

Selection Effects Associated with Leaf Area and Stomatal Density Drive Productivity of Young Temperate Tree Communities Under Different Water Exclusion Treatments

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20 **Abstract**

21 1. A positive relationship between species richness and productivity has been observed
22 in forests around the world. The two classes of mechanisms thought to underlie this
23 relationship, complementarity effects and selection effects, both rely on species' traits,
24 whereby the diversity of traits (under complementarity effects) or the presence of specific
25 trait values (under selection effects) can increase productivity. However, while it has been
26 established that species richness increases productivity, few studies have tested which traits
27 underpin this relationship.

28 2. To address this gap, we examined which traits underpin the diversity-productivity
29 relationship in early-establishment temperate tree communities, and whether they act via
30 complementarity or selection effects. In addition, we tested how the observed relationship
31 and its underlying traits change among environments with different water availabilities.

32 3. These questions were answered using an experimental plantation of young temperate
33 tree communities with water exclusion treatments. Six temperate tree species were planted
34 in this experiment, either in a monoculture or in three-species mixed communities. To
35 separate the effects of species and trait diversity, the mixed tree communities had a fixed
36 species richness but varied in trait diversity. Leaf area, leaf mass per area, stomatal density,
37 chlorophyll concentration, specific root length, root tissue density, and root diameter were
38 measured in each community. Community productivity was measured both as aboveground
39 and belowground biomass. We compared our results from trait-based analyses of selection
40 and complementarity effects to results from classical additive partitioning analyses.

41 4. Using trait-based analyses, neither selection nor complementarity effects were
42 detected with belowground biomass as a productivity metric. Complementarity effects were

43 not detected with aboveground biomass, but the trait combinations of leaf area and leaf
44 mass per area, leaf area and stomatal density, and of stomatal density and specific root
45 length were associated with the selection effect in different environments. Similarly, classical
46 additive partitioning analyses found a larger selection effect but also revealed some
47 complementarity effects across all treatments that were not associated with any of the
48 measured traits. These findings suggest that biodiversity–productivity relationships in young
49 temperate tree communities arise mainly through selection on trait combinations
50 associated with carbon gain and water loss.

51 **1. Introduction**

52 Global anthropogenic change is affecting the richness, composition, and abundance
53 of co-occurring tree species in ecosystems across a range of forest types (Hooper et al.,
54 2005; Vellend et al., 2013; Dornelas et al., 2014). As these changes occur, growing concern
55 for their impact on forests has prompted research into the negative effects of species loss on
56 forest ecosystem functions (Díaz & Cabido, 2001; Balvanera et al., 2006). One such
57 ecosystem function, primary productivity, may be particularly impacted by the loss of
58 species, as it has been shown to increase with species richness in forests around the world
59 (Zhang et al., 2012).

60 Two classes of mechanisms can explain the positive relationship between species
61 richness and productivity: complementarity effects and selection effects. Complementarity
62 effects arise from positive interactions among species, such as niche complementarity and
63 facilitation, whereby the diversity of traits among species allows for a more complete and
64 efficient use of resources (Loreau, 2000; Díaz & Cabido, 2001; Loreau & Hector, 2001). By
65 using resources more efficiently, species perform better on average, thus collectively
66 increasing the productivity of the community (Loreau, 2000; Loreau & Hector, 2001). In
67 contrast, selection effects occur when species with specific traits outperform others in a
68 given environment, leading to the dominance of these highly productive species (Loreau,
69 2000). Here, greater richness increases productivity because highly productive species are
70 more likely to be present in a community with a high initial richness (Loreau, 2000). Loreau
71 & Hector (2001) developed a statistical approach to partition net biodiversity effects into
72 complementarity and selection effects by comparing species biomass observed in mixture to

73 the biomass predicted from monocultures, providing a useful tool to disentangle these two
74 mechanisms.

75 While both mechanisms relate to the species richness of a community, they are more
76 directly linked to the ecophysiological traits of the species present in the community (Díaz &
77 Cabido, 2001). Under complementarity effects, the diversity of traits among species
78 increases community productivity, whereas under selection effects, the presence of specific
79 trait values increases community productivity. Despite the fundamental role of traits in our
80 understanding of these mechanisms, few studies have tested the implicit assumption that
81 ecologically meaningful traits underpin the established species richness-productivity
82 relationship, and fewer have identified the traits underlying these effects (but see Tobner et
83 al., 2016, Jensen et al., 2025).

84 Further, although climate models for Eastern Canada project major shifts in
85 precipitation seasonality (Wang et al., 2022), we do not know how variability in water
86 availability affects these mechanisms and their underlying traits. It thus remains unclear how
87 the traits underlying complementarity and selection effects will be affected by the projected
88 changes in precipitation.

89 To address these gaps, this study uses an experimental plantation of young
90 temperate tree communities to investigate how trait diversity and composition influence
91 community productivity under varying water availability conditions. In each tree community,
92 seven leaf and root traits known to influence plant productivity and survival under drought
93 conditions were measured. Community productivity was estimated using measures of
94 aboveground and belowground biomass.

The objectives of this study are twofold. First, we ask which traits are responsible for the species richness-productivity relationship in temperate tree communities during the early stages of stand development, and whether they act via complementarity or selection effects. If trait diversity underlies the species-richness productivity relationship, then biomass will increase with trait diversity in the three-species communities. If trait composition underlies the species-richness productivity relationship, communities with a high abundance of specific trait values associated with increased productivity will have a higher biomass. Second, we ask how do complementarity and selection effects and their underlying traits change in environments with different water availabilities by assessing which traits are associated with productivity in each environment. We measure complementarity and selection effects based on trait metrics as well as the additive partitioning method developed by Loreau and Hector (2001).

2. Materials & Methods

2.1 Study Site

This study was conducted at the IDENT-Outaouais plantation, established in 2020, near Notre-Dame-de-la-Paix, Qc, Canada (45.7742, -75.0066). This site is a repurposed agricultural field, characterized by a 2021-2024 average temperature of 16 °C and an average total precipitation of 578 mm during the growing season (May to September inclusively), and a sandy loam soil.

Following the initial establishment of the experiment, seedlings were watered for two years, before the implementation of a water exclusion system in 2022. To further help seedling establishment, herbaceous vegetation was manually removed during the growing

117 season from 2020 to 2024 inclusively, and the study area was fenced to reduce mammalian
118 herbivory.

119 **2.2 Experimental Design**

120 Following a similar design to other plantations in the IDENT network (Tobner et al.,
121 2014), this study site is composed of replicated high-density tree communities. Each
122 community contains a 7x7 assemblage of temperate trees, planted as seedlings at regular
123 intervals of 0.5 m. The close-proximity design was implemented to accelerate interactions
124 among individuals at early stages of their development.

125 Six native temperate tree species (*Acer saccharum*, *Betula alleghaniensis*, *Larix*
126 *laricina*, *Picea glauca*, *Pinus resinosa*, and *Quercus rubra*) from local provenances in
127 Maniwaki, Qc for conifers, and in Berthierville, Qc for broadleaves, were planted in seven
128 three-species mixes (authorities in Burns & Honkala, 1990). The community compositions of
129 the three-species mixes were selected to form a gradient of functional diversity using 22
130 traits from the TRY dataset, with communities where species have similar traits at the low-
131 diversity end of the gradient and those where species have the most dissimilar traits at the
132 high-diversity end (Kattge et al., 2011) (Table S1). Later, trait values measured in situ were
133 used to determine the realized diversity gradient among mixtures. By maintaining a
134 functional diversity gradient while keeping species richness fixed, the effects of trait diversity
135 could be separated from the effects of species richness. Reference monoculture
136 communities for five of the listed species were also included in the study. Due to a limited
137 supply of *L. laricina* seedlings at the time of planting, it could not be planted in monoculture.
138 Overall, 12 unique communities (7 three-species mixes and 5 monocultures) were planted in
139 this experiment (Fig. 1).

