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RESEARCH ARTICLE

Self-pruning in tree crowns is influenced by functional strategies and neighbourhood interactions

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Abstract

1. As canopy closure imposes light limitation in forests, the dieback of trees' lower branches, known as self-pruning, defines their live crown base and shapes the structure and function of entire stands.
2. Self-pruning is often thought to occur after shading causes individual branches to transition from carbon sources to sinks. Under this assumption, we would expect resource-conservative and shade-tolerant species to initiate self-pruning under deeper shade because their branches require less light to maintain a positive carbon balance. However, this pattern may be complicated by 'correlative inhibition,' which may cause plants to preferentially allocate resources towards sunlit branches. Consistent with this idea, we predicted that within species, trees with sunlit tops would initiate self-pruning at a higher light threshold. Lastly, we predicted that community-level diversity in self-pruning strategies would correlate with productivity and total crown volume.
3. We tested these predictions in an experiment where 12 temperate tree species were planted in plots of varying diversity and composition. We measured crown dimensions and position as well as the fraction of light reaching the crown base (denoted L_{base}), which we took as an estimate of the light threshold of self-pruning.
4. As predicted, shade-tolerant and resource-conservative species self-pruned at a deeper level of shade (lower L_{base}). Within species, trees generally had higher L_{base} when they had more light at the crown top, suggestive of correlative inhibition. With respect to their neighbours' traits, though, conservative and acquisitive species showed contrary patterns of plasticity: conservative species had lower L_{base} around conservative neighbours, and acquisitive species around acquisitive neighbours. As predicted, plots with a greater diversity of L_{base} had greater basal area and crown volume. Using simulations, we showed that adjustment of crown depth from monocultures to mixtures strengthened the relationship between diversity of L_{base} and crown volume, primarily due to competitive release that benefited acquisitive species.

5. We provide evidence that self-pruning strategies are intimately connected to resource acquisition strategies and propose that L_{base} may serve as a functional trait to quantify them. Our results reinforce the role of tree architectural diversity in the functioning of light-limited forests.

KEYWORDS
canopy packing, crown architecture, IDENT, light competition, self-pruning, shade tolerance, stand development, tree diversity

1 | INTRODUCTION

The arrangement of tree crowns in three-dimensional space contributes to determining how much light they can capture, thereby exerting a strong influence on forest productivity and development. The shape and size of these crowns are influenced by the process of self-pruning—the regulated loss of branches. Self-pruning in the lower parts of a tree crown defines the live crown base, and thus (along with tree height) determines crown depth (Mäkelä, 1997), contributing to the complex, multi-layered vertical structure of light-limited forests. From a silvicultural perspective, since knots left by branches' attachments to the trunk are a main cause of reductions in lumber grade, self-pruning and natural occlusion of knots over time often increase the value of wood (Trincado & Burkhart, 2009). As a result, foresters often aim to choose species, environments or planting conditions that reduce branching and increase self-pruning rates without compromising stand growth (Garber et al., 2008; Kint et al., 2010; Mäkinen, 2002). Because dead branches lose carbon through time, self-pruning can also have a large, often overlooked influence on forest carbon accounting (Lim et al., 2024). However, there is little comparative research on self-pruning that might contribute to a more general, mechanistic understanding of these consequences.

Self-pruning tends to occur in older branches of the lower crown as they become more and more shaded during stand development. Researchers have often conjectured or assumed that individual branches are pruned as diminishing access to light causes them to transition from net carbon sources to sinks (Prentice & Leemans, 1990; Sorrensen-Cothern et al., 1993)—an idea that has received some empirical support (Witowski, 1997). This decline in carbon balance could be exacerbated by factors like water limitation, herbivory or pathogen damage that influence photosynthetic function (Protz et al., 2000).

For simplicity, branches are often taken to be autonomous—they do not rely on carbon from other branches, and they live or die regardless of the carbon status of the whole plant (Sprugel et al., 1991). However, some studies have challenged the idea of branch autonomy (Henriksson, 2001; Schoonmaker et al., 2014; Sprugel, 2002). For example, trees whose upper crowns are well-lit sometimes prune their lower branches at a higher level of light than trees that are fully shaded, an instance of 'correlative inhibition' (Novoplansky et al., 1989; Sprugel, 2002; Stoll & Schmid, 1998; Takenaka, 2000). This phenomenon may result from preferential allocation of water and nutrients to branches that assimilate the most carbon and are expected to contribute most to future growth, which may cause photosynthetic decline or hydraulic failure in shaded lower branches (Protz et al., 2000). Although these findings are consistent with the perspective that self-pruning results from declines in branch carbon balance, they hint at greater complexity than complete branch autonomy would imply.

Under a carbon balance-based explanation, shade-tolerant species may be expected to self-prune at a lower level of light. This hypothesis is based on the assumption that shade-tolerant species have a lower light compensation point (LCP) than shade-intolerant species, meaning that the amount of light required for their carbon balance to break even is lower (Craine & Reich, 2005; Givnish, 1988; Lusk & Jorgensen, 2013). (In this case, the relevant definition of the LCP may include respiration not just by the branch and its leaves, but also by any other living tissues that would no longer be needed if the branch were shed—an idea closely related to the 'effective light compensation point' of Givnish, 1988). The idea that late-successional, shade-tolerant species require deeper shade to initiate self-pruning may help explain why they have longer crowns with lower bases (Poorter et al., 2006) and themselves cast a deeper shade (Canham et al., 1994). Like shade tolerance, conservative leaf-economic traits (sensu Wright et al., 2004) may be expected to reduce the LCP and dark respiration (Baltzer & Thomas, 2007a, 2007b; Falster et al., 2018), causing self-pruning to be initiated at a lower light level.

Variation in self-pruning strategies could contribute to the emergent canopy structure of diverse forests. More generally, variation in crown architecture and position may permit forests to achieve greater: (1) crown complementarity, such that crowns overlap less in space (Williams et al., 2017); and (2) canopy packing, such that there is more total crown volume per unit ground area (Pretzsch, 2014; Jucker et al., 2015). These phenomena may allow the community to capture the available light more completely and use it more efficiently (Sapijanskas et al., 2014; Pretzsch, 2014; Williams et al., 2017; Rissanen et al., 2019; Forrester et al., 2019; Duarte et al., 2021). Once the canopy closes and light becomes a limiting resource, canopy packing and complementarity are likely to help explain the positive influence of diversity on productivity often observed across a variety of forested ecosystems (Feng et al., 2022; Paquette & Messier, 2011).

Past studies have noted that crown complementarity (Williams et al., 2017) and canopy packing (Jucker et al., 2015) are greater in mixtures that vary in shade tolerance, considered as the ability to survive under low light (Valladares & Niinemets, 2008). These effects arise from a combination of vertical stratification and differences in crown shape due to both interspecific variation and plasticity. If commonly measured functional traits and shade tolerance are related to crown architecture—via their influence on self-pruning or otherwise—it may help explain why both functional diversity (Bongers et al., 2021; Urgoiti et al., 2022) and heterogeneity in shade tolerance (Morin et al., 2011; Zhang et al., 2012) are linked to the over-performance of mixed-species plots. We may expect to see likewise that variation in self-pruning strategies correlates with productivity.

Aside from a tree's own traits, various characteristics of the surrounding tree community may be expected to influence the onset of self-pruning. The intensity of competition could alter the light threshold below which self-pruning occurs through correlative inhibition or plasticity in photosynthetic traits. But even if a certain tree species always initiated self-pruning at a fixed light threshold, the neighbourhood could influence the height where that threshold is reached. A dense stand would be expected to have less light at any given height than a much sparser stand. Indeed, it is common for trees to have higher crown bases and lower crown depths in denser stands (Mäkelä, 1997; Mäkinen, 2002). Neighbourhood characteristics could thus influence the light threshold of self-pruning and the crown depth. Plastic adjustment in crown depth could conceivably either increase or decrease the extent of canopy packing in diverse tree mixtures relative to monocultures.

Although self-pruning clearly has a role in shaping how forest stands are structured, not much is known about its ecology, especially in a comparative perspective that would permit generalization across stands with varying species composition. To address this lack, we examined inter- and intraspecific variation in self-pruning among temperate trees within the context of a diversity experiment in southern Québec, Canada. Concerning interspecific variation, we posed the hypothesis that more shade-tolerant and resource-conservative species would initiate self-pruning at a deeper level of shade. This hypothesis is premised on the assumption that carbon depletion due to shading is an important part of the causal chain that leads to self-pruning in light-limited forests. Concerning intraspecific variation, we proposed that crowns that are well-lit at the top would also have a higher (i.e. less shaded) light threshold for self-pruning, in accordance with the notion of correlative inhibition. Consistent with this prediction, we also expected larger trees to have more light at the crown base (Nock et al., 2008). Lastly, we expected crown depth to decline with the intensity of competition in the local neighbourhood.

