consistently above zero by a cambial age of 100, suggesting that "old" trees tend to have slower growth rates within ITRBD collections for this species as well (Figure 4).

Discussion

We provide evidence that within species, long-lived trees show uniquely slower growth trajectories in comparison to trees sampled at younger ages. There are, however, several limitations in the data that could affect the analysis and must be considered. The first of these is that we don't know the specific objectives or sampling strategy used when each collection was taken, although most trees were sampled as overstory trees and for their potential longevity and a high sensitivity to drought or temperature (Meko *et al.,* 1993; Grissino-Mayer & Fritts, 1997). Each ITRDB collection includes location to within a minute of latitude

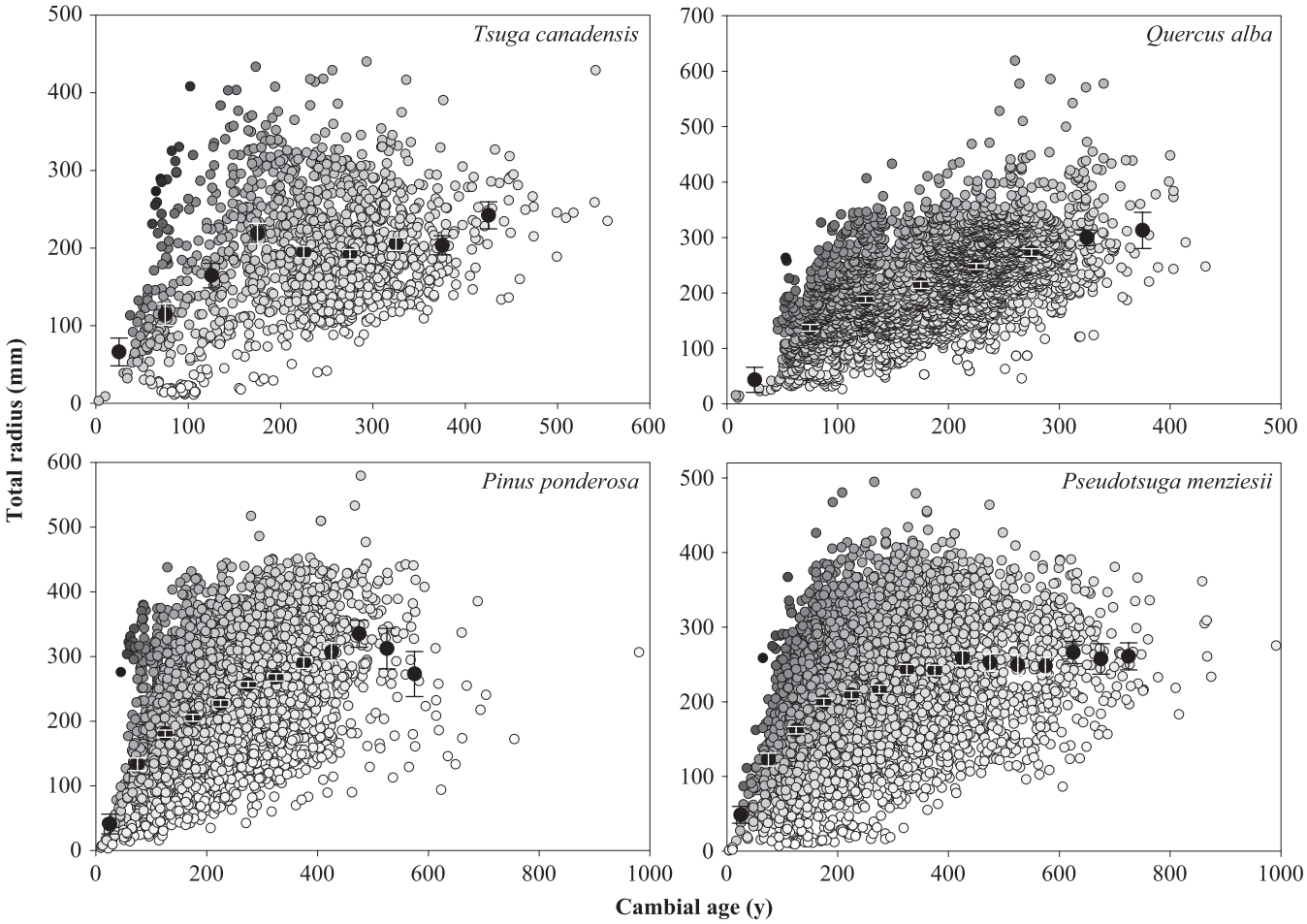

FIGURE 3. Total radius and total age of each measurement time series. Data points are shaded with respect to mean growth increment from small (white) to large (black). Mean values and 95% confidence intervals are shown for each 50-y age class.

