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Research article

Patterns of belowground overyielding and fine-root biomass in native and exotic angiosperms and gymnosperms

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Mixing tree species can lead to more productive forests, but how belowground productivity is affected by mixtures of trees of diverse phylogenetic and eco-evolutionary histories is unclear. Here, we examine how species origin and phylogeny affect belowground productivity in tree communities of varied richness and functional diversity. We measured standing fine-root biomass and annual fine-root production across 41 assemblages of 12 tree species, representing both angiosperms and gymnosperms originating from North America and Europe. Increasing functional diversity of mixtures stimulated overyielding of annual production but did not affect standing biomass. In general, annual productivity of mixtures of species that were less productive in monoculture had neutral (angiosperms) to positive (North American species: +16%) responses to mixing, whereas annual productivity of mixtures of species that were more productive in monoculture had neutral (European species) to negative (gymnosperms: −6%) responses to mixing. These differences translated into angiosperm mixtures overyielding in standing biomass by 16% but no effects of mixing on gymnosperm mixtures. The trends we observed between North American and European species annual production were reversed when considering standing biomass. European mixtures had 14% more standing biomass and North American mixtures had 10% less standing biomass than expected from monocultures.

Our study offers a rare examination of the combined roles of origin and phylogeny in forest fine-root productivity, and suggests varied consequences of biodiversity change for forest belowground productivity based on composition. In North America, belowground productivity of young forests composed of angiosperms and native tree species may be more tightly linked to diversity than that of forests dominated by gymnosperms or European species. This suggests that increased diversity may lead to the greatest enhancement of belowground productivity in native, North American forests dominated by angiosperms, but also that declines in diversity may be felt most strongly in these forests as well.

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Introduction

Belowground production constitutes a major carbon sink globally (Luyssaert et al. 2008, Clemmensen et al. 2013, Dawud et al. 2016, Yang et al. 2019), and is comparable to aboveground production in many forests (Jackson et al. 1996, Cairns et al. 1997, Helmisaari et al. 2002, Kroon et al. 2012). Aboveground, it is well documented that more diverse grasslands (Tilman et al. 2001, Dimitrakopoulos and Schmid 2004, Reich et al. 2004, Hooper et al. 2005) and forests (Leuschner et al. 2009, Morin et al. 2011, Zhang et al. 2012, Forrester and Bauhus 2016, Liang et al. 2016, Tobner et al. 2016, Williams et al. 2017) are often more productive than similar systems of lower diversity. However, the mechanisms governing belowground productivity are less well understood. Despite sizable differences in other forest functions based on diversity, species' geographical origin and phylogeny (Lemma et al. 2007, Liang et al. 2016, Finér et al. 2017), how the functional composition of communities impacts belowground productivity remains unclear and understudied (Augusto et al. 2015, Tobner et al. 2016).

Belowground productivity of tree communities can respond to changes in species richness in diverse ways. Some communities show signs of overyielding belowground (Kawaletz et al. 2013, Ma and Chen 2017), wherein community-level productivity is greater than the expected value based on the weighted mean of each species in monoculture. Other communities under yield (Domisch et al. 2015, Archambault et al. 2019, Martin-Guay et al. 2020) – having lower productivity than expected – and others still show no effect of species mixing (Lei et al. 2012, Jacob et al. 2014, Finér et al. 2017), wherein community-level productivity is as expected based on monocultures.

One of the most commonly assumed mechanisms for overyielding of forest ecosystems is resource partitioning (Fornara and Tilman 2008). Resource partitioning reduces competition between individuals and occurs when species access distinct resource pools and/or together increase soil nutrient availability (Reich et al. 2012, Mueller et al. 2013, Oram et al. 2018, Chen et al. 2021). However, which traits are most relevant to defining species' rooting niches and associated resource partitioning is unclear (Leps et al. 2006, von Felten and Schmid 2008, Roscher et al. 2012, Weemstra et al. 2016).

Many studies of belowground productivity focus on the distribution and structure of roots within the soil column, suggesting that variation between species' rooting depth (Dimitrakopoulos and Schmid 2004, Kulmatiski and Beard 2013) or root structure (Chen et al. 2016, Bu et al. 2017, Liese et al. 2017) is tightly linked to belowground productivity of forests and other systems. Yet, studies finding a lack of evidence for spatial niche partitioning belowground (Meinen et al. 2009, Barry et al. 2020) suggest that it may either be rare, hard to measure or both. Alternatively, resources may be partitioned temporally instead of spatially: differences in species' root phenology could lead to resource partitioning if root growth or resource acquisition of neighboring species occur over different time periods (Ashton et al. 2010, Schwinning and Kelly 2013, Furze et al. 2018, Makoto et al. 2020). By partitioning resources either spatially or temporally, more diverse forests may be able to increase belowground productivity.