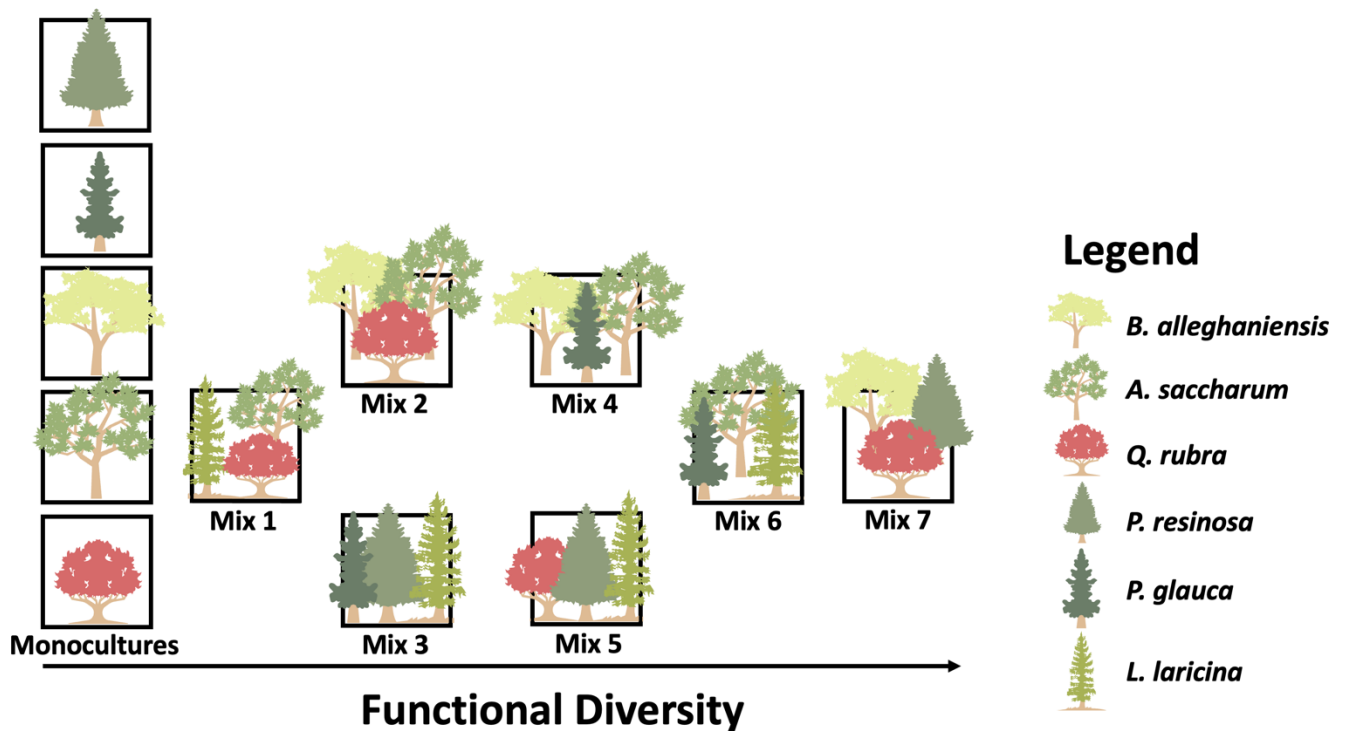


Figure 1. Three-species and monoculture temperate tree communities established along a functional diversity gradient in the IDENT-Outaouais experiment. The functional diversity gradient was established based on 22 traits from the TRY dataset (Kattge et al., 2011).

2.3 Water Exclusion Treatments

A water availability gradient was implemented during the growing season using slightly elevated gutters placed between trees to naturally collect and funnel rainwater downslope from the experimental site. Three water availability treatments were applied: a control (no precipitation removal, with gutters turned upside down to remove the gutter effect), a press water removal stress (25% precipitation removal annually), and a pulse water removal stress (50% precipitation removal biennially). The press treatment simulates a low but persistent water limitation scenario, whereas the pulse treatment represents a stronger

but annually variable water limitation scenario. Over time, the cumulative amount of water removed from each treatment was similar (25% per year on average). Both water exclusion treatments were started in 2022 and thus in 2024, all three water removal treatments were implemented. Each combination of community composition and treatment was replicated three times and spatially arranged into blocks, forming a total of 108 communities (36 control, 36 press, 36 pulse).

To quantify the effects of the water exclusion treatments, soil moisture content was measured weekly from June to October 2024. These measurements were taken at least three days after a precipitation event to allow the soil to return to field capacity. Soil moisture content was recorded in nine locations per community to account for spatial variability within plots. All soil moisture content measurements were taken integrating the top 5 cm of soil, using a FieldScout TDR 350 soil moisture meter.

2.4 Leaf Trait Measurements

Leaf trait measurements were collected from the nine centrally located trees in each community ($n = 972$) between July 3rd, 2024 and August 15th, 2024. From these individuals, a sun exposed lateral branch was randomly selected and cut from the top third of the tree crown. When individuals were shaded, one of the most sun exposed branches was cut. Branches were collected in the morning and stored on ice in plastic bags with damp paper towels, until processing the same afternoon.

Four leaf traits were measured on each branch: leaf area (LA), leaf mass per area (LMA), chlorophyll concentration (CHL), and stomatal density (SD). These traits were chosen as they are known to reflect the resource acquisition and the architectural strategy of trees and have been shown to be affected by drought conditions. LA is related to the light capture,

water loss, and thermoregulation of trees (Givnish, 1979; Olson et al., 2009; Lambers & Oliveira, 2019). LMA reflects the carbon cost of light interception at the leaf level (Wright et al., 2004). CHL affects light capture and is therefore correlated with photosynthetic capacity (Lambers & Oliveira, 2019). SD affects gas exchange, which then affects transpiration and photosynthetic rates (Evans & Loreto, 2000; Lambers & Oliveira, 2019).

Leaf trait measurements were collected differently for broadleaf species and conifer species. On broadleaf species, LA (cm^2) and LMA (g cm^{-2}) were measured without the petiole on three intermediate sized and relatively intact mature leaves, which were selected at random. On conifer species, LA (cm^2) and LMA (g cm^{-2}) were measured on twenty mature needles taken, at random, from the top side of the branch.

CHL (mg m^{-2}) and SD (stomata mm^{-2}) were measured on a second set of three randomly selected leaves in broadleaved species. On conifer species, these traits were measured on the same set of 20 needles. CHL on the adaxial side of the leaves was recorded using a CCM-300 chlorophyll content meter from the chlorophyll fluorescence ratio F_{735}/F_{700} (Opti-Sciences; Gitelson et al., 1999). For broadleaves, a stomatal density imprint was made on the abaxial side of each leaf using clear nail polish and clear tape ($n=3$). For conifers, the abaxial side of three needles was scanned at 4800 dpi to measure SD, using an Epson Perfection V850 Pro scanner.

2.5 Root Trait Measurements

For each species three root traits were measured: specific root length (SRL), root diameter (RD), and root tissue density (RTD). These traits were chosen as they are known to describe the important aspects of the morphology-based resource acquisition strategies of trees. SRL is generally higher in fast-growing species, as these species produce cheap roots

for rapid soil exploration and are suggested to invest less carbon into their mycorrhizal symbionts (Eissenstat, 1991; Comas & Eissenstat, 2004; Bergmann et al., 2020). RD is negatively correlated to SRL, with thin roots being associated to high SRL (Comas et al., 2002; Comas & Eissenstat, 2004). As a result, fast-growing species tend to have smaller RD (Comas et al., 2002; Comas & Eissenstat, 2004). RTD also varies along the fast-slow growth axis, with slow growing species typically having a higher RTD (Ryser, 1996; Kramer-Walter et al., 2016; Bergmann et al., 2020).

Root traits were measured at the species level in each community. Within the area delineated by the central 9 trees, three soil cores ($\varnothing$ 10 cm x 14 cm) were collected between July 23rd, 2024 and August 13th, 2024. Soil cores were taken at the centre point between four adjacent trees, so that each species was equally represented across the three cores. After collection, soil cores were bagged and kept frozen at -20 °C until processing.

Before being processed, soil cores were thawed for 12 hours at 4 °C. Thawed soil cores were then soaked in water for up to three hours and passed through a 5 mm and a 2 mm sieve. Roots retained in the sieves were gently rinsed to remove more soil, then resuspended in a bucket of clean water. Once the roots were mostly clean, they were transferred to a tray of water for further cleaning and sorting. Organic matter, debris, and grass roots were removed using tweezers, and the tree roots were sorted by species based on their morphology.