We also posed hypotheses about the influence of variation in self-pruning on ecosystem function. We proposed that plots whose species vary in the light threshold of self-pruning would show greater productivity and total crown volume. We proposed further that intraspecific adjustment in crown depth from monocultures to mixtures would tend to increase crown volume and strengthen the effect of diversity on crown volume.

2 | METHODS

2.1 | Site and experimental design

We conducted this study at IDENT-Montréal, which is part of the IDENT network of tree diversity experiments (Tobner et al., 2014) and the larger TreeDivNet (Paquette et al., 2018). The experiment was planted in spring 2009 on abandoned farmland in Ste-Anne-de-Bellevue, Québec, Canada (45° 25′ 30.1″ N, 73° 56′ 19.9″ W). Details about climate, soils and preparation can be found in Tobner et al. (2016).

The experiment comprises 256 plots arrayed into four blocks, surrounded by a fence that excludes large herbivores. The plots were planted with varying species diversity and composition, drawing on a pool of 19 species. Here, we focus on plots that include only the 12 species native to North America—six evergreen conifers, one deciduous conifer and five deciduous broadleaf species (Table 1). The distinct all-native species compositions included monocultures of all 12 species, 14 two-species mixtures, 10 four-species mixtures and a 12-species mixture. Each composition was replicated once at a random position within each block.

Each plot was 4×4 m and had 64 trees planted in a 0.5×0.5 m grid. Within blocks, plots were separated by a 1.25 m buffer. Trees were planted at 1–2 years old. Tree species in a given plot were planted with equal frequency. By the time we conducted this study in 2018, the canopy had effectively closed in all plots.

2.2 | Self-pruning survey

We collected self-pruning measurements over 1 month in July and August 2018. We focused on two of the four blocks (A and D) and left out the 12-species plots. From each of the 72 selected plots, we randomly chose four living trees of each species when possible, excluding the plot edges. However, there were not always enough living trees to sample four per species per plot, particularly in four-species plots; this left us with $n = 546$ (out of a potential 640) living trees.

We made the key assumption that each tree's crown base was defined by self-pruning of lower branches in the past, such that the present amount of light at the crown base could serve as a measure of the threshold beneath which self-pruning had occurred. This assumption could be complicated by epicormic sprouting on lower crowns, but there was seldom any evidence of it. Defining the crown base can pose a challenge when crowns are ragged and vertically non-continuous; we defined it as the point on the trunk above which there are relatively continuous branches bearing live foliage that is typical for its species (USDA Forest Service, 2024; Figure 1; Figure S1) (This definition stands in contrast to those often used in fire ecology,

TABLE 1 The 12 native species in IDENT-Montréal and their characteristics. The shade tolerance values come from Niinemets and Valladares (2006). Average basal diameter and height are calculated using only monoculture plots in 2018. Basal diameter measurements come from the tree inventory, while height measurements come from the self-pruning survey.

Species	Species code	Family	Leaf habit	Leaf morphology	Shade tolerance	Average basal diameter (mm)	Average height (cm)
Abies balsamea (L.) Mill.	ABBA	Pinaceae	Evergreen	Needleleaf	5.01	46.7	357
Acer rubrum L.	ACRU	Sapindaceae	Deciduous	Broadleaf	3.44	53.8	682
Acer saccharum Marshall	ACSA	Sapindaceae	Deciduous	Broadleaf	4.76	43.2	622
Betula alleghaniensis Britton	BEAL	Betulaceae	Deciduous	Broadleaf	3.17	48.6	716
Betula papyrifera Marshall	BEPA	Betulaceae	Deciduous	Broadleaf	1.54	55.2	795
Larix laricina (Du Roi) K. Koch	LALA	Pinaceae	Deciduous	Needleleaf	0.98	52.2	772
Picea glauca (Moench) Voss	PIGL	Pinaceae	Evergreen	Needleleaf	4.15	45.9	336
Picea rubens Sarg.	PIRU	Pinaceae	Evergreen	Needleleaf	4.39	45.6	378
Pinus resinosa Aiton	PIRE	Pinaceae	Evergreen	Needleleaf	1.89	33.8	222
Pinus strobus L.	PIST	Pinaceae	Evergreen	Needleleaf	3.21	47.2	531
Quercus rubra L.	QURU	Fagaceae	Deciduous	Broadleaf	2.75	66.5	810
Thuja occidentalis L.	THOC	Cupressaceae	Evergreen	Scaleleaf	3.45	46.1	386

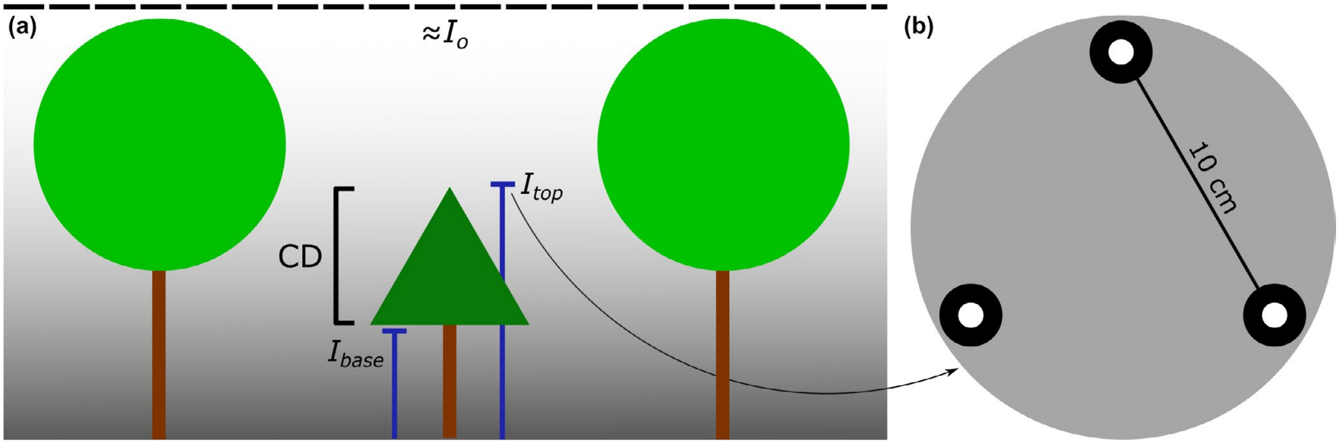

FIGURE 1 A diagram of our self-pruning measures. (a) For each focal tree (center), we calculated the crown depth (CD) as the difference between the height at the top and base of the crown. We used an apparatus (represented here by the blue T-shaped figures) consisting of an extensible pole bearing a top plate to measure the amount of light at the top and base of the crown (I_{top} and I_{base}). These values were compared to the amount of light in an adjacent open environment (I_o), a proxy for light above the canopy of the entire experiment (dashed line). (b) The design of our apparatus's top plate, comprising three light sensors fixed to a disk in an equilateral triangle. The pole held the plate horizontal, parallel to the ground.

where self-pruning is considered not to occur until dead branches physically detach from the trunk [Schwilk & Ackerly, 2001]). On each tree, we measured the height of both the crown top and the crown base and estimated the crown radius as the average of measurements in the four cardinal directions from the central stem to the periphery. We calculated the crown depth as the vertical distance between the crown top and the crown base (Figure 1a).

We also characterized the general availability of light (as photosynthetic photon flux density) at both the crown top and the crown base. Following Messier and Puttonen (1995), we calculated the ratio between the amount of light at each site of interest and in an adjacent open environment, which we took as representative of conditions above the canopy. All measurements were conducted under clear-sky conditions due to the rarity of consistently overcast conditions; this method estimates average light availability with little bias, but with greater temporal and spatial noise compared to overcast conditions (Messier & Puttonen, 1995). We only collected measurements from 9:00 to 16:00 to avoid times when the sun was close to the horizon (median solar zenith angle: 36.6°; 2.5th–97.5th percentile: 25.5°–55.2°).