If resource partitioning drives belowground productivity in forests, then forests composed of more functionally diverse species should be more prone to overyielding (as reviewed by Hooper et al. 2005, Cardinale et al. 2006). Broad categorizations of phylogeny and geographic origin may succinctly reflect some ecologically relevant differences that affect the propensity of a mixture to overyield (Augusto et al. 2015). Compared to angiosperms, gymnosperms on average invest more heavily belowground in the early stages of growth (Lei et al. 2012, Domisch et al. 2015, Archambault et al. 2019). Gymnosperms also prioritize root growth in more shallow soil strata (Finér et al. 2017), have less variable root phenology (Makoto et al. 2020, but see Withington et al. 2020) and have higher root turnover rates (An et al. 2017) than angiosperms. Finally, there is a trend of gymnosperms maintaining higher root:shoot ratios than angiosperms in experiments (Archambault et al. 2019, but see Reich 2014). These differences between angiosperms and gymnosperms may facilitate resource partitioning when the two groups are mixed and result in belowground overyielding in angiosperm–gymnosperm mixtures.

Species geographic origin may also be important to belowground overyielding. Many species that are exotic to North America benefit from an extended growing season that can lead to greater carbon assimilation at the expense of less effective nutrient resorption during senescence (McEwan et al. 2009, Fridley 2012, Paquette et al. 2012, Jo et al. 2015). This tradeoff increases exotic species' demand for soil nutrients and may cause them to invest more heavily in root growth than native species (Kawaletz et al. 2014, Jo et al. 2015, Caplan et al. 2019). Exotic species may also invest more belowground to compensate for weakened mycorrhizal mutualisms (Vogelsang and Bever 2009). Consequently, intense competition between highly-productive exotic species can cause underyielding in some mixtures of exotic species (Kawaletz et al. 2013). In contrast, differences in belowground productivity between native and exotic species may lessen belowground competition and facilitate overyielding of some native–exotic mixtures (Kawaletz et al. 2013). These observations may be part of a more general trend, whereby mixtures containing species with lower root productivity (typically angiosperms and native species) are more likely to overyield than more productive species (typically gymnosperms and exotic species) that saturate soil space and suppress productivity of other species (Kawaletz et al. 2013, Wright et al. 2021). However, no study to date has reported the combined roles of species origin (native or exotic) and phylogeny (angiosperm or gymnosperm) in forest root productivity, leaving these hypotheses to be tested.

Here, we consider the roles of functional, phylogenetic and taxonomic diversity vis-à-vis fine-root productivity within two experiments on two distant sites of distinct soil and climatic conditions along the boreal-temperate ecotone of North America. By using a common garden design across two sites, we offer greater generality by conducting the experiment in divergent settings. Unlike many biodiversity experiments, our experiment also varies in species richness and functional diversity in such a way that each richness level spans an orthogonal and independent gradient of functional diversity (Tobner et al. 2014), and includes factorial combinations within phylogenetic groups (angiosperms and gymnosperms) and species origin (North America or Europe). Particularly within the context of species origin, our study is novel and made rigorous by the inclusion of congeneric pairs that minimize the effects of phylogeny and functional differences on cross-origin comparisons – an important but often overlooked component in studies of exotic species (Diez et al. 2008, Procheş et al. 2008, Ma et al. 2016). The inclusion of congeneric pairs that have high functional similarity also allows us to isolate the role of traits from species' shared ecological histories, such that congeneric pairs should be interchangeable in mixtures if traits are the only factor regulating belowground interactions. In our work, we address three central hypotheses of the effects of diversity on fine-root biomass and productivity:

1) Greater diversity within species mixtures (in terms of species richness or functional diversity) results in greater overyielding of standing fine-root biomass and annual productivity of fine roots.
2) Mixing species with less fine-root biomass and annual productivity of fine roots in monoculture results in greater overyielding of standing fine-root biomass and annual productivity of fine roots
3) Mixing North American species or angiosperm species results in greater overyielding of standing fine-root biomass and annual productivity of fine roots compared to mixing European species or gymnosperm species.

Material and methods

IDENT experiment

We conducted this study within common garden plots established simultaneously in Cloquet, Minnesota, USA (42°21'36.36''N, 92°31'08.4''W) and Auclair, Québec, Canada (47°41'49.2''N, 68°39'18''W), during the spring of 2010. Together, these two sites form one experiment that is part of the International Diversity Experimental Network with Trees (IDENT) (Tobner et al. 2014). The Cloquet site was previously forested and has a sandy loam soil whereas the Auclair site was an abandoned pasture and has a loam soil. Mean annual temperature is 4.8 and 2.3°C, and mean annual precipitation is 783 and 965 mm at the Cloquet (Rich et al. 2015) and Auclair sites (www.climate-data.org), respectively.

The Cloquet and Auclair forest biodiversity experiment was designed to independently vary in functional diversity and species richness. This experiment uses a set of 12 tree species (Table 1), namely six angiosperms and six gymnosperms, each represented by three congeneric pairs of species from North America and Europe. Congeneric pairs were selected to minimize differences in traits (Tobner et al. 2014). At each site, containerized seedlings were planted into 7 × 7 grids spaced 40 cm apart (2.8 × 2.8 m plots) in spring of 2010. All seedlings originated from the same nursery stocks and were divided into two groups at random, with one group going to Auclair and the other to Cloquet in refrigerated trucks. Plots contained either one, two or six species resulting in 48 different assemblages in total that were replicated in four blocks (mixture descriptions presented in the Supporting information). Plots were randomly ordered within blocks in an 8 × 6 grid with each plot spaced 1 m apart. Once the tree seedlings were established, we allowed herbaceous ground cover to establish within plots, but continued to remove any woody species other than those that were planted. Due to practical

Table 1. Description of species used in the IDENT experiment.