For trait measurements, ten branches of live fine roots from 1st -3rd order were selected at random for each species. These roots were scanned in a clear tray of deionized water at 1200 dpi on a backlit Epson Perfection V850 Pro scanner to avoid shadows. The fine roots were dried at 60 °C until their dry weight stabilized and weighed using an XSR205DU

analytical scale (Mettler Toledo). Root scans were then processed in Rhizovision Explorer (Version 2.0.3), to obtain measurements of average root diameter (mm), root length (mm), and root volume (mm³) (Seethepalli & York, 2020). From the measurements obtained, RTD was calculated as the dry weight divided by the volume of fresh root (g cm⁻³), and SRL was calculated as the length of root divided by its dry weight (m g⁻¹).

2.6 Biomass Measurements

In October 2024, the height (cm) and basal diameter (cm) of each tree was measured. Using these values, aboveground biomass was estimated following allometric equations for temperate tree species, where biomass is calculated as the square of the basal diameter multiplied by height and by wood density ($D^2 \times H \times WD$) (Tobner et al., 2016; Williams et al., 2017). Wood density values specific to Montreal were obtained from Belluau et al., (2021).

The aboveground biomass of each community was measured as the sum of the aboveground biomass of the nine central trees. A standardized measure of belowground biomass of each community was measured as the sum of the dry weight of all tree roots across the three soil cores collected in each community.

2.7 Testing Mechanisms Based on Traits

2.7.1 Testing Complementarity Effects

Univariate and multivariate metrics for complementarity effects were obtained for each community. For single traits, the variance in trait values within a community was used as the metric for complementarity effects, with complementarity increasing with variance. For multiple traits, Functional Dispersion (FDis), calculated using the FD package in R, was

used as the metric of complementarity (Laliberté & Legendre, 2010; Laliberté et al., 2014) (See equations S1, S2). In each community, FDis was calculated using all seven measured traits, as well as with each possible combination of trait pairs. Here, complementarity increases with FDis.

2.7.2 Testing Selection Effects

Univariate and multivariate metrics for selection effects were obtained for each community. To quantify selection effects for a single trait, community weighted distance to the ‘best’ trait values (CWD) was measured following this equation:

$$CWD = \sum_{j=1}^n p_j |b_j - x_j| \quad \text{Eqn. 1}$$

where p_j is the relative abundance of species j , b_j is the reference trait value from the most productive species in the monocultures of the experiment (the ‘best’ trait value), and x_j is the trait value of species j . This equation was derived from the calculation of community weighted mean presented in Lavorel et al. (2008). The CWD metric allowed us to compare the trait values in the community to those of the most productive conifers and broadleaves in the system, thus indicating selection for that particular trait value. If the trait values of the most productive species were associated with the selection effect, we would expect communities with low CWD (more similar to the ‘best’ traits) to produce more biomass.

Given the strong life history, anatomical, and physiological differences between angiosperms and gymnosperms, a different ‘best’ trait value was identified for each of these two clades. Since we test which traits predict the mixtures with the highest biomass, we could not also use the traits from those mixtures as the ‘best’ trait values. Instead, to avoid circularity, the ‘best’ trait values within each clade were defined as the traits of the

monocultures with the highest biomass. As there were no *L. laricina* monocultures, the ‘best’ trait values were obtained by averaging the traits of all *L. laricina* individuals across mixtures in each treatment. This was sound because the mean trait values of *L. laricina* showed no plastic response to community composition.

To quantify selection effects for multiple traits, the Functional Dispersion index was modified to be centered around the weighted community best trait value rather than the weighted trait centroid of the community. This provided us with a multivariate equivalent (FDis_{CWD}) to the community weighted distance from the ‘best’ trait value used previously. We calculated FDis_{CWD} in the following way:

$$\text{best trait centroid} = [c_{bi}] = \frac{\sum a_j b_{ij}}{\sum a_j} \quad \text{Eqn. 2}$$

$$\text{FDis}_{CWD} = \frac{\sum a_j z_{bj}}{\sum a_j} \quad \text{Eqn. 3}$$

where a_j is the abundance of species j , b_{ij} is the best trait value of species j for trait i , and z_{bj} is the Euclidean distance of species j to the multivariate ‘best trait’ centroid. In each community, FDis_{CWD} was calculated using all seven measured traits, as well as with each possible combination of trait pairs. Here, lower FDis_{CWD} values represent convergence towards the traits of the most productive species. Thus, selection increases as FDis_{CWD} decreases.

2.8 Testing Mechanisms Based on Additive Partitioning

Complementarity and selection effects were also calculated using the additive partitioning method developed by Loreau & Hector (2001), based on the difference between

the observed biomass in mixtures and the expected biomass under the null hypothesis that neither complementarity nor selection effects are present (See equations S3-S5).

For these calculations, the biomass of *L. laricina* in monocultures from three plots in an adjacent experiment were used. These *L. laricina* monocultures were planted in an 8 x 8 grid in 2020, and no water exclusion treatments were applied to these plots. The biomass in these monocultures was measured from the 12 central individuals and was used in calculations for all three treatments because there was no effect of treatment on the biomass of individual species, including *L. laricina*, nor on community-level productivity (Figs S1, S2).

Replication Statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates for each level of treatment or factor
Communities	Plot	3 treatments: Control, Pulse, Press 3 replicate blocks per treatment 12 plots per block (12 different community compositions)
Individuals	Plot	9 individuals per plot, 3 from each of 3 species (mixes) and 9 from one species (monocultures)

2.9 Statistical Analyses

All statistical analyses were performed in R (Version 4.5.1; R Core Team, 2025). To determine which angiosperm and gymnosperm planted in the experiment were most productive in monoculture in each treatment, a two-way ANOVA was conducted to test the effects of species, treatment, and their interaction on aboveground biomass (Table S2). The same approach was used to examine the effects of species, treatment, and their interaction on

303 trait values. When significant effects were detected, a post-hoc TukeyHSD was used to
 304 identify pairwise differences among groups.

305 To determine if water availability differed across water exclusion treatments,
 306 differences in the mean percent volumetric water content (VWC%) across communities in
 307 each treatment was tested using a one-way ANOVA (Fig. S3). Using the lme4 and emmeans
 308 packages in R, temporal changes in VWC% were analysed using a linear mixed-effects model
 309 (LME) with a post-hoc estimated marginal means test (EMM), predicting VWC% as a function
 310 of treatment, date, and their interaction, and with plot ID a random effect (Bates et al.,
 311 2015; Lenth, 2025). One-way ANOVAs and post-hoc TukeyHSD tests were also used to
 312 compare mean aboveground and belowground biomass among treatments and to assess the
 313 effects of treatments on species traits (Figs S2, S4).

314 To determine if biomass increased with diversity due to trait complementarity in
 315 each treatment, we tested whether aboveground and belowground biomass increased with
 316 trait variance and with FDis using linear regressions. To determine if biomass increased with
 317 diversity due to selection for the 'best' traits in each treatment, we tested whether
 318 aboveground and belowground biomass increased with CWD and with FDis_{CWD}. One-way
 319 ANOVAs and post-hoc TukeyHSDs tests were used to assess if complementarity and selection
 320 effects measured using the additive partitioning method varied among treatments. T-tests
 321 were also used to determine if either mechanism was more prominent in each treatment.

322 Model assumptions were checked using the procedure described in Zuur & Ieno
 323 (2016). When model assumptions of homoscedasticity were not met, independent variables
 324 were log-transformed or square root transformed as needed to produce homoscedasticity.

325 The Benjamini-Hochberg procedure was used to control the experiment-wide false discovery
 326 rate and calculate adjusted p-values.

327 **3. Results**

328 **3.1 Effects of Water Exclusion Treatments**

329 Of the three water exclusion treatments applied in 2024, only the pulse treatment
 330 resulted in soil that was drier than the control, although this difference was marginal. On
 331 average, the percent soil volumetric water content (VWC%) in the pulse treatment was
 332 14.86%, which is 20% drier than the press treatment (mean VWC% = 18.16%) and 16% drier
 333 than the control treatment (mean VWC% = 17.36%) (ANOVA & TukeyHSD post-hoc, Press: p
 334 = 0.020, Control: p = 0.1). Overall, all treatments followed the same temporal trends and
 335 maintained consistent VWC% differences during the growing season (LME & EMM post-hoc,
 336 p < 0.001; Fig. 2).