and longitude, and most report an elevation, but the exact site conditions or area sampled is often not described. The second, and perhaps more important, limitation is that the majority of these trees were sampled while they were still living (Melvin, 2004). Under these conditions, we lose ability to isolate trees that will ultimately have a short lifespan, particularly among trees sampled at relatively young ages for a given species (*i.e.,* sampled at 100 or 150 y of age). Some of these trees may die in the very near future, while others may live for several more centuries. As trees are sampled at greater ages, the data will represent an increasing percentage of long-lived trees to the point where the oldest sampled age class will include only the longest-lived individuals. Despite the mixing of ultimately short-lived individuals and long-lived individuals among trees sampled at early ages, growth trajectories consistently separate as age at the time of sampling increases. If trees that ultimately die young could be isolated, we hypothesize that separations in growth trajectories would likely become more pronounced.

Another major limitation is that pith was probably not reached on the majority of samples, and at least some, particularly from the western US, may have been sampled as woody debris long after the outer rings decomposed. In addition, trees in this data set were probably not sampled at the base, but at breast height or elsewhere on the bole. All these sources of error would contribute to underageing. Our use of 50-y classes should mitigate at least some of this error, yet extreme underageing will have the effect of falsely placing older trees into younger age classes, thereby adding more noise to the data set. The slow-growing long-lived trees that were underaged would be mixed with their faster-growing, shorter-lived counterparts, diminishing the signal strength of the results. If pith is missed, the earliest growth increments would be truncated, potentially lowering our estimate of mean growth rate early in life if a geometrically- (*i.e.,* age-) related growth decline is assumed. If pith is missed by a consistent number of years across all sampled trees, the effect should be a consistent underestimation of growth rate across all classes. Although this would add error to the analysis, the relative differences among classes should be preserved. Considering borer limitations, rot, and the general difficulty of reaching the centre of older, larger trees, a potentially more problematic and realistic scenario is that pith is missed by a greater number of years in trees sampled at an old age. In this case, a greater number of years will be truncated in the oldest sampled trees, erroneously lowering growth rates early in life (assuming geometrically-related growth declines) and falsely accentuating the differences between