Species	Abbreviation	Phylogenetic group	Phenology	Origin
Acer platanoides	ACPL	angiosperm	deciduous	Europe
Acer saccharum	ACSA	angiosperm	deciduous	N America
Betula papyrifera	BEPA	angiosperm	deciduous	N America
Betula pendula	BEPE	angiosperm	deciduous	Europe
Larix decidua	LADE	gymnosperm	deciduous	Europe
Larix laricina	LALA	gymnosperm	deciduous	N America
Picea abies	PIAB	gymnosperm	evergreen	Europe
Picea glauca	PIGL	gymnosperm	evergreen	N America
Pinus strobus	PIST	gymnosperm	evergreen	N America
Pinus sylvestris	PISY	gymnosperm	evergreen	Europe
Quercus robur	QURO	angiosperm	deciduous	Europe
Quercus rubra	QURU	angiosperm	deciduous	N America

limitations of time and resources, we focused on 41 (of the 48) assemblages on three (of the four) blocks at each site for this study, rather than all assemblages and blocks. This subset was selected such that each species was present in monoculture and in mixtures of species of the same origin (i.e. NA–NA and EU–EU mixtures) and mixtures of species of differing origin (i.e. NA–EU mixtures).

Fine-root assessments

We considered two metrics of fine-root productivity. First, we sampled existing standing fine-root biomass (SFRB) at both the Auclair site and the Cloquet site in September 2015. This measurement reflects the sum of the current year's growth and any remaining fine roots from previous years and is therefore a combined function of productivity and fine-root decay. Second, we installed two root ingrowth cores in each plot at the Cloquet site concurrent with our initial sampling in order to measure annual fine-root production (AFRP) for the following three years. Limited resources prevented us from also conducting ingrowth core measurements at the Auclair site.

SFRB in both Cloquet and Auclair, as well as AFRP in Cloquet, were sampled in each plot. Within each plot, we randomly selected two positions that were each at least 60 cm from the plot edge (i.e. within the central 6 × 6 area of the 7 × 7 grid plot). If a position was bordered by one or more dead trees at the time of coring, we sampled in a randomly determined adjacent grid position (approximately 40 cm away). At each sampling positon, we first cleared away existing intact leaf litter, exposing the organic layer below. We then used a soil corer (5 cm diameter) to harvest root biomass within the top 15 cm of soil at each of the two positions within each plot. Harvesting at this depth has accounted for the majority of root biomass in a similar, nearby IDENT experiment (Archambault et al. 2019), and likely allowed us to account for the majority of fine-root biomass in our sites as well (but see Brassard et al. 2013). Combined soil and root mass from each core were stored at 3°C until processed (typically within 30 days). At Cloquet, once soil had been extracted from each position, we inserted a 5 cm diameter and 15 cm deep cylindrical ingrowth core made of 1 cm welded wire mesh. We then refilled ingrowth cores with soil taken from areas adjacent to each experimental block that was sieved to 2 mm. Ingrowth cores were packed to roughly the same bulk density as the surrounding soil. We harvested and refilled ingrowth cores in early October of 2016, 2017 and 2018 following the same process. We followed a one-year sampling interval since fine root turnover rate in our experiments was unknown at the start of our study, and estimates of fine root turnover vary greatly based on site and methodology (Gill and Jackson 2000).

Roots collected from Cloquet were separated from soil by emptying soil samples onto a 2 mm mesh and gently washing them with water. Roots collected from Auclair were separated from soil using a root washing machine, Hydropneumatic Elutriation System (Gillison's Variety Fabrication Inc., Benzonia, Michigan, USA). This difference in protocol between the two sites requires that we consider it as a potential contributor to significant differences between sites in total SFRB (and should be considered in interpretation of relevant results). However, we are primarily interested in the productivity of mixtures relative to monocultures within each site, and since all roots within each site were processed consistently, we are still able to confidently make these comparisons within each site. All root material was collected from each sample, sorted into living fine (< 2 mm diameter) and living coarse (≥ 2 mm diameter) roots, placed in a coin envelope, and dried at 65°C for 7 days (herbaceous roots and dead roots – i.e. those that were dark and brittle – were discarded). Once roots achieved constant mass, we weighed them and recorded fine-root mass. Here, we consider only SFRB (g m^{-2}) and AFRP (g m^{-2} $year^{-1}$) values. Coarse roots were contained in relatively few samples, and were not sufficiently abundant for rigorous statistical analyses. Masses of the two samples within a plot were averaged to provide a single value for each plot within a block.

Statistical analyses

Our statistical analyses considered either the SFRB, the response ratio of SFRB (deviation of observed SFRB from expected SFRB based on monoculture), annual fine-root production (AFRP) or the response ratio of AFRP (deviation of observed AFRP from expected AFRP based on monoculture). Analyses of both SFRB and AFRP followed a similar structure. We will describe those for SFRB first. Full descriptions and output of each model are presented in the Supporting information.