337 The water exclusion treatments did not affect aboveground and belowground
 338 biomass (ANOVA, aboveground: p = 0.588, belowground: p = 0.27) or net biodiversity effect
 339 (ANOVA, p = 0.52). The treatments also had a minimal effect on traits, as a significant plastic
 340 response in monocultures across treatments was only observed in the CHL of *B.*
 341 *allegghaniensis* (ANOVA & Tukey post-hoc, Pulse-Press: p = 0.009, Pulse-Control: p = 0.007)
 342 and in the RTD of *P. resinosa* (ANOVA & TukeyHSD post-hoc, Press-Pulse: p = 0.002, Press-
 343 Control: p = 0.002) (Fig. S5).

344

345

346 **Figure 2.** Change in percent volumetric soil water content during the growing season, by
 347 treatment. All treatments followed the same temporal trends and maintained consistent
 348 percent volumetric water content differences throughout the growing season, as indicated
 349 by the loess curve. The percent volumetric soil water content in the pulse treatment was
 350 consistently lower than in the control and the press treatments ($p < 0.001$).

351

352 **3.2 Which Traits Affect Biomass (and by Which Mechanism)**

353 We found no evidence of complementarity effects based on the studied traits in this
 354 system because neither metric of community productivity increased with community trait
 355 variance or with FDis. We also found no evidence of univariate selection effects in this
 356 system because neither metric of community productivity decreased with CWD for any trait.
 357 In contrast, multivariate analyses with aboveground biomass provided evidence of selection
 358 effects (Table 1). Belowground biomass was not related to any metrics of complementarity
 359 or selection effects (all $p > 0.05$).

Table 1. Trait combinations significantly (*) and marginally significantly (.) associated with selection effects. No traits were associated with complementarity effects. Bolded traits are under selection in multiple treatments and grouped by row.

Analyses	Treatment	Press	Pulse	Control
Trait pairs		LA & SD (*)	LA & SD (.)	LA & SD (.)
			SD & SRL (*)	
		LA & LMA (*)		LMA & SD (.)

In multivariate analyses, aboveground biomass decreased with the community weighted distance to best of trait pairs that included LA in the press treatment. Here, aboveground biomass decreased threefold with multivariate distance ($FDis_{CWD}$) to the best LA and LMA values (Linear model, $R^2 = 0.45$, $p = 0.027$; Fig. 3). Aboveground biomass also decreased threefold with the log of the distance to the best trait value ($\log FDis_{CWD}$) for the combination of LA and SD (Linear model, press: $R^2 = 0.47$, $p = 0.027$; Fig. 3). In addition, the trait pair of SD and SRL was associated with the selection effect in the control. Aboveground biomass decreased fourfold with the log of the distance to the best SD and SRL values ($\log FDis_{CWD}$) (Linear model, $R^2 = 0.53$, $p = 0.049$; Fig. 3).

There was also weak evidence of selection for the trait pairs of LA and SD, and of LMA and SD. Aboveground biomass decreased marginally with the log of the distance to the best trait value ($\log FDis_{CWD}$) for the combination of LA and SD in the pulse and the control treatments (Linear model, Pulse: $R^2 = 0.34$, $p = 0.062$, Control: $R^2 = 0.35$, $p = 0.059$) and with the log of the distance to the best trait value ($\log FDis_{CWD}$) for the combination of LMA and SD in the control (Linear model, $R^2 = 0.30$, $p = 0.099$).

In some cases, relationships between the complementarity and selection metrics and biomass were in the opposite direction of the predictions. Because these relationships do not provide support for either mechanism, they are reported in the supporting materials but not discussed further (Table S3).

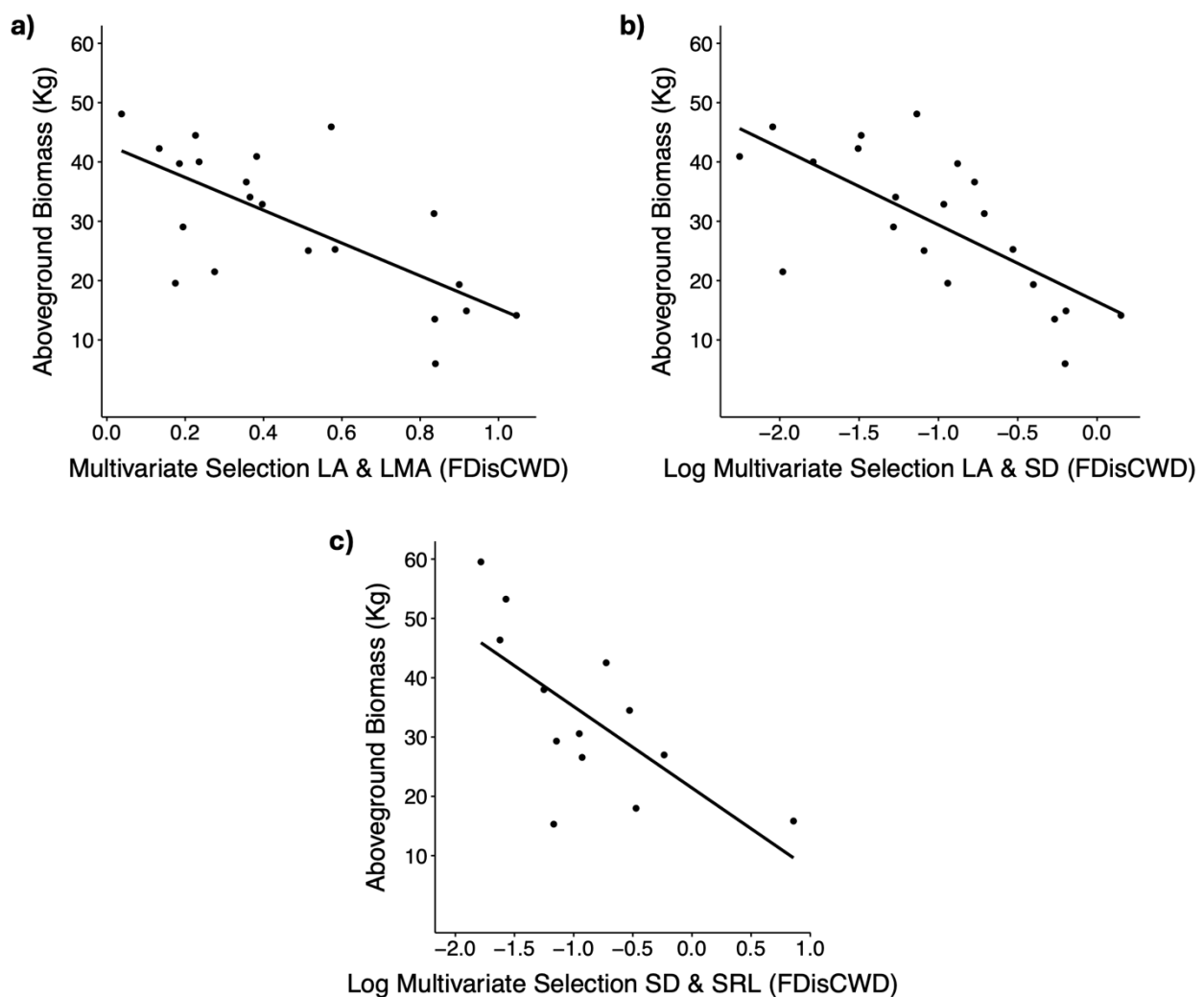


Figure 3. Linear regressions of aboveground biomass, in kilograms per plot, against the multivariate metric for selection effects ($FDis_{CWD}$). Panel a) against the $FDis_{CWD}$ of LA and LMA in the press treatment ($R^2 = 0.45$, $p = 0.027$). Panel b) against the $FDis_{CWD}$ of LA and SD

389 in the press treatment ($R^2 = 0.47$, $p = 0.027$). Panel c) against the $FDis_{CWD}$ of SD and SRL in
390 the control ($R^2 = 0.53$, $p = 0.049$).