We measured a time series of light in the open (I_o) using an LI-190R quantum sensor (LI-COR Biosciences, Lincoln, NE, USA) mounted on a tripod and connected to a data logger. We measured light in the experiment using three LI-190R sensors arrayed in an equilateral triangle with a side length of 10 cm on a round wooden plate (Figure 1) mounted on an extensible pole. For each selected tree, we went in each of the four cardinal directions from the trunk, stopping short of the edge of the crown base. Just below the base in each direction, we took simultaneous readings from the three sensors three times, rotating the plate between readings, to measure I_{base}. Each measurement was thus an average of 36 individual sensor readings (4 directions × 3 rotations × 3 sensors). We then repeated this procedure just above the crown top to measure I_{top}, although for some trees that were visibly the tallest within a large neighbourhood, we assumed I_{top} to be equal to I_o. We summarized the properties that determine light at the crown base and top by calculating the values $L_{base} = \ln (I_{base}/I_o)$ and $L_{top} = \ln (I_{top}/I_o)$, extracting I_o from the time series based on measurement time. These log-light fractions reach a maximum of 0 under open conditions. The formulas are based on an idealization of light transmission through the canopy as an exponential decay described by the Beer–Lambert law (Ponce de León & Bailey, 2019). Besides this theoretical justification, the log-transformation also helps to linearize the relationships between these quantities and their predictors.

Both L_{base} and crown depth can serve as measures related to self-pruning, but in different ways. In theory, a crown could be as deep as the tree is high, but due to self-pruning, it seldom is. Although L_{base} describes the putative threshold of light needed to cause self-pruning, the height where this threshold is reached depends on the pattern of light extinction through the canopy, which could vary strongly across neighbourhoods even if L_{base} were constant. Variation in both L_{base} and the light environment is integrated into crown depth, which captures the influence of self-pruning on tree architecture.

2.3 | Tree inventory

We measured the basal diameter (15 cm above the ground) of every live tree in the experiment in late autumn of 2018. We estimated the productivity of each native-species plot, including 12-species plots and all four blocks, as the basal area of the inner 6 × 6 trees (i.e. excluding edges). Trees that died by 2018 were considered to make no contribution to basal area.

We characterized the competitive environment in each focal tree's neighbourhood using the neighbourhood competition index, calculated as $\text{NCI} = \Sigma_i A_i/D_i$, where for each tree i in the neighbourhood, A_i is the stem cross-sectional area (cm^2) and D_i is the distance (m). In effect, this index simplifies the more complex NCI of Canham et al. (2004) by assuming that a tree's competitive effect is independent of its species identity and by setting the parameters α and β—exponents of tree diameter in the numerator and distance in the denominator—to 2 and 1. We considered these simplifications appropriate since our aim is inference rather than prediction. We defined the neighbourhood to include all trees within a radius of 1.1 m from the focal tree (the 90th percentile of crown radius measurements).

2.4 | Functional identity and diversity

To describe the functional identity of each species, we used a set of five traits describing plant economics: specific leaf area (SLA), leaf nitrogen concentration (%N), leaf dry matter content (LDMC), wood density (WD) and specific root length (SRL). These traits were not measured locally but rather were previously compiled from trait databases for IDENT-Montréal species (Belluau, 2020). We used principal components analysis on the correlation matrix to identify major axes of species-level variation (Figure S2). The first principal component explained 56.5% of trait variation, so we took species' positions along this axis to represent their functional identity. The axis separated the evergreen needleleaf species at low values from the deciduous broadleaf species at high values, with the one deciduous needleleaf species (*L. laricina*) in between (Urgoiti et al., 2022); higher values correspond to higher SLA, %N, WD and SRL. We label this axis 'acquisitiveness' based on correspondence to the global whole-plant economic spectrum (Díaz et al., 2016). While the loading for wood density is contrary to expectations based on global patterns (Díaz et al., 2016), it is consistent with a typical split between coniferous softwoods and broadleaf hardwoods in North American temperate forests. Past studies in the experiment noted that deciduous species had greater above-ground growth than evergreen species, as evaluated from the annual survey (Tobner et al., 2016; Urgoiti, Messier, Keeton, & Paquette, 2023). Because this division persisted at the time of our measurements, acquisitiveness was to some degree confounded with tree size across species. For each focal tree in our self-pruning survey, we described the functional identity of trees within the 1.1 m radius neighbourhood by calculating the community-weighted mean (CWM) of acquisitiveness ('neighbourhood acquisitiveness'), with weights determined by the number of trees planted of each species.

Aside from the trait-based dimension of acquisitiveness, we described focal tree strategies using the shade tolerance index of Niinemets and Valladares (2006), which was compiled on a 1–5 scale based on empirical measurements and expert opinion on the amount of light trees of various species require for survival. We also used previously compiled leaf lifespan for each species (Belluau, 2020). Although leaf lifespan is often considered a leaf-economic trait (Wright et al., 2004), we considered it separately here to investigate relationships between leaf and branch longevity.

While we carried out analyses of inter- and intraspecific variation in self-pruning at the scale of individuals and their neighbourhoods, we examined their influence on ecosystem function at the scale of entire plots. To enable these analyses, we calculated various metrics of diversity at the plot level, including the diversity of functional traits, of shade tolerance values and of L_{base}. We calculated diversity of L_{base} using species means across all plots to make it analogous to the functional traits and shade tolerance values, which were also available only at the species level. In these calculations, we used the abundance-weighted version of Scheiner et al. (2017)'s $^qD(TM)$, with weights determined by the number of trees of each species planted among the plot's inner 6 × 6 trees. This metric is calculated as the product of species richness, mean dispersion, and a Hill diversity-derived functional evenness, and corresponds to the effective number of species with maximal distinctness. The Hill number q was set to 1, resulting in measures analogous to the exponential of Shannon diversity (Jost, 2006). To calculate functional trait ${}^{q}D(TM)$, we used a matrix of Euclidean distances among species, calculated with the five aforementioned functional traits (*z*-standardized).

2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Species	12
Individual	Individual	546 total; 27–69 per species
Plot	Plot	148 (for basal area analyses); 69 (for crown volume analyses)

2.6 | Statistical analyses

We conducted all analyses in *R* v. 4.4.0 (R Core Team, 2024). To examine how self-pruning behaviour relates to other aspects of trees' strategies, we used ordinary least-squares (OLS) regression to evaluate relationships between species-level properties (acquisitiveness, shade tolerance and leaf lifespan) and species mean L_{base}.

To understand drivers of variation among individual trees, we tested the influence of four variables on L_{base}. Two of these variables were properties of the focal individual itself (height and light fraction at the crown top), and two were properties of its neighbourhood (NCI and CWM acquisitiveness). Using package *lme4* v. 1.1.35.3 (Bates et al., 2015), we built mixed-effects models testing how L_{base} is influenced by the interactive effects between one individual-level variable at a time and species identity, with plot as a random intercept. We used *lmerTest* v. 3.1.3 (Kuznetsova et al., 2017) to calculate *p*-values using Satterthwaite's method to estimate degrees of freedom, noting that such estimates should be interpreted conservatively. We used analysis of covariance (ANCOVA) with Type III sums of squares to test the significance of each main effect and their interaction. Under the hypothesis of correlative inhibition, we expected L_{top} to have a positive effect on L_{base}. Whether or not there was a significant interaction between species and each individual-level variable, we extracted the species-specific slopes using package *emmeans* v. 1.10.3 (Lenth, 2023) and used OLS regression to evaluate whether these slopes covaried with shade tolerance or acquisitiveness.

We likewise tested the influence of these same four variables on crown depth using ANCOVAs with identical structure to the models of L_{base}. Crown depth was strongly dependent on tree height, which varied considerably among species, making it challenging to interpret species-specific slopes. For this reason, we were primarily interested in the significance and direction of the main effects of the four individual variables rather than their interactions with species identity. Accordingly, we also did not analyse trends in species-specific slopes.

We were interested in whether diversity in L_{base}—considered as a putative functional trait at the species level—could explain productivity across plots, analogous to previous studies using better-studied functional traits (Bongers et al., 2021; Urgoiti et al., 2022). We used OLS regression to test whether diversity in functional traits (not including L_{base} or leaf lifespan), shade tolerance and L_{base} were correlated with productivity at the plot level. In this analysis alone, we used all native-species plots (including those with 12 species) in all four experimental blocks, since the analysis depended only on species means rather than individual measurements of L_{base}.

2.7 | Simulations of canopy packing

In evaluating the influence of intraspecific variation in self-pruning on canopy packing, we used crown depth as a metric of how neighbourhoods influenced crown shape via self-pruning. We relied on a simple, stylized representation of crown structure developed by Purves et al. (2007) and adopted by Jucker et al. (2015) in the context of canopy packing. In this representation, tree crowns are defined by the positions of their base and top, their radius and a shape parameter that influences concavity. This representation makes it tractable to estimate the volume of individual crowns. We fixed the shape parameter at the species level using estimates provided by Purves et al. (2007). Further details on calculating crown volume are found in Appendix S1.