Response ratio was calculated as the proportional difference between a plot's observed SFRB and what would be expected based on the weighted mean SFRB of that plot's species in monocultures at that site ((observed − expected)/expected). Positive response ratios indicate mixtures are overyielding (i.e. producing more biomass than expected based on their component species in monoculture), and negative response ratios indicate mixtures are underyielding (i.e. producing less biomass than expected based on their component species in monoculture).

We then identified differences in species' fine-root mass to establish a baseline for our comparisons. To do this, we analyzed the initial SFRB of monocultures as a function of species identity (a 12-level factor) and site (Cloquet or Auclair), with block included as a random factor in a mixed model. We also analyzed SFRB as a function of mixture identity and site for all 2- and 6-species mixtures.

Our first hypothesis (more diverse mixtures overyield more) was tested with a model of SFRB as a function of species richness (1, 2 or 6) and a second model analyzing SFRB in mixed species plots as a function of a continuous index of functional diversity presented by Tobner et al. (2014). Functional diversity was calculated using the functional dispersion index, which calculates the mean distance of species in mixture to a centroid in trait space (Laliberté and Legendre 2010), using three traits: wood density, seed mass and leaf nitrogen concentration. Although this metric is based on aboveground traits taken from the literature, we posit that it adequately describes differences in whole-plant resource use strategy (Westoby 1998, Reich 2014) and can therefore provide a proxy for niche separation and potential complementarity. Site and its interaction with either richness or functional diversity were included in each model. We then repeated these analyses considering response ratios (i.e. analyzed SFRB response ratios as a function of species richness or functional diversity).

We tested our second hypothesis (mixtures of less productive species overyield more) in two parts. First, we analyzed mixtures' expected values as a function of a factorial combination of 1) site and 2) either richness, functional diversity, origin (North America, Europe or both) or phylogenetic group (angiosperm, gymnosperm or both). We also included the interaction between site and the second factor. We then analyzed mixtures' observed values as a function of expected values and compared that to a 1:1 line. Positive deviations from this line indicate overyielding and negative deviations from the 1:1 line indicate underyielding. This approach allowed us to evaluate if more productive mixtures are more likely to overyield (as well as identify which types of mixtures those are) without encountering collinearity that would result from analyzing response ratios as a function of expected values. Both expected and observed values were log-transformed to meet assumptions of normality.

We tested our third hypothesis (North American species and angiosperm species overyield more than European species or gymnosperm species) by analyzing mixed species plots' SFRB as a function of their species' origins or phylogenetic group. We then performed these same analyses considering SFRB response ratios instead of absolute SFRB. Note that we were unable to isolate the effects of phylogeny from deciduousness since all of the considered angiosperms are deciduous, and all but two of the considered gymnosperms are evergreen (only *Larix* spp. are deciduous).

The aforementioned analyses were repeated using three years (2016–2018) of AFRP at the Cloquet site as the response variable. These analyses did not include site or its interaction since AFRP data were only available for one site. However, they did include year and its interaction with other main factors as a repeated measure with plot nested within block as a random effect.

Block was included as a random factor in all analyses and was nested within site for SFRB analyses. All statistical analyses were performed using PROC MIXED in SAS ver. 9.4.

Results

Fine-root standing biomass (within and among sites)

The mean SFRB was 206 ± 9 g m^{-2} (mean ± SE) at the Cloquet site and 98 ± 5 g m^{-2} at the Auclair site ($F_{2,5.47} = 30.50$, $p < 0.01$). Notably, SFRB differed appreciably between sites in every analysis presented here (Supporting information). We did not detect significant differences in SFRB among species in monoculture ($F_{11,45.1} = 1.12$, $p = 0.37$), but there were significant differences in the SFRB of different mixtures ($F_{28,111} = 2.13$, $p < 0.01$). Averaged across both sites, the mixture of six North American species had the lowest SFRB and the *Picea abies* – *Acer platanoides* mixture had the greatest SFRB (Supporting information).

Across both sites, SFRB of mixtures was often different than we expected based on the SFRB of each species grown in monoculture. Response ratios of SFRB were positive (indicating overyielding) in mixtures containing species that had less biomass in monoculture, but became progressively more negative (indicating underyielding) in mixtures containing more productive species (Fig. 1A–B). After accounting for block and site effects, observed and expected SFRB values were sufficiently decoupled such that expected values were a poor predictor of observed SFRB values overall ($F_{1,165} = 0.92$, $p = 0.34$).

SFRB of mixtures differed depending on whether the mixtures included gymnosperms, angiosperms or both gymnosperms and angiosperms. Gymnosperms had greater SFRB on average in monocultures than angiosperms, particularly in Cloquet (Fig. 1A, $F_{2,52} = 4.70$, $p = 0.01$). However, gymnosperm mixtures produced comparable SFRB to angiosperm mixtures and 18% less SFRB than angiosperm–gymnosperm mixtures (Fig. 2A; $F_{2,163} = 3.54$, $p = 0.03$). SFRB of angiosperm mixtures overyielded by 16 ± 8% and gymnosperm mixtures' SFRB underyielded by 6 ± 7% (Fig. 2C; $F_{2,163} = 3.17$, $p = 0.04$). Response ratios for SFRB in mixtures containing both angiosperms and gymnosperms did not differ from zero and indicated additive species interactions (i.e. SFRB did not differ from expected values) on average.