391

392 **3.3 Which Mechanisms Affect Biomass Based on Additive Partitioning**

393 The biomass-based measures of complementarity and selection effects obtained
394 using the additive partitioning method showed that selection effects were more prominent
395 than complementarity effects in the pulse treatment (T-test, $p = 0.01$; Fig. 4). In the control
396 and the press treatments, complementarity and selection effects were not different (T-test,
397 Con: 0.80, Press: 0.11). Across treatments, there were stronger complementarity effects in
398 the control than the pulse treatment (ANOVA & TukeyHSD post-hoc; $p = 0.022$), whereas
399 selection effects did not differ among treatments (ANOVA; $p = 0.80$; Fig. 4).

400

401

Figure 4. The average biodiversity effect on aboveground biomass in plots each treatment, partitioned between complementarity and selection effects. Red and blue error bars represent 95% confidence intervals for complementarity and selection effects, respectively.

4. Discussion

Our first objective was to determine which traits are responsible for the species richness-productivity relationship in young temperate tree communities, and whether they act via the complementarity or the selection effect. We found that selection was the dominant mechanism driving increased productivity during early stand development. This pattern was detected for aboveground biomass but not belowground biomass. We found that selection effects were associated with pairs of traits which included LA, LMA, SD, and SRL. Our second objective was to determine how complementarity and selection effects and their underlying traits change across environments with different water availabilities. We found that complementarity effects changed among the water availability treatments, whereas the strength of selection effects was consistent across treatments. However, the trait pairs associated with selection effects differed among treatments.

4.1 Selection for Leaf Area & Leaf Mass per Area

The trait combination of LA with LMA was associated with the selection effect in the press treatment. Small leaves are characteristic of the dominant species in our system, *L. laricina* and *B. alleghaniensis*. Given the open nature of the canopy at the time of establishment, light conditions likely favoured the successful dominance of *L. laricina* and *B. alleghaniensis*, which depend on abundant light to compete and grow successfully (Burns &

Honkala, 1990). Under these high light conditions, small leaves are less prone to overheating due to their thinner air boundary layers (Parkhurst & Loucks 1972; Givnish, 1979). The thin boundary layers of small leaves facilitate convective heat dissipation, allowing the leaf to avoid overheating, which in turn, reduces the rate of transpiration (Parkhurst & Loucks, 1972; Givnish, 1979). Smaller leaves may therefore confer an advantage by decreasing the amount of water lost during cooling (Givnish & Vermeij, 1976).

In combination with smaller leaves, low LMA was associated with the selection effect in both conifers and broadleaves. Low LMA reflects a lower leaf dry-mass investment per unit of light-intercepting area produced at the leaf level (Wright et al., 2004). By investing less mass per unit area of leaf tissues, low LMA species can benefit from a quicker photosynthetic carbon return on investment, allowing them to grow faster (Wright et al., 2004; Poorter et al., 2009). LMA can also be related to water use efficiency (WUE), the rate of CO₂ uptake for a given rate of water loss (Cernusak, 2020). This relationship has been reported at multiple scales, however, contrary to the selection for low LMA values observed here, previous studies have reported increases in WUE with LMA (Poorter et al., 2009; Baird et al., 2017; Messier et al., 2018). If LMA reflects carbon use, selection for more acquisitive leaves in a water-limited environment (press treatment) would be counter-intuitive. If LMA reflects water-use efficiency, it is also unclear why non-efficient leaves would be selected for in that type of environment. We therefore interpret selection for low LMA in our system as reflecting indirect selection for shorter leaf lifespans, which we did not measure here. *L. laricina* is the only deciduous gymnosperm included in this study and thus has a shorter leaf lifespan, whereas *B. alleghaniensis* is an intermediate-growth angiosperm, such that each leaf lasts less than a full growing season. Leaf abscission by *B. alleghaniensis* throughout the

growing period could serve to reduce transpiration when water is limited (Taylor & Whitelaw, 2001).

4.2 Selection for Leaf Area & Stomatal Density

LA was also associated with the selection effect in combination with SD. Although both dominant species in our system had smaller leaves than the other species of the same leaf habit, they differed in their stomatal densities, with high SD in *L. laricina* and low SD in *B. alleghaniensis* (Fig. S4). Like LA, SD affects gas exchange; while leaf area constrains the physical surface available for heat exchange and water loss, stomatal traits determine how gas exchange and transpiration are regulated at that surface. However, the high- and low- SD of *L. laricina* and *B. alleghaniensis* do not necessarily indicate high- and low- leaf gas exchange, as this property is determined by other stomatal traits such as stomatal size, with larger stomata providing faster evaporative cooling (Boardman, 1977; Abrams, 1990). Gas exchange rates can also be affected by the opening and closing of stomata in response to environmental cues (Wolz et al., 2017). Intrinsic water use efficiency (WUE_i) can be used to determine stomatal responsiveness, as species that close their stomata rapidly in response to environmental cues tend to have a high WUE_i (Brodribb et al., 2009; Cernusak, 2020; Ozeki et al., 2022). The environmental threshold at which trees reduce their stomatal conductance varies across species, therefore differences in the stomatal responses of *L. laricina* and *B. alleghaniensis*, reflected in their WUE_i , may also explain why these species exhibited diverging SD (Wolz et al., 2017).

Based on the observed selection on LA and SD, evapotranspirative and photosynthetic functions are likely the targets of selection during stand establishment. If LA and SD were only associated with the selection effect due to the high light conditions to

which the trees were exposed, we would expect these trait pairs to be selected in other treatments. Given that selection for these trait pairs was only observed in the press treatment, which should represent a low but persistent reduction in water availability, belowground resources may have affected aboveground processes. Small leaves and effective gas exchange may provide a greater advantage in dry conditions, where trees cannot afford to lose as much water.

Notably, these trait combinations were not associated with the selection effect in the pulse treatment, suggesting that the effect of the treatments may be cumulative. For example, shoot formation often occurs over two years, with bud development starting in the first year and bud elongation in the second year (Bréda et al., 2006). As a result, water availability can affect shoot formation in either or both years (Bréda et al., 2006). Similarly, some roots persist from previous years, such that not all sampled roots were produced during the pulse year. Since water availability was not reduced in the pulse treatment in 2023, selection from lower water availability in the second year alone may be harder to detect. This could explain the marginal effect of LA and SD in the pulse and control treatments.

4.3 Selection for Stomatal Density & Specific Root Length

The trait combination of SD and SRL was associated with the selection effect in the control treatment, indicating coordination between aboveground and belowground strategies. For each of these traits, the best trait values for conifers and broadleaves differed with high SD and low SRL in *L. laricina* and low SD and high SRL in *B. alleghaniensis*.

Although more traits are needed to fully understand gas exchange in these species, the low SRL in *L. laricina* and high SRL in *B. alleghaniensis* may be indicative of their

respective water use strategies. Seedlings of *Larix* species have been shown to have a conservative water use strategy, whereas seedlings of *Betula* species used water more liberally (Gao et al., 2017). *B. alleghaniensis* may thus require a more acquisitive root system, as reflected in its high SRL, to sustain this greater water use. In contrast, selection effects on low SRL paired with high SD in *L. laricina* might reflect the conservative water use of this species. It is, however, unclear why this relationship between SD and SRL and aboveground biomass only occurred in the control treatment.

Alternatively, in gymnosperms, selection acted on an unmeasured axis of plant strategy, with SD and SRL responding jointly due to underlying trait integration as these traits were strongly negatively correlated within the clade (Gymnosperms: R^2 : -0.93, Angiosperms: R^2 : 0.04). Given the strong correlations between these traits, but the lack of strong selection for either trait individually, variation in another, unmeasured trait may be driving the observed variation in SRL and SD in gymnosperms. Future work can explore additional traits related to gas exchange (as suggested by SD), and to nutrient acquisition (as suggested by SRL) to investigate the integration of other traits. The consistent selection for pairs of traits or all traits highlights that physiological coordination, rather than individual traits, underlies differences in productivity.