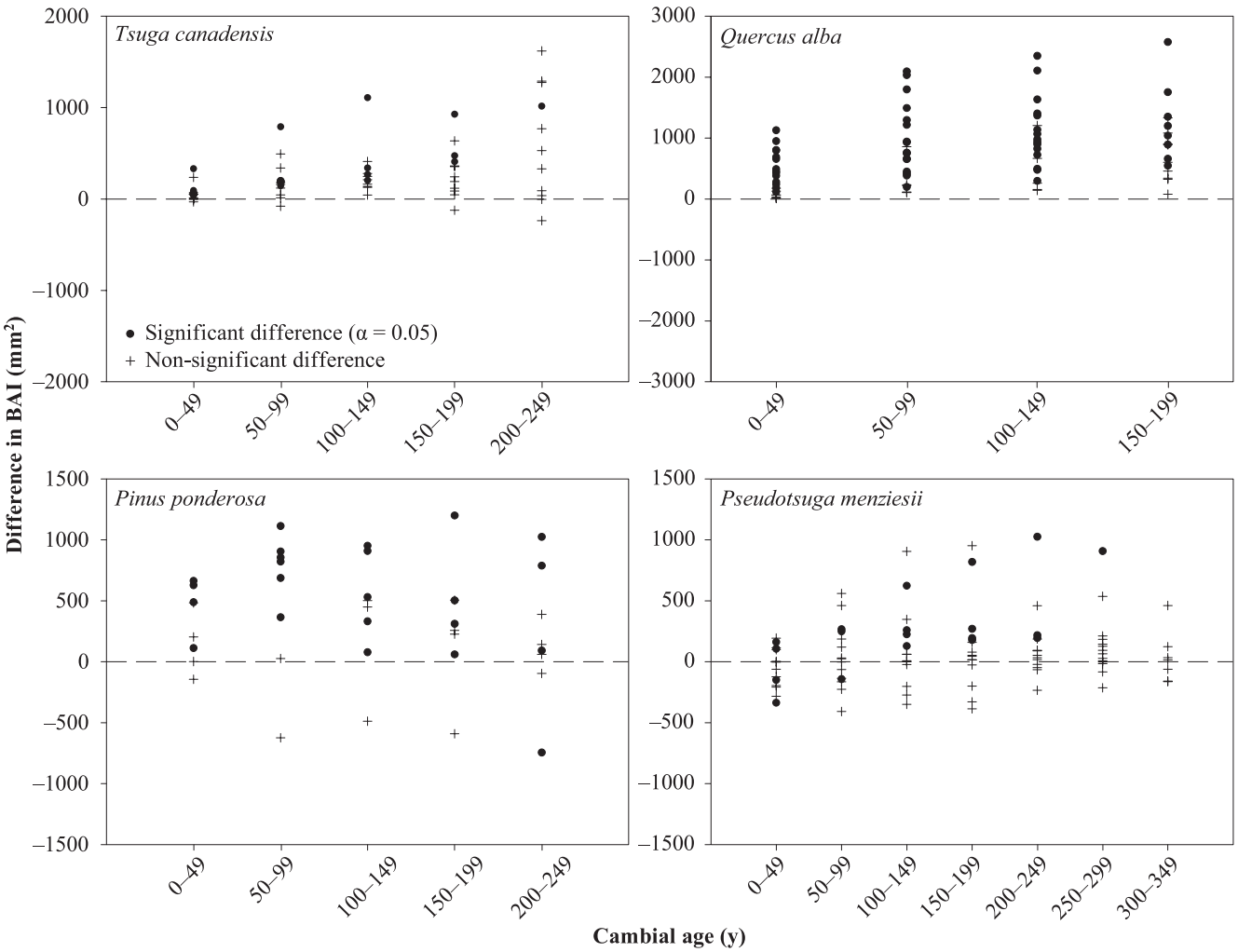

FIGURE 4. Differences between mean basal area increment (BAI) of "young" and "old" trees (see Table I) within each ITRDB collection. Differences are calculated for each 50-y interval beginning with the first cambial year of recorded growth. A positive value represents faster growth in the "young" group in the ITRDB collection. The number of comparisons depends on the number of 50-y intervals shared by the "young" and "old" groups. Statistical significance of mean differences was tested using *t*-tests assuming unequal variance.

the growth trajectories of long- and short-lived trees. To first evaluate whether this effect influences our results, we truncated the first 10% of all growth increments in each sampled tree. For a tree sampled at 100 y in age, the first 10 y were dropped, while the first 50 y of growth were dropped from a tree sampled at 500 y in age. Yet we found that inducing this extra error made very little difference in the results of our analysis (data not shown). For a second test, we identified a smaller collection of 171 *Quercus alba*, 107 *Quercus prinus*, and 44 *Liriodendron tulipifera* measurement time series collected in forests along the Appalachian Mountain chain. Tree samples were fully crossdated and likely within 10 y of pith, with most likely to be within 2–5 y of pith (Pederson, 2005). For *Quercus alba*, differences in growth trajectories were somewhat more pronounced and very consistent with the full ITRDB data set (Figures 2 and 5). Likewise, *Quercus prinus* and *Liriodendron tulipifera* also show strong separation among classes of trees sampled at increasing ages (Figure 5). Thus, we believe any error due to missed pith does not alter our conclusion that long-lived trees grow significantly more slowly than shorter-lived trees.