Origin also contributed to differences in SFRB between mixtures. Although expected SFRB values in monocultures did not differ by origin ($F_{2,52} = 0.40$, $p = 0.67$), SFRB in mixed plots containing species from North America tended to be 20% less than that of mixtures of European species, with plots containing species from both North America and Europe producing an intermediate SFRB (Fig. 2B; $F_{2,163} = 2.90$, $p = 0.06$). SFRB of mixtures from North America underyielded by 10 ± 8%, whereas the European mixtures' SFRB overyielded by 14 ± 9% (Fig. 2D; $F_{2,163} = 3.31$, $p = 0.04$).

In contrast to phylogeny and origin, SFRB was insensitive to richness and functional diversity. Across both sites, expected values from monoculture ($F_{1,54} = 0.07$, $p = 0.79$) and observed SFRB ($F_{2,236} = 1.46$, $p = 0.24$) did not differ by richness level, and we did not detect significant differences between 2- and 6-species mixtures' SFRB response ratios ($F_{1,165} = 3.20$, $p = 0.08$). Similarly, neither expected values from monoculture ($F_{1,54} = 0.05$, $p = 0.82$) nor observed SFRB ($F_{1,165} = 0.12$, $p = 0.73$) changed with increasing functional diversity across plots and did not show signs of SFRB overyielding across levels of functional diversity ($F_{1,165} = 0.05$, $p = 0.82$).

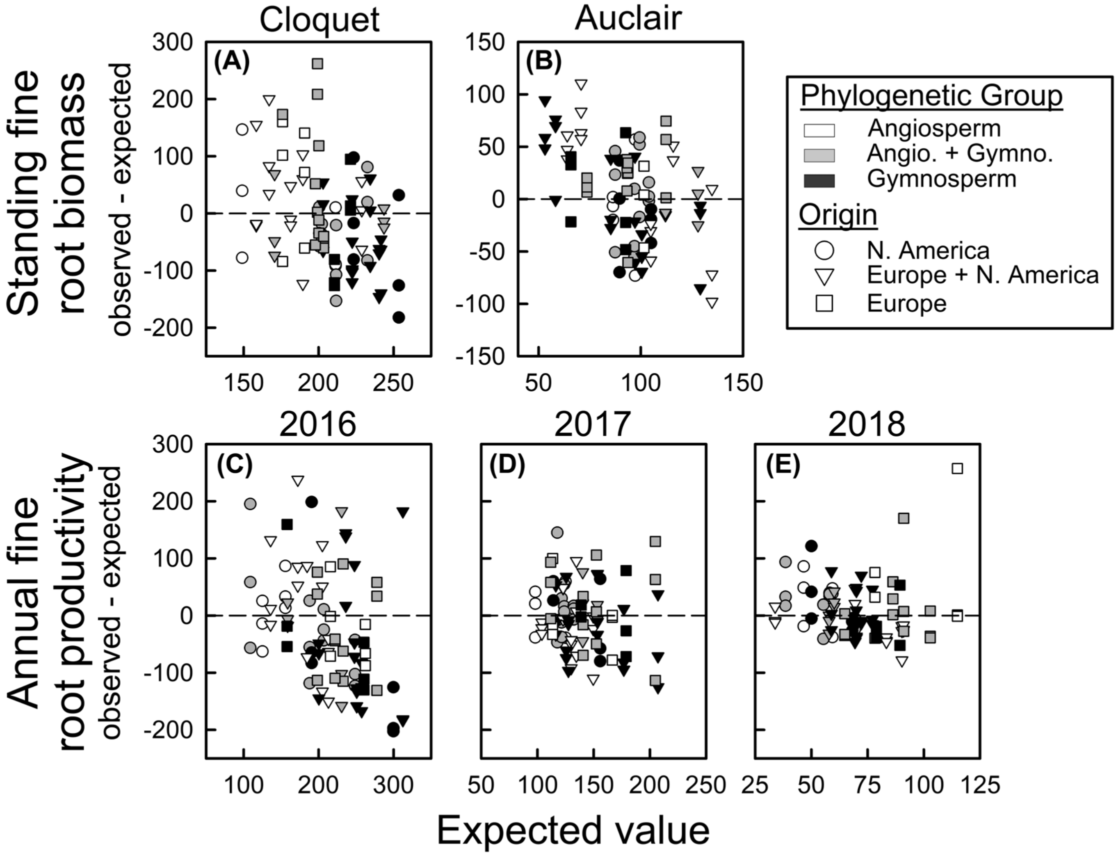

Figure 1. Difference in observed and expected standing fine-root biomass of mixtures in Cloquet (A) and Auclair (B) relative to expected values, as well as difference in observed and expected annual fine-root productivity of mixtures in Cloquet 2016–2018 (C and D) relative to expected values. Expected values are based on constituent species standing fine-root biomass or annual fine-root production in monoculture for the respective site and time period. Shading corresponds to mixture phylogeny (angiosperms only: white, gymnosperms only: black, or a combination of angiosperms and gymnosperms: gray) and origin (North America: circle, Europe: square, or a combination of North America and Europe: triangle). Axis are scaled in (A) and (B) to reflect differences in total values between sites; (C) – (E) are scaled equally.