4.4 Comparison of Trait Data and Biomass Data

Evidence for complementarity and selection effects from the trait-based measurements and the biomass-based measurements were largely consistent with each other: in both types of analyses, selection was identified as the main mechanism driving increases in community productivity. This finding is consistent with previous studies, which

516 have shown that selection effects contributed more to the productivity of young forest
517 stands than complementarity effects (Tobner et al., 2016; Jensen et al., 2025). While
518 evidence for selection was consistent in all treatments based on the biomass metrics, the
519 trait metrics highlighted that the traits associated with the selection effect differed across
520 treatments.

521 The main difference between the biomass-based and the trait-based metrics
522 occurred in the detection of complementarity effects. Using the biomass metrics,
523 complementarity was detected in all three treatments, whereas no complementarity was
524 detected using the trait-based metric. This difference was most notable in the control,
525 where complementarity effects were nearly as prominent as selection effects. The lack of
526 evidence for complementarity using the trait-based metrics likely indicates that the
527 complementarity traits were missed, which is to be expected when measuring specific
528 aspects of the phenotype. For example, Jensen et al., (2025) observed that stronger
529 complementarity effects were associated with lower community-weighted means of wood
530 density, a trait not measured here.

531 In conclusion, together the biomass-based and the trait-based metrics provide a
532 fuller picture of the mechanisms at play in a system. The biomass-based metrics are reliable
533 for detecting the mechanisms at play because complementarity and selection effects will
534 always produce a biomass response. In contrast, the trait metrics can be used to identify the
535 traits underlying each mechanism. Here, selection for LA, SD, LMA and SRL point to
536 coordinated regulation of carbon gain and water loss as a key driver of productivity during
537 early stand establishment.

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Supporting Information

Selection Effects Associated with Leaf Area and Stomatal Density Drive

Productivity of Young Temperate Tree Communities Under Different

Water Exclusion Treatments

Supplementary Tables

Table S1. Summary of the 22 traits from the TRY dataset (Kattge et al., 2011), used to select the community composition of the three-species mixes planted in this study.

Trait Acronym	Trait Name	Trait TRY ID
RootN	Fine root nitrogen (N) content per fine root dry mass	475
LA	Leaf area (in case of compound leaves: leaf, petiole included)	3110
SLA	Leaf area per leaf dry mass (specific leaf area, SLA or 1/LMA): petiole excluded	3115
CN	Leaf carbon/nitrogen (C/N) ratio	146
LDM	Leaf dry mass (single leaf)	55
LL	Leaf length excluding petiole (leaf lamina length)	940
Na	Leaf nitrogen (N) content per leaf area	50
Nm	Leaf nitrogen (N) content per leaf dry mass	14
NP	Leaf nitrogen/phosphorus (N/P) ratio	56
Pm	Leaf phosphorus (P) content per leaf dry mass	15
Photoa	Photosynthesis rate per leaf area	53
Photom	Photosynthesis rate per leaf dry mass	40
Rd	Leaf respiration rate in the dark per leaf dry mass	41
LitterCN	Litter carbon/nitrogen (C/N) ratio	150
LWR	Plant biomass and allometry: Leaf dry mass per plant dry mass	110
RGR	Plant growth rate relative (plant relative growth rate, RGR)	77
PHV	Plant height vegetative	3106
Lifespan	Plant lifespan (longevity)	59
RRT	Root rooting depth	6
SDM	Seed dry mass	26
SCm	Stem carbon (C) content per stem dry mass	407
SSD	Stem specific density (SSD, stem dry mass per stem fresh volume) or wood density	4

Table S2. Results of the two-way ANOVA conducted to test the effects of species, treatment, and their interaction on aboveground biomass. While some species differed in their aboveground biomass production, the water exclusion treatments and the interaction between species and treatments did not have an effect on aboveground biomass.

	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
Species	5	160425781	32085156	42.360	<2e-16 (*)
Treatment	2	2147880	1073940	1.418	0.250
Species:Treatment	10	3197486	319749	0.422	0.931

Table S3. List of regressions that were significant (*) or marginally significant (.) but did not provide evidence of either complementarity or selection effects. In cases where the metric used was functional dispersion (FDis), biomass decreased with the multivariate trait metric for complementarity. This indicates that productivity was lower in communities that had a high trait diversity of a given group of traits. In cases where the metric used was community weighted difference (CWD), biomass increased with the univariate metric for selection (CWD). This indicates that productivity was higher in communities that had trait values that diverged from the traits of the most productive species.

Treatment	Metric	Trait	Productivity metric	R²	Adjusted p-value
Control	Log(FDis)	LA & SRL	Aboveground biomass	0.62	0.027 (*)
Control	Log(FDis)	LA & SD	Belowground biomass	0.37	0.049 (*)
Control	Log(FDis)	LMA & SD	Belowground biomass	0.37	0.049 (*)
Control	Log(FDis)	LA & RD	Aboveground biomass	0.50	0.059 (.)
Control	CWD	LMA	Aboveground biomass	0.33	0.068 (.)
Press	Log(FDis)	LA & RTD	Aboveground biomass	0.76	0.010 (*)
Press	FDis	LA & SD	Aboveground biomass	0.51	0.020 (*)
Press	Log(FDis)	LA & RD	Aboveground biomass	0.69	0.025 (*)
Press	Log(FDis)	RTD & SRL	Aboveground biomass	0.63	0.030 (*)
Press	Log(FDis)	RTD & RD	Aboveground biomass	0.57	0.049 (*)
Press	Log(FDis)	SRL & RD	Aboveground biomass	0.57	0.049 (*)
Press	Log(FDis)	LA & SRL	Aboveground biomass	0.61	0.032 (*)

Press	FDis	All traits	Aboveground biomass	0.63	0.030 (*)
Press	FDis	LMA & RD	Aboveground biomass	0.49	0.077 (.)
Pulse	Log(CWD)	LMA	Aboveground biomass	0.63	0.0042 (*)