To evaluate how self-pruning alters canopy packing, we simulated crown volume under two scenarios: (1) one where trees in each plot show the same crown depth as in the monoculture of their species, and (2) one where trees may plastically adjust their crown depth when growing in mixtures. To carry out scenario (1), we simulated 500 crowns of each species in each plot; the radius was sampled from among the trees of that species in that plot measured in the self-pruning survey, but the depth was sampled from monocultures of the same species in the same block. To carry out scenario (2), we sampled both the crown depth and radius independently from the focal plot. (When the focal plot was a monoculture, the two scenarios were of course identical.) We took the second scenario as an estimate of the actual crown volume in the plot (Figure S3). We performed this procedure for each plot included in the self-pruning survey. Further details on these simulations are presented in Appendix S1.

For both scenarios, we scaled up individual crowns to estimate the total crown volume per unit area in each plot's inner 6×6 trees (9 m^2). Since our self-pruning survey only included living trees, we used the tree inventory to calculate the fraction of living trees of each species in each plot in 2018. We then estimated the total crown volume per unit area (V, in $m^3\ m^{-2}$ or simply m) in each plot as:

$$V = \frac{1}{9}\sum_{s}\overline{v}_s l_s n_s$$

where $\overline{v}_s$ is the mean crown volume of measured (living) trees of species s in the plot, l_s is the fraction of trees of species s in the plot that were still living, and n_s is the number that were planted at the outset of the experiment.

3 | RESULTS

3.1 | Species-level predictors of self-pruning

Of the individual-level variation in the log-light fraction at the crown base (L_{base}), 51.3% could be explained by species identity alone. Average species L_{base} across all plots was tightly correlated with average L_{base} in monocultures alone (t (10) = 7.80, $R^2 = 0.859$, $p < 0.001$), with a relationship that does not significantly differ from the 1:1 line (Figure S4). The L_{base} values were lower among the six evergreen species than the six deciduous species. Given that evergreen species were also less acquisitive than deciduous species, there was a strong positive species-level correlation between L_{base} and acquisitiveness (t (10) = 4.36, $R^2 = 0.655$, $p = 0.001$; Figure 2). Shade tolerance was not linked to leaf habit, but showed a moderate negative correlation with L_{base} (t (10) = −2.64, $R^2 = 0.411$, $p = 0.025$). Shade tolerance and acquisitiveness were uncorrelated (t (10) = −0.63, $R^2 = 0.038$, $p = 0.542$), and the two variables could additively explain by far most of the variation in L_{base} ($R^2 = 0.897$). In addition, L_{base} had a strong negative correlation with log-leaf lifespan both across all species (t (10) = −7.40, $R^2 = 0.846$, $p < 0.001$) and among just the evergreen species (t (4) = −4.32, $R^2 = 0.824$, $p < 0.001$; Figure 2).

3.2 | Neighbourhood-level predictors of self-pruning

We considered the interactive effects of species identity and each of four individual-level predictor variables (neighbour acquisitiveness, NCI, focal tree height and L_{top}) on L_{base} in our mixed-model ANCOVA analyses. The four variables had clear but noisy correlations with each other within species (Figure S5), most likely because more acquisitive neighbours increased competition, suppressed the growth of the focal individual and reduced L_{top}. There was strong evidence for a species × height interaction and weaker evidence for a main effect of height (Table 2). In the species × L_{top} model, there were strong main effects of species and L_{top}, but much more modest evidence for an interaction. In the species × neighbour acquisitiveness model, we found evidence for a main effect of species and modest evidence for an interaction with acquisitiveness, but no main effect of acquisitiveness. In the species × NCI model, there was only a significant effect of species.

Even though we only found any evidence for species variation in slopes for two individual-level predictor variables, we extracted the species-specific slopes from the mixed models to evaluate whether there were any suggestive patterns for further exploration. There was no evidence for any correlations between these slopes and shade tolerance (all $p > 0.05$); however, there were varying degrees of evidence for correlations with the focal species' acquisitiveness (Figure 3). There was no significant correlation for L_{top} (t (10) = 1.59, $R^2 = 0.202$, $p = 0.143$), but progressively stronger correlations for NCI (t (10) = −3.298, $R^2 = 0.521$, $p = 0.008$), neighbour acquisitiveness (t (10) = −3.759, $R^2 = 0.586$, $p = 0.004$) and tree height (t (10) = 6.058, $R^2 = 0.786$, $p < 0.001$). In particular, the most acquisitive species had a greater L_{base} when their neighbourhood had lower NCI and acquisitiveness, and when they themselves had greater height and light at the crown top as a result. This trend was reversed among the most conservative species, which had a lower L_{base} when their

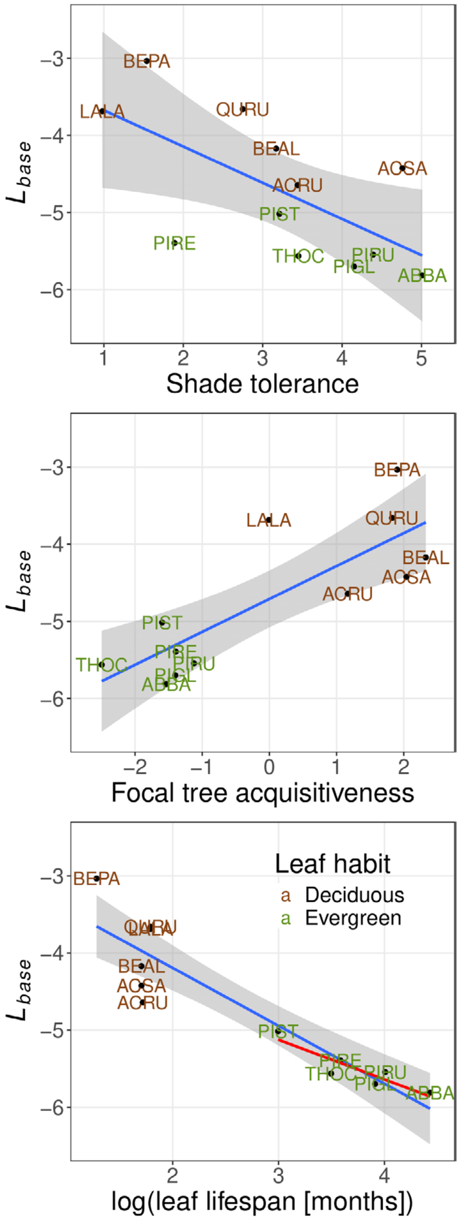

FIGURE 2 Species-level correlations between the light threshold of self-pruning (L_{base}) and shade tolerance (top), acquisitiveness (middle) and leaf lifespan (bottom). Labels are species codes, which are found in Table 1. Blue lines represent OLS regression lines, with a 95% confidence interval shown in grey. The red line in the bottom panel is the OLS regression line for only evergreen species, with no confidence interval shown.

TABLE 2 Output from analysis of covariance (ANCOVA) models with Type III sums of squares designed to test how log-transformed light fraction at the crown base (L_{base}) and crown depth (CD) are influenced by each of four individual/neighbourhood-level variables (continuous), focal species identity (categorical) and their interactions. All models included a random effect for experimental plot, which is left out from the model structure for concision. As is typical for mixed-effects models, denominator degrees of freedom (df) varied for terms within a model and were estimated using Satterthwaite's method. Abbreviations: neighbour acq = neighbour acquisitiveness; NCI = neighbourhood competition index; L_{top} = log-transformed light fraction at the crown top.