Annual fine-root production (Cloquet site only)

AFRP at the Cloquet site averaged 137 ± 5 g m^{-2} $year^{-1}$ across plots and years. *Picea abies* had the greatest AFRP of monocultures (223 ± 171 g m^{-2} $year^{-1}$) and *Acer saccharum* had the lowest AFRP (73 ± 26 g m^{-2} $year^{-1}$; $F_{11,70}=2.44$, $p=0.01$). Monoculture AFRP did not differ between angiosperms and gymnosperms ($F_{1,100}=2.50$, $p=0.17$), but European species were 35% more productive than North American species on average ($F_{1,100}=5.99$, $p=0.02$). Of mixtures, *Picea abies–Acer platanoides* had the greatest AFRP (212 ± 37 g m^{-2} $year^{-1}$) and *Quercus rubra–Quercus robur* had the lowest AFRP (81 ± 17 g m^{-2} $year^{-1}$; $F_{28,172}=1.9$, $p < 0.01$). In analyses of AFRP, year was always significant and reflected declining AFRP over time (Supporting information).

As with SFRB, AFRP overyielded in mixtures containing species that were less productive in monocultures, but underyielded in mixtures containing species that were more productive in monocultures (Fig. 1C–E, $F_{1,253}=8.72$, $p < 0.01$). The magnitude of over- and under-yielding was greatest in 2016 (Fig. 1C), when both observed ($F_{2,224}=116.07$, $p < 0.01$) and expected ($F_{2,81}=69.62$, $p < 0.01$) values were large, but dissipated as values became more constrained after multiple years of sampling. The pattern of mixtures composed of more productive species underyielding also corresponded with changes in mixture origin and – to a lesser extent – phylogeny.

Based on monocultures, mixtures of European species were expected to have 33% larger AFRP than North American mixtures (compare symbol shapes in Fig. 1C and D, $F_{2,78}=10.62$, $p < 0.01$). Consistent with this expectation, European mixtures had greater AFRP than North American mixtures or combined North American–European mixtures (Fig. 3B; $F_{2,250}=4.88$, $p < 0.01$). However, the difference between European mixtures and others was only 22–27%. This reduced difference was associated with North American mixtures' AFRP overyielding by 16 ± 7% (Fig. 3D; $F_{2,250}=3.48$, $p=0.03$). In contrast, other mixtures did not show signs of overyielding.

Gymnosperm mixtures tended to have larger expected AFRP than angiosperm mixtures (compare symbol shading in Fig. 1C– D, $F_{2,78}=2.57$, $p=0.08$). However, AFRP