Supplementary Figures

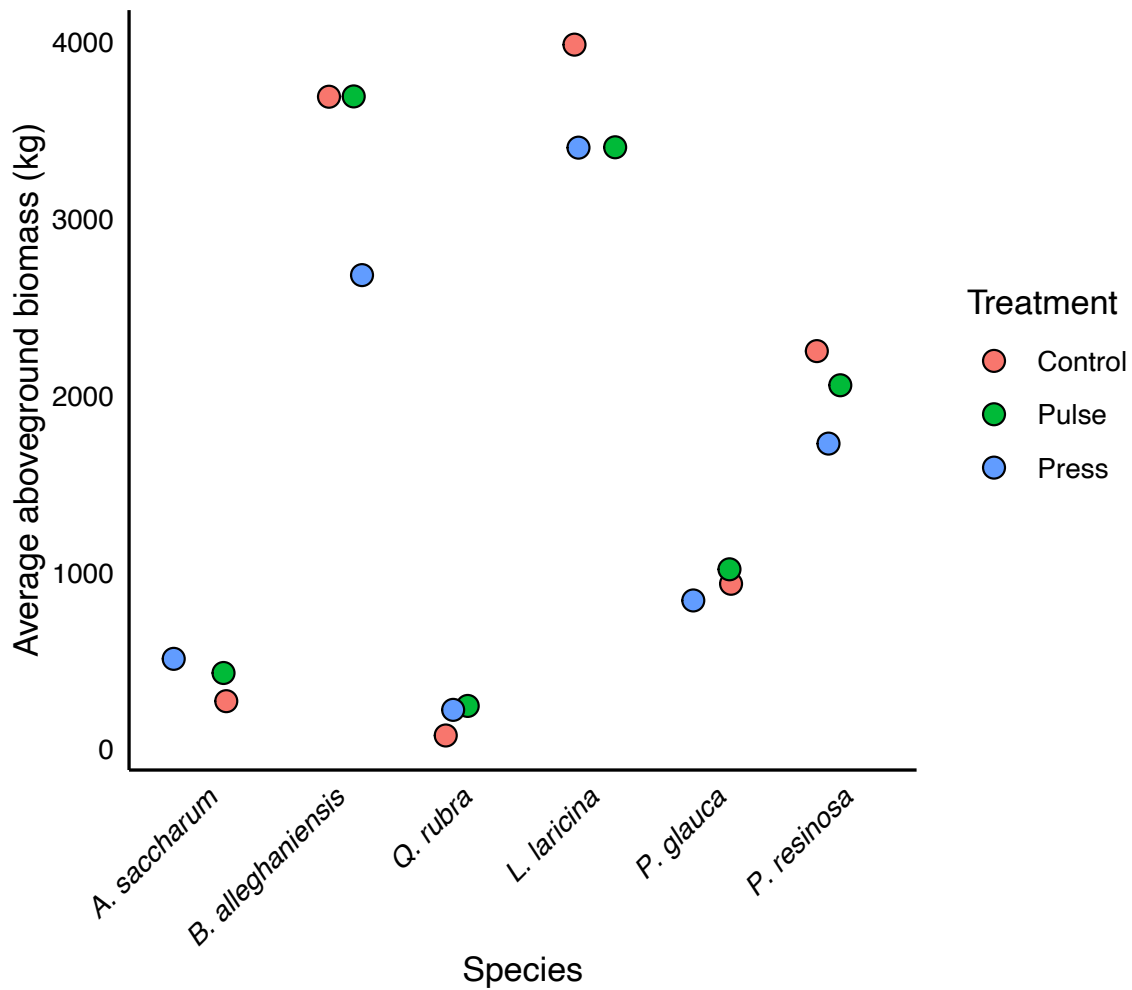


Figure S1. Differences in average aboveground biomass (Kg) across species, in each water exclusion treatment. For *L. laricina*, aboveground biomass was averaged across all individuals for each treatment. For all other species, aboveground biomass was averaged across individuals growing in monoculture for each treatment. Across all treatments, *L. laricina* and *B. alleghaniensis* had the highest aboveground biomass.

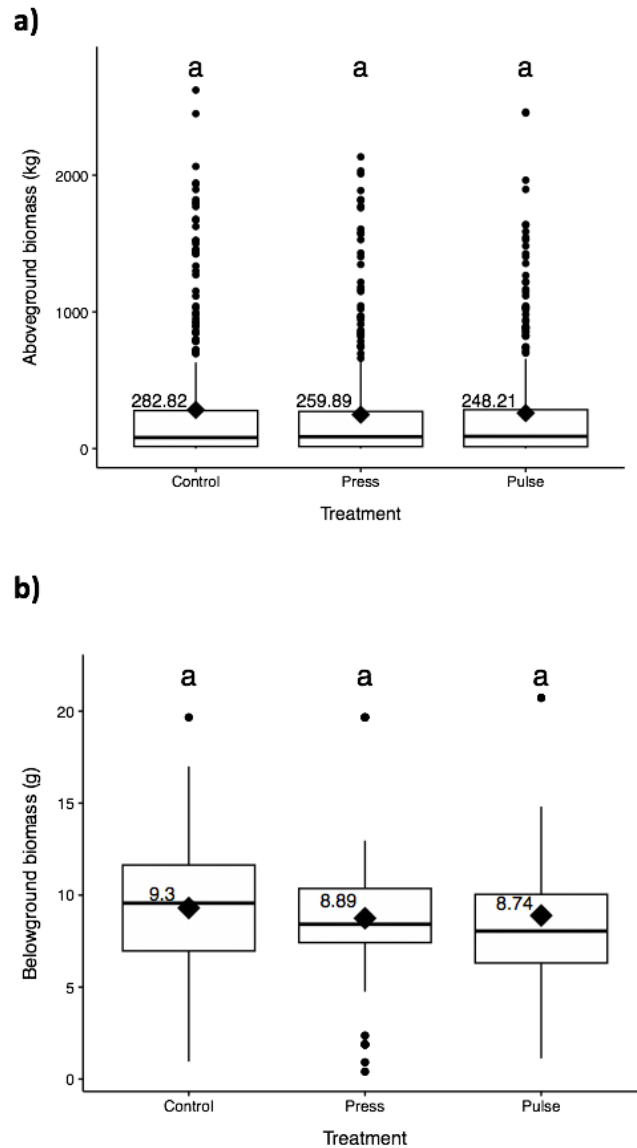


Figure S2. Differences in plot biomass across treatments. Panel a) illustrates the effects of the water exclusion treatments on aboveground biomass, in kilograms. Aboveground biomass for each tree was calculated as height x diameter² x wood density. The total aboveground biomass in 2024 did not differ across treatments ($p = 0.588$). Panel b) illustrates the effects of the water exclusion treatments on belowground biomass, in grams. Belowground biomass for each plot was calculated as the total dried weight of tree roots collected from three soil cores. The belowground biomass in 2024 did not differ across treatments ($p = 0.27$).

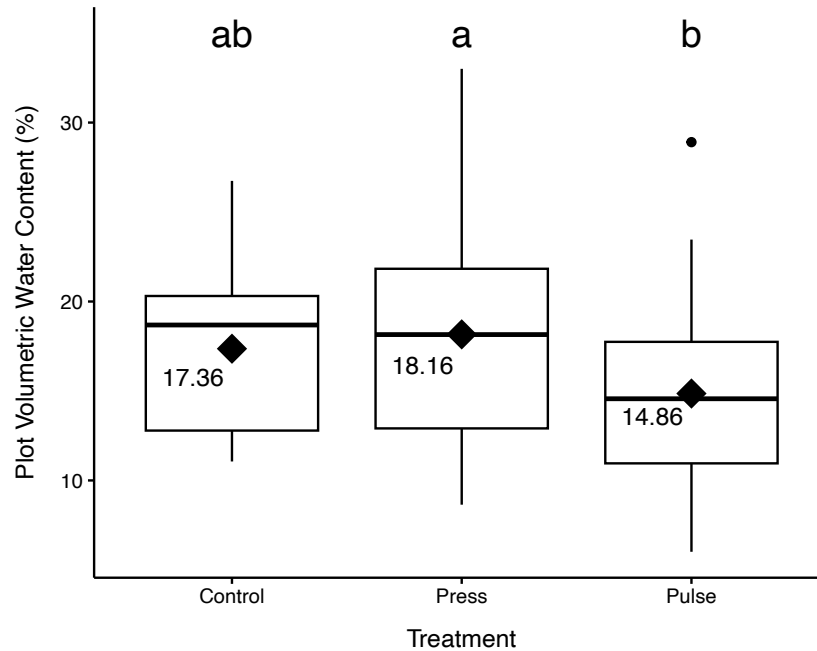


Figure S3. Differences in the percent volumetric water content (VWC%) of each treatment over the 2024 summer. Plot volumetric water content represents the percent volumetric water content averaged across nine measurements within a community for each day of measurement. Across all plots, the average volumetric water contents were significantly different between the pulse and the press treatments ($p = 0.020$), marginally different between the pulse and the control treatments ($p = 0.1$), and not different between the press and the control treatments ($p = 0.785$).