Beyond any effect of lifespan, factors such as climate, site productivity, and forest density could also influence tree growth. Over the past 200 y, these factors have changed, often profoundly, as a consequence of such phenomena as 20th century warming, altered disturbance regimes that followed European settlement, and fertilization effects from nitrogen deposition and increased CO_2. Large-scale studies in Europe have generally detected positive growth trends over the past several decades, which may be linked to such changes (Spiecker *et al.,* 1996). If indeed the modern era is more productive, then faster growth would be expected in younger trees, as observed in the results of our study. However, the relationship between growth and lifespan persists even when all growth increments formed after the year 1800 AD are dropped from the data set. When these more recent data points are excluded, significant ($P < 0.001$) separations in BAI still occur through the cambial ages of 150 y, 100 y, 300 y, and 450 y for *Tsuga canadensis*, *Quercus alba, Pinus ponderosa*, and *Pseudotsuga menziesii,* respectively (data not shown).

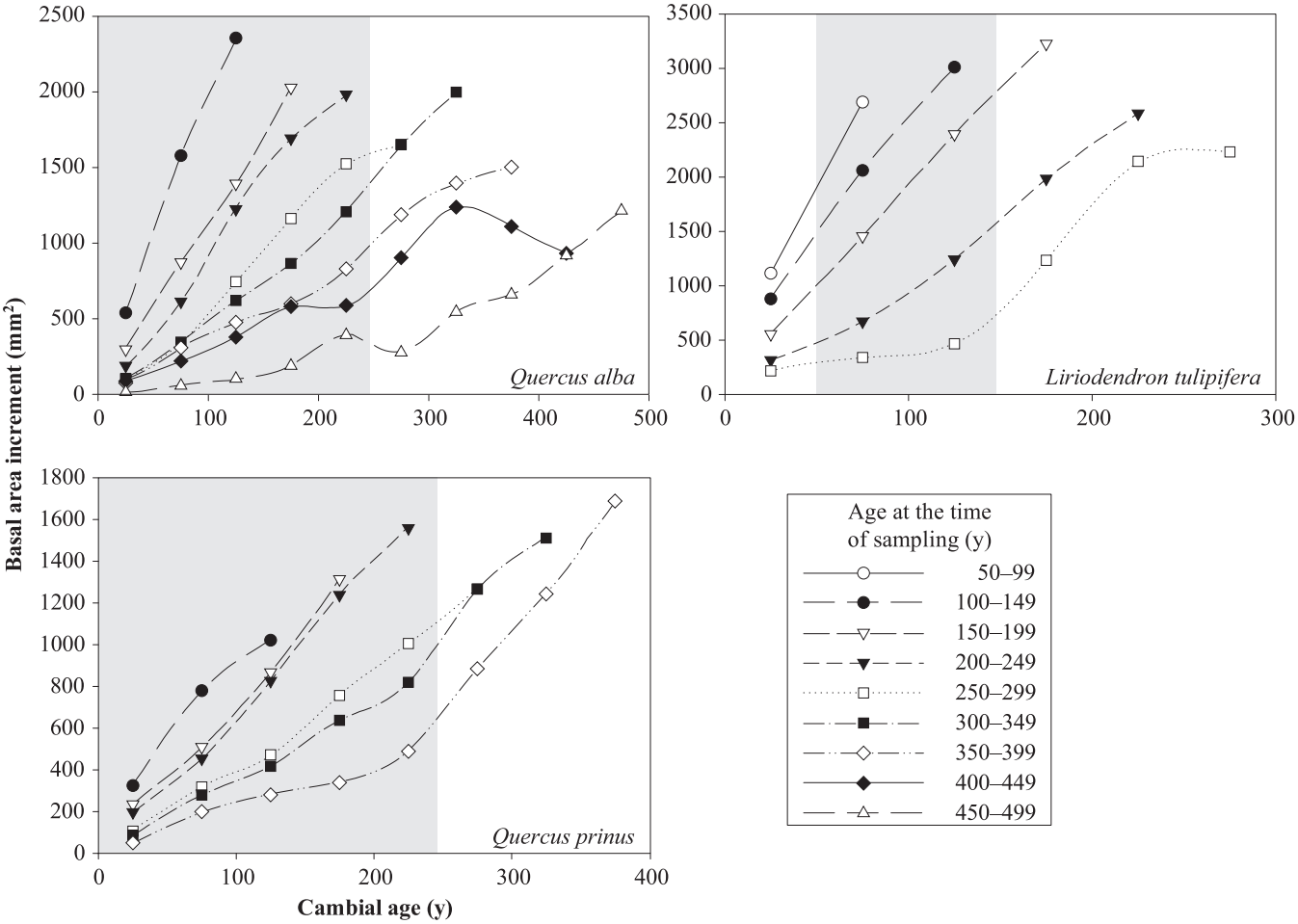

FIGURE 5. Mean annual basal area increment (BAI) for trees grouped with respect to the age at which they were sampled. Within each group, mean BAI was calculated across 50-y intervals (cambial age classes) beginning with the first year of recorded growth. Only those groups with more than 5 measurement time series are included. All samples used in this analysis were measured to within 10 y of pith. Cambial age classes in which significant ($P < 0.001$) differences in BAI occur are shaded.

On longer timescales, climate fluctuations such as the Little Ice Age may also affect radial growth, but climate appears to be an unlikely explanation for the patterns observed in this study. If these patterns were climate related, we would expect to see other evidence, such as fluctuations in the growth trajectories of the longest-lived age classes. Yet growth trends in these older age classes follow rather consistent trends through time. Furthermore, to induce the growth and lifespan relationship observed in this study, environmental conditions would have to have steadily improved over the past thousand years, and with consistently positive impacts on growth. Given that we included 6 species in this study and have also found similar results in European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), European silver fir (*Abies alba*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and post oak (*Quercus stellata*) (data not shown), a relationship between growth and lifespan appears to be the most likely explanation for our finding of slow growth in the longest-lived individuals.