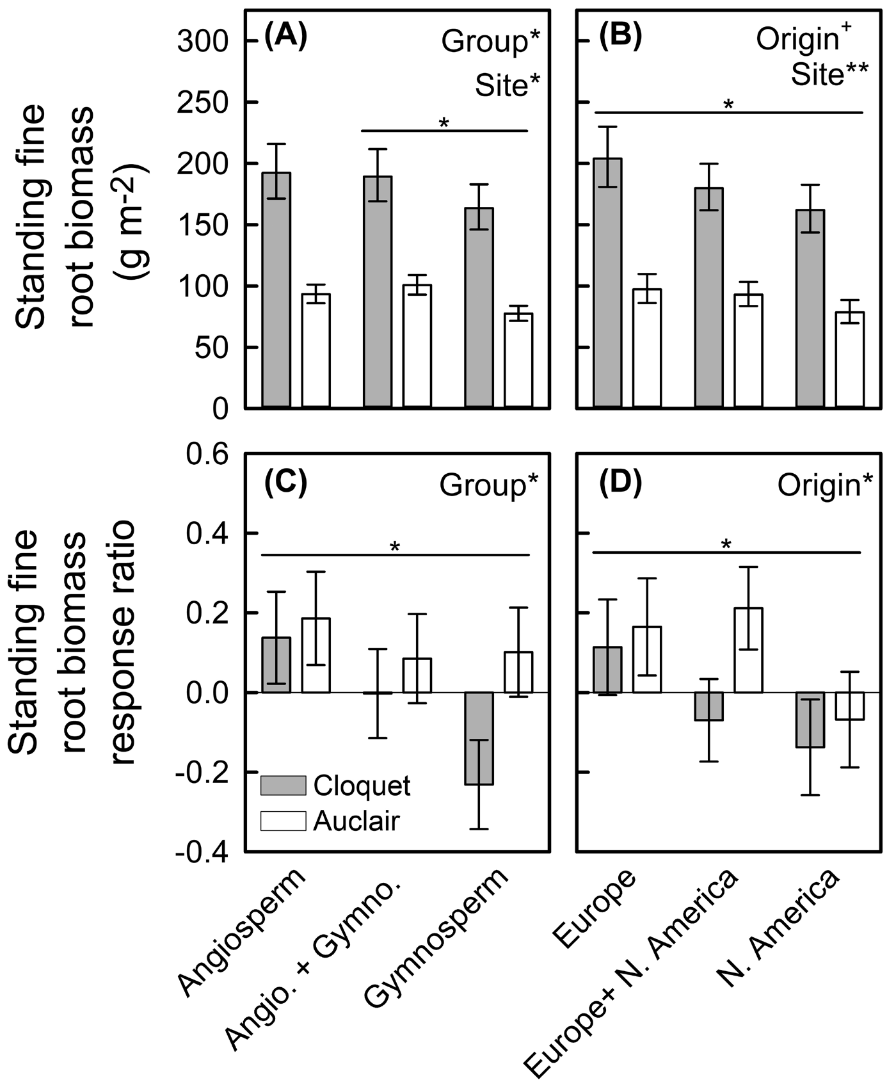

Figure 2. Least-squared mean (± SE) fine-root standing fine-root biomass and standing fine-root biomass response ratios (calculated as (observed − expected)/expected) based on mixture composition: angiosperm only, gymnosperm only or angiosperm–gymnosperm mixtures; or European only, North American only or European–North American mixtures. Includes data from both Cloquet and Auclair sites. Lines indicate statistically distinct values based on group or origin. Effect significance: $^+$ indicates $0.05 < p \leq 0.10$, * indicates $0.01 < p \leq 0.05$ and ** indicates $p \leq 0.01$.

was similar across mixtures containing angiosperms, gymnosperms or a combination of angiosperms and gymnosperms (Fig. 3A; $F_{2,250} = 1.40$, $p = 0.25$). This meant that while gymnosperms underyielded in AFRP on average, and angiosperms overyielded in AFRP on average, the difference between angiosperms and gymnosperms was too weak to reach statistical significance (Fig. 3C; $F_{2,250} = 2.41$, $p = 0.09$).

Increasing species richness of plots had inconsistent impacts on belowground productivity. Expected AFRP from monocultures did not differ across richness levels ($F_{1,81} = 0.04$, $p = 0.84$), but 6-species mixtures tended to be more productive than monocultures or 2-species mixtures (Fig. 1; $F_{2,358} = 2.26$, $p = 0.10$). Consequently, 6-species mixtures were more likely to overyield in AFRP on average and 2-species mixtures were more likely to underyield in AFRP on average, although statistical confidence of these trends was weak ($F_{1,253} = 2.55$, $p = 0.11$).

Increasing functional diversity increased both AFRP and response ratios. Increasing functional diversity stimulated AFRP ($F_{1,253} = 8.76$, $p < 0.01$), although there was high variability within this trend (adj. $R^2 = 0.01$). Between the least functionally diverse and the most functionally diverse mixtures we considered, AFRP increased by 46% on average (Fig. 4A). However, functional diversity did not affect expected AFRP values from monocultures ($F_{1,81} = 2.48$, $p = 0.12$). Consequently, more functionally diverse mixtures also had greater response ratios of AFRP (Fig. 4B; $F_{1,253} = 15.85$, $p < 0.01$, adj. $R^2 = 0.05$), indicating an increased propensity for AFRP overyielding with greater diversity.