Model structure	Term	Sum of squares	Mean squares	Numerator df	Denominator df	*F*	*p*-value
$L_{\text{base}} \sim$ neighbour acq × species	Neighbour acq	0.249	0.249	1	414.7	0.425	0.515
	Species	99.9	9.084	11	460.2	15.510	$<10^{-3}$
	Interaction	11.6	1.053	11	467.3	1.798	0.052
$L_{\text{base}} \sim$ NCI × species	NCI	0.394	0.394	1	489.7	0.655	0.419
	Species	60.3	5.48	11	476.4	9.114	$<10^{-3}$
	Interaction	3.07	0.280	11	508.4	0.465	0.925
$L_{\text{base}} \sim$ tree height × species	Tree height	2.89	2.89	1	455.3	4.906	0.027
	Species	4.83	0.439	11	514.8	0.744	0.696
	Interaction	22.4	2.04	11	495.5	3.454	$<10^{-3}$
$L_{\text{base}} \sim L_{\text{top}}$ × species	L_{top}	5.48	5.48	1	518.2	9.653	0.002
	Species	68.0	6.18	11	475.6	10.890	$<10^{-3}$
	Interaction	9.91	0.901	11	512.0	1.587	0.099
CD ~ neighbour_acq × species	Neighbour acq	70,948	70,948	1	388.7	8.884	0.003
	Species	1,190,804	108,255	11	444.1	13.555	$<10^{-3}$
	Interaction	136,914	12,447	11	452.6	1.559	0.108
CD ~ NCI × species	NCI	47,536	47,536	1	460.6	5.784	0.017
	Species	464,877	42,262	11	461.0	5.142	$<10^{-3}$
	Interaction	60,639	5513	11	510.2	0.671	0.767
CD ~ tree height × species	Tree height	1,608,601	1,608,601	1	487.3	608.872	$<10^{-3}$
	Species	166,282	15,117	11	512.7	5.722	$<10^{-3}$
	Interaction	58,917	5356	11	506.5	2.027	0.024
CD ~ L_{top} × species	L_{top}	1,199,701	1,199,701	1	488.3	225.623	$<10^{-3}$
	Species	446,413	40,583	11	424.2	7.632	$<10^{-3}$
	Interaction	211,907	19,264	11	507.6	3.623	$<10^{-3}$

neighbourhood had lower NCI and acquisitiveness and when they had greater height. However, no species had highly negative correlations between L_{top} and L_{base}.

There was strong evidence that crown depth was greater for individuals with lower NCI, lower neighbour acquisitiveness, higher focal tree height and higher light at the crown top (Table 2; Figure 4). Besides these main effects, species identity and (for all models except the one with NCI) the interaction term also had significant effects, implying that species varied in crown depth even accounting for their other individual and neighbourhood characteristics.

3.3 | Self-pruning and productivity

We used plot-level diversity (^{q}D(TM)) in functional traits, shade tolerance and L_{base} as predictors of plot basal area. Log-transforming our diversity measures nearly always improved model fit. After this log-transformation, diversity in L_{base} was better correlated with basal area (t (146) = 5.71, $R^2 = 0.182$, $p < 0.001$; Figure 5) than diversity in functional traits (t (146) = 3.81, $R^2 = 0.090$, $p < 0.001$) or diversity in shade tolerance (t (146) = 3.42, $R^2 = 0.074$, $p < 0.001$). Similar results hold when considering the net biodiversity effect (NBE) on productivity, defined as the over-performance of mixtures relative to monoculture-based expectations (Figure S6; see Appendix S1 for further details).

3.4 | Canopy packing

Estimated total crown volume per plot (based on simulations under the scenario with plasticity) was moderately correlated with basal area (t (67) = 5.35, $R^2 = 0.299$, $p < 0.001$). Crown volume increased modestly with the diversity (log-transformed ^{q}D(TM)) of L_{base} (t (67) = 4.45, $R^2 = 0.228$, $p < 0.001$; Figure 6) and of functional traits (t (67) = 3.81, $R^2 = 0.178$, $p < 0.001$).

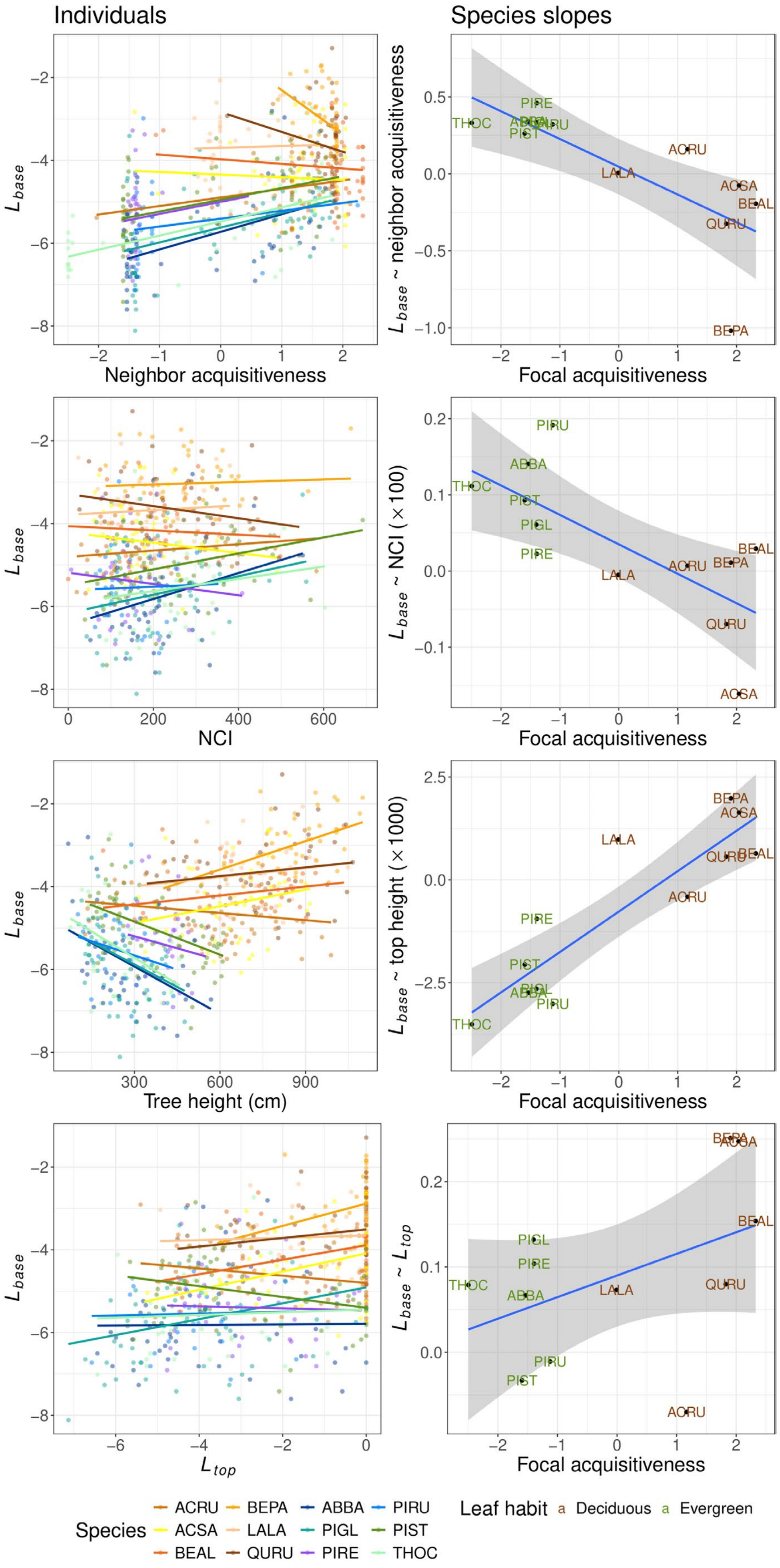

FIGURE 3 Relationships between individual-level variables and L_{base} across species. The individual-level variables are neighbour acquisitiveness (top row), the neighbourhood competition index (NCI; second), the focal tree's height (third) and the light availability at the crown top (L_{top}; bottom). Left panels show the individual-level relationships with species-specific best-fit lines, while right panels show species' slopes in relation to their acquisitiveness. The slopes of the lines in the left panels are not exactly identical to the slopes plotted along the *y*-axis in the right panels, since the former are OLS regression slopes and the latter are based on mixed-effects models that also include a random intercept for plot.