Other studies have widely documented the relationship between growth and lifespan between and within species and noted differences in the ecology between slow-growing, long-lived and faster growing, short-lived individuals. Rapidly growing species quickly occupy space, reach early sexual maturity, are favoured by environments prone to frequent, catastrophic disturbance such as fires, floods, or severe windstorms, and tend to die at relatively young ages. In contrast, slow-growing species tend to live longer and are favoured by stable, predictable environments (MacArthur & Wilson, 1967; Bazzaz, 1979). Slow-growing tree species typically invest heavily in maintenance and defensive compounds, resist rot formation, and form hard, high-density wood, all of which would favour longevity (Loehle, 1988; 1996). Within a species, slow-growing trees also appear to maximize durability while minimizing the potential for damage. For example, the mechanical strength of wood in slow-growing eastern white cedar trees is substantially greater than that formed in faster growing individuals (Larson, 2001). In combination with a small stature less prone to snow accumulation or windthrow, these long-lived, slow-growing trees are well adapted to maintaining structural integrity (Larson, 2001). On the other extreme, fast-growing trees are more likely to be emergent in the canopy and

therefore more vulnerable to the full force of storm events (Putz & Sharitz, 1991).

In recent years, an increasing number of studies have demonstrated that within species, tree size is closely linked with physiological processes traditionally associated with ageing, including declines in gas exchange, photosynthesis, and growth rate (Ryan & Yoder, 1997; Hubbard, Bond & Ryan, 1999; Mencuccini *et al.,* 2005). These changes may not be due to age *per se*, but instead appear to be related to increases in size and the associated difficulties in transporting water over longer distances. As tree height increases, water must overcome additional gravitational and frictional forces to reach the top. Eventually resistance becomes so great that leaf water stress increases, inducing stomata to close, thereby limiting gas exchange and photosynthesis, and ultimately reducing growth (Ryan & Yoder, 1997; Hubbard, Bond & Ryan*,* 1999). As evidence of this "hydraulic limitation hypothesis" (Ryan & Yoder, 1997), water relations and their effects on photosynthesis appear to explain maximum height in California redwoods (Koch *et al.,* 2004). Just as importantly, tips of old trees grafted onto young rootstocks resume normal growth, indicating size matters more than age within each of 4 diverse species (Mencuccini *et al.,* 2005). Furthermore, old trees do not show evidence of genetically controlled cellular senescence and instead retain cambial function, reproductive output, and capacity for photosynthesis (Hubbard, Bond & Ryan, 1999; Lanner & Connor, 2001; Martinez-Vilalta, Vanderklein & Mencuccini, 2006). Eventually, research might show that genetically and biochemically controlled factors play at least some role in processes traditionally associated with ageing, but size is clearly a very important variable (Mencuccini *et al.,* 2005).