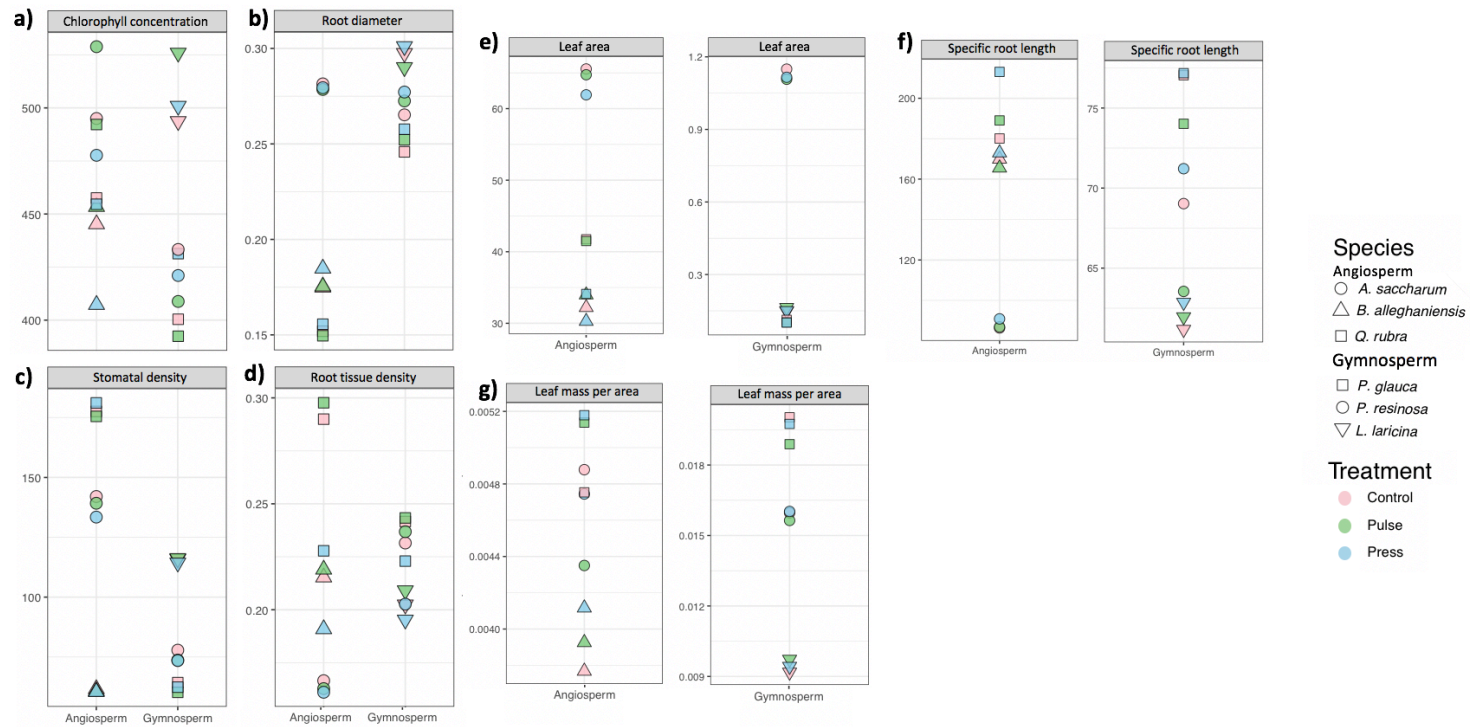


Figure S4. Differences in trait values across individuals of each species and water exclusion treatments. The angiosperms and the gymnosperms were included in the same panel when scales were comparable and in separate panels when scales were not comparable. The dominant species for each clade are identified by triangles. Trait differences are illustrated in panels: a) chlorophyll concentration (mg m^{-2}), b) root diameter (mm), c) stomatal density (stomata mm^{-2}), d) root tissue density (g cm^{-3}), e) leaf area (cm^2), f) specific root length (m g^{-1}), and g) leaf mass per area (g cm^{-2}).

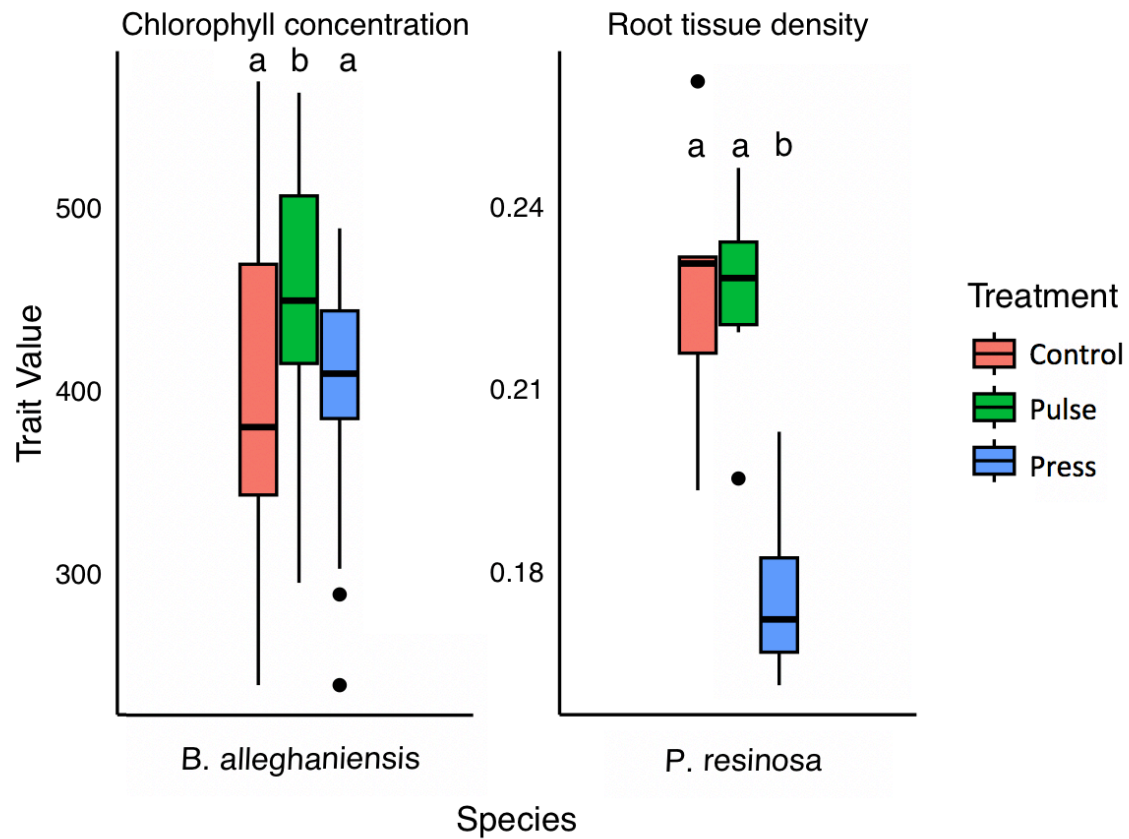


Figure S5. Differences in trait values of monoculture communities where trait plasticity was observed. The trait values of monocultures were grouped by treatment for comparisons. Three-species communities were not included, to isolate the effects of the water exclusion treatments from those of neighbouring species. In *B. alleghaniensis* monocultures, chlorophyll concentration was higher in the pulse treatment than in the press and the control treatments (Press: $p = 0.009$, Control: $p = 0.007$). In *P. resinosa* monocultures, root tissue density was lower in the press treatment than in the pulse and the control treatments (Pulse: $p = 0.002$, Control: $p = 0.002$).

Supplementary methods: Trait-based metrics of complementarity and selection effects

Functional Dispersion (FDis) was used as the multivariate metric of complementarity effects in this study. FDis was calculated for each community as:

$$\mathbf{FDis} = \frac{\sum a_j z_j}{\sum a_j} \quad \text{Eqn. S1}$$

where a_j is the abundance of species j and z_j is the Euclidean distance of species j to the community's weighted trait centroid (Laliberté & Legendre, 2010). In turn, the weighted centroid of each community is the abundance-weighted mean multivariate trait value, calculated as:

$$\mathbf{centroid} = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j} \quad \text{Eqn. S2}$$

where a_j is the abundance of species j , and x_{ij} is the trait value of species j for trait i (Laliberté & Legendre, 2010).

Supplementary methods: Additive partitioning of complementarity and selection effects

In this study, complementarity and selection effects were also calculated using the additive partitioning method developed by Loreau & Hector (2001). Here, ΔY , the net biodiversity effect (the sum of complementarity and selection effects) is calculated as:

$$\Delta Y = Y_O - Y_E = \sum_i RY_{Oi} M_i - \sum_i RY_{Ei} M_i = \sum_i \Delta RY_i M_i \quad \text{Eqn. S3}$$

where Y_O is the total observed yield of the mixture, Y_E is the total expected yield of the mixture, RY_{Oi} is the observed relative yield of species i in the mixture, RY_{Ei} is the expected relative yield of species i in the mixture, M_i is the yield of species i in monoculture, and ΔRY_i is the deviation from the expected relative yield of species i in the mixture (Loreau & Hector, 2001).

From this equation, complementarity effects (CE) and selection effects (SE) are then calculated as:

$$CE = N \overline{\Delta RY} \overline{M} \quad \text{Eqn. S4}$$

$$SE = N \text{cov}(\Delta RY, M) \quad \text{Eqn. S4}$$

where N is the number of species in the mixture (Loreau & Hector, 2001).

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