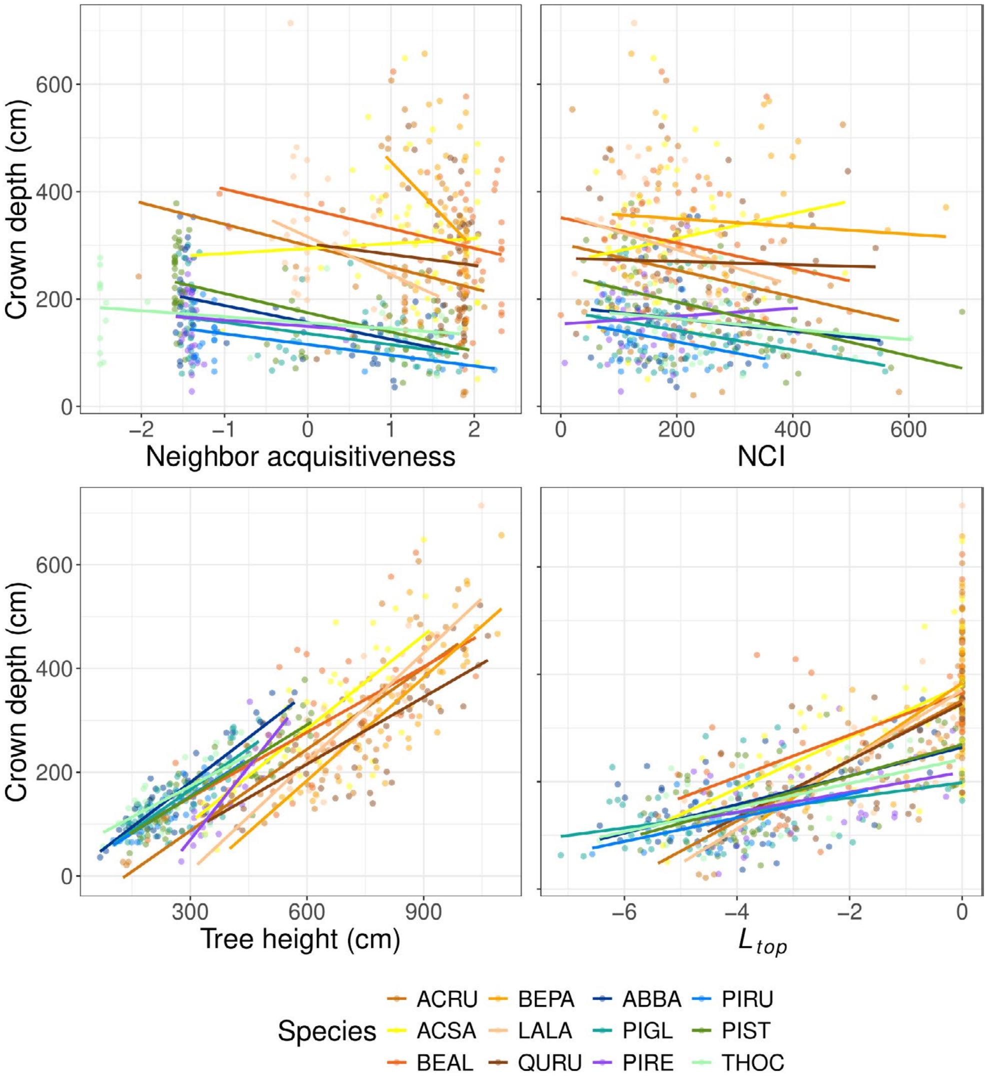

FIGURE 4 Relationships between individual-level variables and crown depth across species. The individual-level variables are neighbour acquisitiveness (top), the neighbourhood competition index (NCI; second), the focal tree's height (third) and the light availability at the crown top (L_{top}; bottom). The best-fit lines are derived from species-specific OLS regressions.

To evaluate whether the plastic adjustment of crown depth influences canopy packing, we compared simulated mixture plots where crown depths were drawn from monoculture plots (without plastic adjustment) to those where crown depths were drawn from the focal plot (with plastic adjustment). Simulated mixture plots without plastic adjustment showed less total crown volume than those with plastic adjustment (paired *t*-test; $t(44) = 3.05$, $p = 0.004$, mean difference = 0.810 m). The greatest source of this disparity was in the most productive mixtures, which yielded as much or more crown volume than the most productive monocultures in actual data, but considerably less in simulations (Figure 6). As a result, in these simulations without plastic adjustment in crown depth the relationship between total crown volume and diversity in functional traits ($t(67) = 2.35$, $R^2 = 0.076$, $p = 0.022$) or L_{base} ($t(67) = 3.10$, $R^2 = 0.125$, $p = 0.003$) was attenuated. Similar results hold when considering the net biodiversity effect on crown volume (Figure S7; see Appendix S1 for further details).

4 | DISCUSSION

We found considerable variation in the threshold of light availability below which trees pruned their lower branches. This value, which we called L_{base}, was lower for more conservative and shade-tolerant species, and plots whose species had greater diversity in L_{base} were more productive. However, there were also notable intraspecific patterns: while acquisitive species had lower L_{base} with acquisitive neighbours, conservative species had lower L_{base} with conservative neighbours. Moreover, there was a general tendency for L_{base} to be higher in crowns with sunlit tops. Most species had deeper crowns when surrounded by smaller and more conservative neighbours. In simulations, we found that plasticity in crown depth increased the total crown volume in diverse plots, strengthening the relationship between crown volume and functional diversity. Our findings suggest that self-pruning plays a role in defining trees' functional strategies, and that diversity in self-pruning strategies may contribute

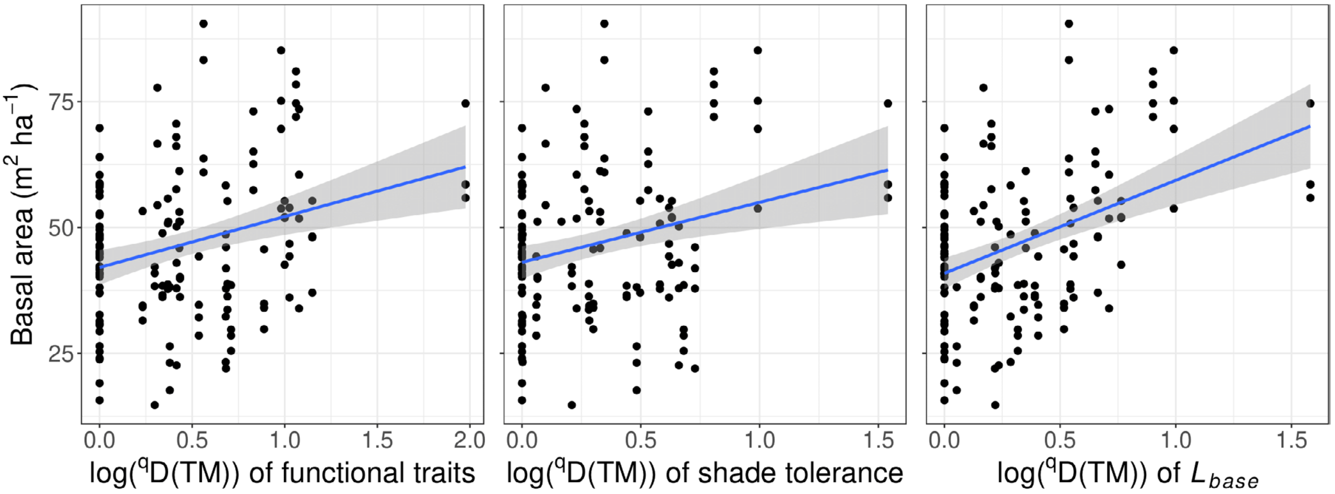

FIGURE 5 Correlations between basal area and diversity of functional traits (left), shade tolerance (middle) and L_{base} (right) among plots. Blue lines are OLS regression lines, with 95% confidence intervals shaded in grey.

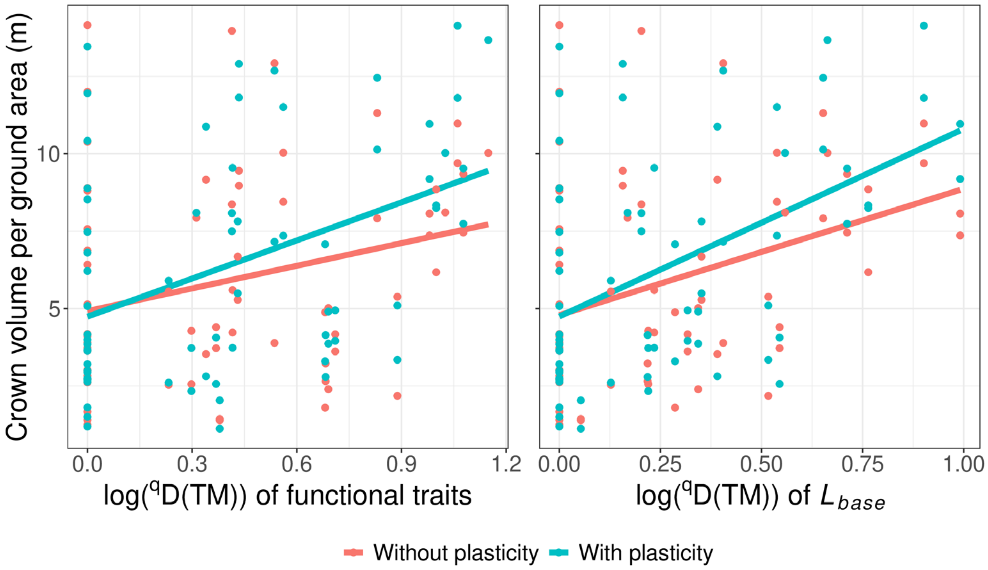

FIGURE 6 The relationship between total crown volume and diversity in functional traits (left) or L_{base} (right) in simulations where plasticity in crown depth between monoculture and mixtures is or is not allowed. Although we base the ground area on the 9 m^2 that contains the inner 6×6 trees, the trees' entire crown volume is included even when part of it would extend beyond the boundaries of that area. Lines represent OLS regression fits.

to biodiversity–ecosystem functioning relationships in light-limited mesic forests.