Despite the fact that we cannot investigate the mechanisms underlying growth and lifespan relationships, our meta-analysis provides wide-ranging evidence that long-lived trees maintain relatively slow growth and that these low growth rates begin at an early age. Also, old trees maintain relatively small statures, probably due to such consistently low growth rates. In this data set the oldest trees were not necessarily the widest and probably not the tallest, assuming a functional relationship between diameter and height (West, Brown & Enquist, 1999). Although slow growth is associated with many attributes that favour longevity, a potential drawback is that slow growth may also carry certain risks. Specifically, slow growth has been linked with higher susceptibility to disease, insect infestation, and increased probability of mortality (Clinton, Boring & Swank, 1993; Bleiker & Uzunovic, 2004). The results of our study do indicate that long-lived trees grow more slowly than average, but also that these growth rates have lower limits. In all 4 species, minimum size consistently increases with age, suggesting lower boundaries to sustainable growth rates (Figure 3). Slow growth may be favourable for longevity to a point, but extremely slow growth could decrease chances for survival.

As almost certainly occurs in this data set, long-lived individuals are more likely to occur on the borders of a species' range or on stressful sites with extreme climatic conditions or low availability of nutrients, water, or light (Schulman, 1954; Fritts, 1976; Nienstaedt & Zasada, 1990; Larson, 2001). Generally, separation between long-lived slow-growing trees and faster-growing shorter-lived trees is thought to occur on broad spatial scales. Yet, somewhat surprisingly, growth trajectories of older trees are uniquely slow even when compared to other trees in the same ITRDB collections. The area covered by each collection is unknown, but when sampling, dendrochronologists generally attempt to select trees in relatively homogenous stands to ensure similar climate–growth relationships or forest histories. Thus, the results of this study indicate that tradeoffs between growth and longevity may also occur on fine scales, with slow-growing, long-lived trees commingling with faster growing trees on the same sites. If predictive models of lifespan can be developed from early growth rates, the spatial extents and mechanisms behind growth and lifespan could be more thoroughly addressed in later studies.

An important issue to determine in future research is whether this intraspecific relationship between growth rate and lifespan is due to genotypic plasticity, phenotypic plasticity, or some combination of the two. In other words, do some trees innately grow slowly and live relatively long lives, or does the environment, such as heavy competition, poor microsite, or climatically unfavourable eras, enforce some type of suppression that induces slow growth and extends lifespan? If phenotypic plasticity plays a major role in determining growth and lifespan, then disturbance regime, as one example, will heavily influence the growth trajectories and lifespans of trees in a given forest. Minor, gap-phase disturbances would promote more long-lived trees, while broad, catastrophic disturbances would promote more short-lived trees. If genotypic plasticity plays a major role in determining growth and lifespan, then disturbance could also act as a selective force. Prolonged periods of catastrophic disturbance could reduce the proportion of slow-growing, long-lived trees to favour faster-growing, shorter-lived individuals.

If diversity of growth trajectories is reduced, what effect would that have on forest dynamics and resiliency following certain disturbance events? Could a reduction in the diversity of growth trajectories reduce ecosystem productivity and carbon sequestration? With respect to management and anthropogenic disturbances, what are the consequences of harvesting regimes, particularly clearcutting followed by broadcast planting of trees genetically selected or developed for rapid growth and wood production? It has been proposed that development of old-growth forests can be accelerated by favouring larger, fast-growing trees to quickly restore structural characteristics. Given linkages between growth and lifespan, could diversity sacrificed in exchange for the accelerated development of old-growth structure produce a forest with a superficially "correct" structure that lacks the "correct" processes or genetic biodiversity? Our study cannot address these questions and only demonstrates the possibility of a variety of growth trajectories and their relationships with lifespan. However, these growth strategies could be an important component of forest biodiversity and should be more thoroughly investigated to determine to what degree they affect the patterns and processes of forested ecosystems.

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