4.1 | Interspecific variation in self-pruning

A large body of research has emphasized the role of shade tolerance in either self-pruning (Schoonmaker et al., 2014) or related aspects of crown and stand structure, including crown shape (Poorter et al., 2006), canopy light transmission (Canham et al., 1994; Valladares & Niinemets, 2008), leaf area index (Niinemets, 2010) and delays in self-thinning (Urgoiti, Messier, Keeton, Belluau, & Paquette, 2023; Urgoiti, Messier, Keeton, & Paquette, 2023). Although L_{base} did correlate with shade tolerance across species, it correlated even more strongly with our index of resource-acquisitiveness. The directions of both relationships agreed with our predictions, which were based on the assumption that branches die when they become carbon-depleted. Furthermore, although shade tolerance is often taken to be strongly influenced by economic traits like dark respiration (Baltzer & Thomas, 2007a, 2007b; Lusk & Jorgensen, 2013), shade tolerance and acquisitiveness were entirely uncorrelated among our species. Future comparative work on the drivers of self-pruning may benefit from directly measuring the light compensation point and dark respiration, rather than taking them to be proxied by broad axes of plant functional variation.

In our experiment, acquisitiveness was tightly linked with both leaf habit/type and focal tree size, since the most acquisitive species were deciduous and fast-growing. These links raise the question of whether acquisitive species only have higher L_{base} due to their size rather than their traits. But were this the case, we would expect the largest and least-shaded trees among the conservative evergreen species to approach the L_{base} of the acquisitive deciduous species, whereas actual patterns of plasticity suggest that these groups diverge with increasing tree size (Figure 3). This potential for confounding could be addressed more directly in the future by measuring isolated trees of similar sizes, or by considering experiments where the relationship between acquisitiveness and tree size is reversed (Augusto et al., 2025; Kothari et al., 2021).

Leaf lifespan was also tightly linked to average L_{base} across species, even among just the evergreen species. There may be something intuitively logical about this link, given that L_{base} could exert a strong influence on branch longevity. One might imagine that, holding constant a stand's timeline of canopy closure and light extinction, a species with lower L_{base} would be expected to retain its lower branches for a longer period. In a deeper sense, both leaf lifespan and L_{base} may be underpinned by economic traits that determine how long it takes for the leaf and branch to fall below their respective light compensation points (Givnish, 1988; Reich et al., 2009).

Recent work has aimed to identify crown economic traits that define fundamental axes of tree architecture, analogous to the leaf economic spectrum (McNeil et al., 2023). We propose that L_{base} could serve as a simple crown economic trait to describe trees' strategies in light-limited environments. Indeed, it may serve as both a response and effect trait (sensu Lavorel & Garnier, 2002): a response trait because it influences how much leaf area a tree retains given the light environment created by its neighbours, and an effect trait because it determines how much shade the tree casts on any plants below itself. Species with lower L_{base} may be able to persist under more closed canopies, and when dominant may prevent establishment of shade-intolerant species in the understory (Craine & Reich, 2005; Rees et al., 2001). Since L_{base} shows strong and fairly consistent interspecific patterns, it may have a role in driving the ratchet of species turnover during succession in light-limited forests. Importantly, however, the hypotheses and interpretations we propose—and the notion of L_{base} as a trait that can be used in comparative ecological research—rely on the oft-assumed premise that the main criterion for whether a branch is retained or pruned is whether it receives enough light to sustain a positive carbon balance. This idea could in theory be complicated by water relations or other factors that may co-limit photosynthesis (Protz et al., 2000) and merits rigorous testing in a wide variety of forest ecosystems.

Our results leave open the question of whether L_{base} is redundant with known dimensions of variation in plant function, including shade tolerance and the plant economic spectrum. If it is, these economic traits may be more strongly intertwined with canopy properties than currently recognized. Regardless, it may not align simply with a general deciduous-evergreen split; for example, some very shade-intolerant pines transmit large fractions of light (>25%) even at fairly high stocking densities (Battaglia et al., 2003; Knapp et al., 2016). Nor, in our opinion, is it likely to represent a straightforward angiosperm–gymnosperm split, despite the conserved ecological and developmental differences between these clades (Chomicki et al., 2017). Notably, the deciduous gymnosperm *L. laricina* resembled deciduous angiosperms in its self-pruning behaviour, which suggests a primary influence of present-day ecological strategies rather than deep evolutionary legacies. These links to other aspects of plant ecology and evolution could be resolved with a broader sampling of species.

4.2 | Plasticity in self-pruning

Besides the clear trends across species, we also found plasticity in L_{base} and crown depth across neighbourhoods. L_{base} showed contrary relationships with neighbourhood characteristics among acquisitive and conservative species. For acquisitive species, L_{base} became more negative with more acquisitive and larger neighbours. Since large neighbours reduced focal tree height—presumably via competition—L_{base} was also more negative among smaller focal trees. For conservative species, L_{base} was less negative with more acquisitive and larger neighbours and thus less negative among smaller focal trees.

The rise in L_{base} with size among more acquisitive species is consistent with findings that deciduous trees decline in leaf area index and transmit more light as they grow (Nock et al., 2008). This pattern may be explained by increasing respiratory load (Givnish, 1988; Sendall et al., 2015) or by greater allocation towards horizontal growth in sunlit parts of the canopy as a form of correlative inhibition (Nock et al., 2008), among other possibilities. It is harder to plausibly explain why L_{base} becomes more negative with size among more conservative species. Because these species tend to be much less dominant in mixture plots, they experience greater shading from acquisitive neighbours alongside self-shading—especially the smallest individuals with the least negative L_{base}. Some of these small individuals of conservative species have crown bases nearly at ground level (Figure S8), so they may not have initiated self-pruning at all.

There was modest evidence that trees had more light at the crown base when they had more light at the crown top. This pattern is consistent with correlative inhibition, in which trees whose crowns are at least partly sunlit tend to drop their lower branches at a higher light threshold than trees that are fully shaded. However, other factors may contribute to this trend: For example, if one of a focal tree's neighbours suddenly dies, it would increase the amount of light at both the crown top and the crown base, but without any relation to self-pruning strategies. Although Schoonmaker et al. (2014) had proposed that correlative inhibition may be strongest in shade-intolerant species because their strategies to acquire and preempt light require stronger preferential allocation to well-lit parts of the canopy, we did not find evidence that shade tolerance influences the relationship between L_{base} and L_{top}. To discern among competing explanations and decisively test how correlative inhibition varies among species, more direct manipulations may be needed (Henriksson, 2001; Schoonmaker et al., 2014).

All species declined in crown depth as the neighbourhood environment became more competitive. This result would be expected even in the absence of plasticity in L_{base}, since (1) competitive environments reduce the focal tree's top height, and (2) more competitive environments result in greater light extinction, which would cause the focal tree's L_{base} to be reached at a greater height. However, the plasticity in L_{base} can be assumed to contribute to variation in crown depth; if they had constant L_{base}, the most acquisitive species would presumably have had steeper declines in crown depth with increasing neighbour size or acquisitiveness, while conservative species would have had shallower declines.

4.3 | Self-pruning, diversity effects and canopy packing

Previous research in IDENT-Montréal has shown that species mixtures show a positive average net biodiversity effect (NBE)—they grow more than expected based on monocultures of their constituent species. In early years, this effect was weak and due almost entirely to the over-performance of high-yielding broadleaf species, which benefited from competitive release in mixtures with less productive species (Tobner et al., 2016). Across plots, the magnitude of the NBE was closely related to the increase in crown complementarity from monocultures to mixtures (Williams et al., 2017), and diverse plots had greater light interception (Rissanen et al., 2019). However, by the time of the self-pruning survey in 2018, there were more consistently positive NBEs that were driven by the over-performance of both high- and some low-yielding species, and the NBE was largest in plots with high diversity in plant economic traits (Urgoiti et al., 2022). There was also strong evidence for transgressive overyielding, in which certain mixtures are more productive than the most productive monocultures.

We found that diversity in L_{base} (as a measure of self-pruning strategies) was better correlated with plot basal area and NBEs than was diversity in functional traits or shade tolerance (Figure 5; Figure S6). Since the functional traits and shade tolerance values are species-level rather than site-specific values, this comparison is not meant to imply the superiority of L_{base}, but simply to benchmark the explanatory power of L_{base} against a commonly used approach in biodiversity–ecosystem function research (Blondeel et al., 2024; Urgoiti et al., 2022). Diversity in functional traits and especially in L_{base} was also positively related to crown volume—a relationship that, as our simulations showed, was strengthened by plasticity in crown depth (Figure 6; Figure S7). The most acquisitive and productive species in the experiment had much deeper crowns in mixtures with less acquisitive species than in the highly competitive environment of monocultures (Figure 4). As a result, mixtures with high diversity in functional traits or L_{base} produced about as much crown volume as the most productive monocultures, even though without plasticity in crown depth they would have produced much less. However, this plasticity in crown depth is not solely responsible for the positive relationship between diversity and crown volume, since the relationship appeared even in simulations without plasticity.

In general, the influence of diversity on productivity arises from multiple mechanisms of species interactions. In a dense, closed-canopy forest undergoing self-thinning (Urgoiti, Messier, Keeton, Belluau, & Paquette, 2023), competition for light can generally be taken as one of the dominant mechanisms. Under competition for light, the influence of species interactions on total productivity arises from a mixture of two effects: (1) competitive relaxation, in which light niche partitioning allows the community to achieve greater total light interception; and (2) competitive imbalance, in which the stark asymmetry of light competition causes most of the light to be intercepted by the most dominant species (Yachi & Loreau, 2007). Competitive imbalance usually has a negative influence, in that the stunted growth or death of deeply shaded species represents lost productivity. However, given that our results and past findings at IDENT-Montréal show evidence for transgressive overyielding and for over-performance of less-dominant species (Figure 3; Urgoiti et al., 2022), it appears that competitive imbalance may not have been strong enough to compromise total growth.

In IDENT-Montréal, deciduous species tended to occupy higher strata of the canopy than evergreen species (Urgoiti, Messier, Keeton, & Paquette, 2023). The species in these groups vary in both height at the crown top (due to variation in productivity) and at the crown base (due to variation in both productivity and self-pruning strategies). When pairing deciduous and evergreen species, deciduous species are likely to have benefited from competitive relaxation, and accordingly constructed much larger crowns (Figure 4). These deciduous species likely have better light-use efficiency under high light, and their sparser crowns allow a relatively high fraction of light to filter down to less-dominant evergreen species. Most of the evergreen species appear to have been able to continue growing under this partial shade, albeit not always as quickly, using much of the light transmitted through the deciduous crowns. As a result, the influence of competitive imbalance may not have been particularly severe. Indeed, shade-tolerant species may even be facilitated by large neighbours that shield them from harsh microclimates (Kothari et al., 2021).

Rapid growth and photosynthesis under high light often come at the cost of greater carbon loss and mortality under low light (Baltzer & Thomas, 2007a; Falster et al., 2018; Lusk & Jorgensen, 2013; Pacala et al., 1994). The success of mixtures after canopy closure may depend on an arrangement where the species that achieve early dominance are those that grow well under high light, and the species relegated to lower strata are those that can keep growing under relatively low light (Williams et al., 2021). This arrangement may be favoured by the fact that rapid growth enables early dominance. However, if the dynamic were inverted—perhaps due to other factors such as dispersal timing—and more shade-tolerant species achieved early dominance, the more shade-intolerant species may not be able to persist underneath. Even without this sort of inversion, extreme competitive imbalance may weaken diversity–productivity relationships (Yachi & Loreau, 2007), and there is some evidence that this may indeed occur in late succession (Yi et al., 2022).

To get a fuller picture of the links between tree diversity, crown architecture and ecosystem function is difficult because traditional methods to measure crown architecture are labour-intensive (Forrester et al., 2019; Williams et al., 2017). Further investigations will likely benefit from the growing accessibility of technologies like above-canopy LiDAR and terrestrial laser scanning (TLS). For example, although we show that total crown volume increases with diversity in self-pruning strategies, we cannot be certain that total leaf area increases without having measured leaf area density. LiDAR and TLS offer the potential to map full leaf area profiles and segment individual trees (Lines et al., 2022), which would provide unprecedented detail on trees' above-ground interactions.

In conclusion, we present the first major comparative study of self-pruning among trees in a light-limited forest. Consistent with the idea that self-pruning follows carbon depletion, we find that species' variation in self-pruning strategies can be explained by major axes of functional variation, including shade tolerance and the plant economic spectrum. Alongside strong interspecific variation, we also found distinctive patterns of plasticity: While acquisitive species self-pruned under deeper shade around acquisitive neighbours, conservative species self-pruned under deeper shade around conservative neighbours. Broader comparative studies could test the generality of these patterns and uncover further nuances in trees' functional strategies. At the plot level, greater diversity in self-pruning strategies corresponds with greater basal area and crown volume. These findings reinforce the strong links between diversity in canopy architecture and productivity in young, light-limited forests. We propose that L_{base} may serve as a simple crown-level functional trait to explain how the interactions between individual trees competing for light shape the structure and development of forest stands.

AUTHOR CONTRIBUTIONS

Alain Paquette and Christian Messier designed the IDENT-Montréal experiment and funded this study. Jon Urgoiti, Alain Paquette, Christian Messier and William S. Keeton conceived the project with substantial later contributions by Shan Kothari. Jon Urgoiti carried out fieldwork and initial data curation with supervision from Alain Paquette, Christian Messier and William S. Keeton. Shan Kothari performed statistical analyses and wrote the first draft of the manuscript with contributions from Jon Urgoiti and Alain Paquette; all authors contributed to revisions and gave approval for publication.

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UQAM and IDENT-Montréal are located on unceded Indigenous land. This land is recognized as the territory of the Kanien'kehà:ka Nation and has long served as a place of meeting and exchange for many other Indigenous nations. We owe our deep thanks to the many researchers and interns who have studied and maintained the IDENT-Montréal experiment during the first 9 years of its existence. McGill University provided access to the land on which IDENT-Montréal sits; no specific permit was needed. Peter Reich contributed to the initial design of the experiment. Daniel Lesieur and Mélanie Desrochers from the Centre d'étude de la forêt provided much valuable help with data management and GIS for positioning trees and plots. Eric Searle provided valuable advice on statistical analyses. Maria Faticov, Sarah Tardif, Charlotte Langlois, Davia Yahia, Elyssa Cameron and other members of the Paquette Lab provided useful feedback on an early draft. Chrystal Ashby offered valuable suggestions on the French abstract. Alain Paquette received funding from the Fonds de recherche du Québec—Nature et technologies (#267091) and the Natural Sciences and Engineering Research Council of Canada (RGPIN-2018-05201). William S. Keeton received funding from the McIntire-Stennis Forest Research Program of the United States Department of Agriculture. Christian Messier received funding from a Canada Research Chair in the Resilience of Forests to Global Change.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All data needed to reproduce analyses are archived at Borealis (Kothari et al., 2025; DOI: 10.5683/SP3/OYURVJ). All original code used in data processing and analysis is on GitHub at https://github.com/ShanKothari/self-pruning-analysis/, and a stable version is archived on Zenodo (Kothari, 2025; DOI: 10.5281/zenodo.15750867).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Analyses of canopy packing and net biodiversity effects.

Figure S1. Illustrations of how the crown base and top were defined in heterogeneous crowns.

Figure S2. A biplot of species in trait space following principal components analysis on the trait correlation matrix.

Figure S3. Estimates of crown volume per unit ground area, comparing the actual crowns approach with the two simulations.

Figure S4. The relationship between species mean L_{base} calculated across all measured plots and calculated only from monocultures.

Figure S5. Pairwise correlations among neighborhood variables.

Figure S6. Correlations between the net biodiversity effect on basal area and diversity metrics.

Figure S7. The relationship between the net biodiversity effect on total crown volume and diversity metrics.

Figure S8. The relationship between neighbor acquisitiveness and crown base height across species.

Figure S9. The relationship between crown depth and average crown radius across species.

Figure S10. The relationship between L_{base} and crown depth across species.

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