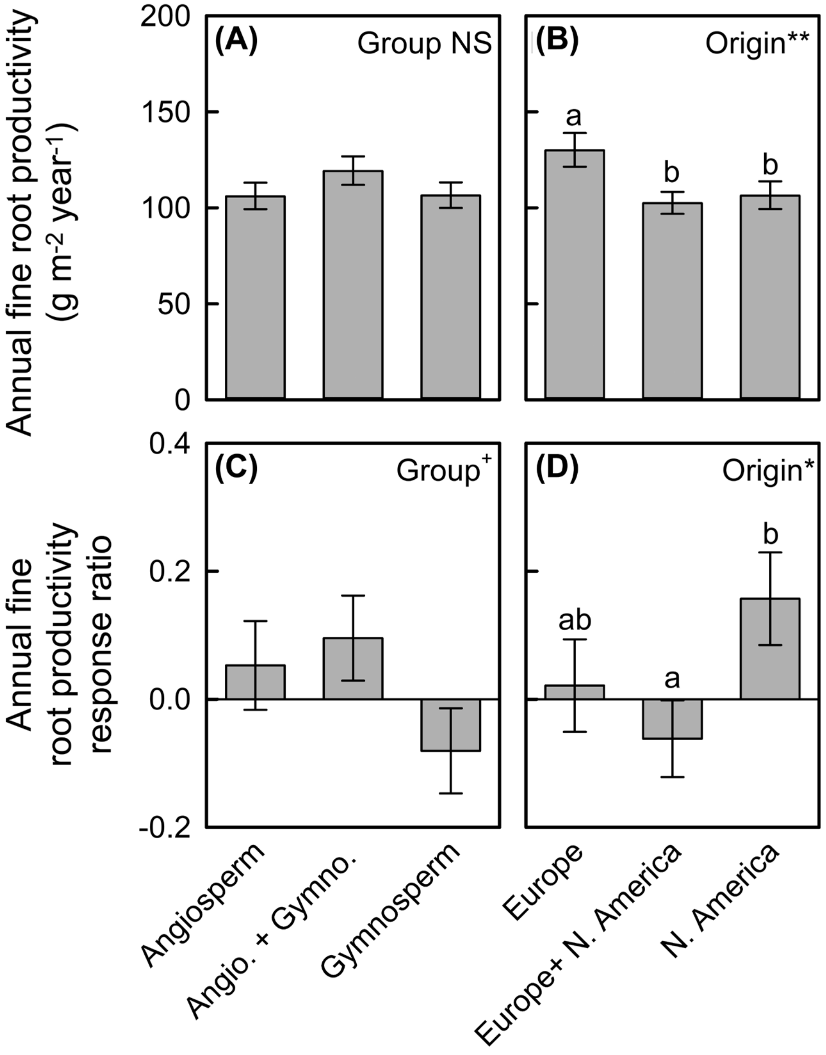

Figure 3. Least-squared mean (± SE) annual fine-root productivity and annual fine-root response ratios (calculated as observed – expected/expected) in Cloquet based on mixture composition: angiosperm only, gymnosperm only or angiosperm–gymnosperm mixtures; or European only, North American only or European–North American mixtures. Statistically similar groups are indicated with lowercase letters. Effect significance: NS indicates $p > 0.10$, $^{+}$ indicates $0.05 < p \leq 0.10$, * indicates $0.01 < p \leq 0.05$ and ** indicates $p \leq 0.01$.

Discussion

Using two common gardens of young trees located at distant sites with different soil fertility and climate in the boreal-temperate ecotone of North America, we investigated the roles of species richness, functional diversity, origin and phylogeny on annual fine-root productivity (one site) and standing fine-root biomass (both sites). We found that in general, mixtures at the Cloquet site that were composed of species with lower AFRP in monoculture were more likely to overyield in AFRP, and that those composed of species with greater AFRP in monoculture were more likely to underyield in AFRP. These patterns in AFRP were often reflected by overyielding SFRB as well. Mixtures' propensity for belowground overyielding was strongly influenced by whether they included angiosperms and/or gymnosperms, or whether they included species from North America and/or Europe. Accordingly, functional diversity, more than species richness, was associated with higher AFRP and overyielding. Our findings add to the growing literature indicating that species richness alone does not moderate belowground biomass and productivity (Mahaut et al. 2020). Instead, our results indicate that productivity and ecosystem function are much more tightly linked to species traits above- and below-ground (Hooper et al. 2005, Cardinale et al. 2006, Tobner et al. 2014, Hisano et al. 2018).

Response ratios are illustrative of the consequences of biodiversity, but cannot alone identify the mechanism underlying the effects of biodiversity on ecosystem function (Barry et al. 2019). Identifying species by their roots is challenging, making it difficult to untangle the relative contributions of individual species to enhanced belowground

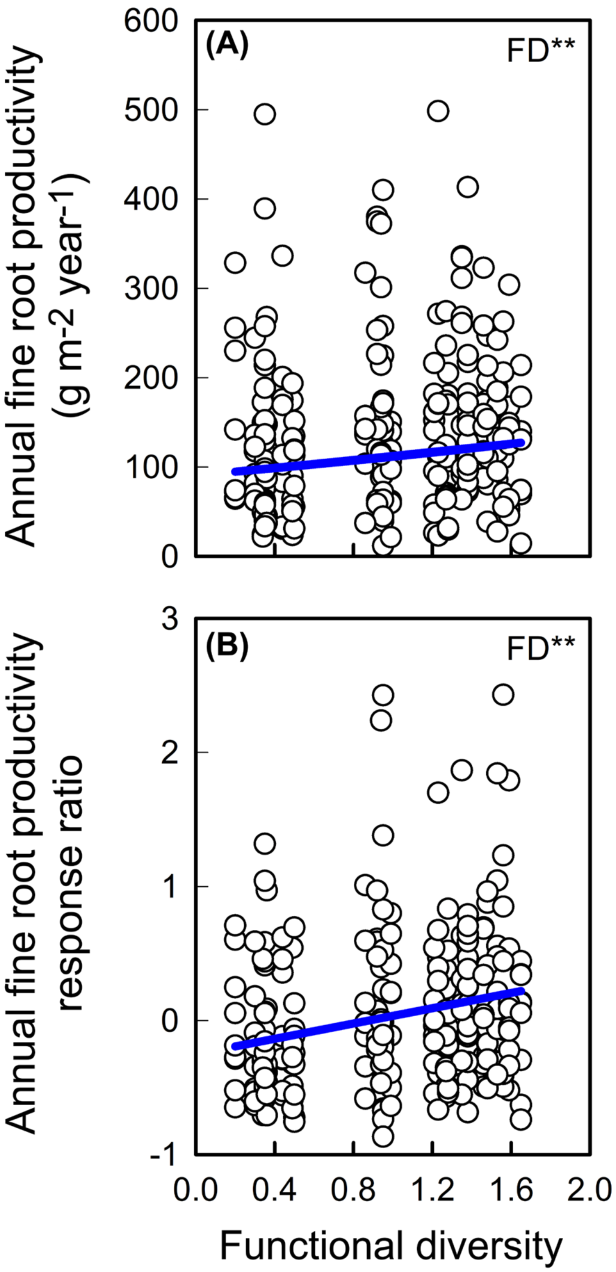

Figure 4. Least-squared mean (± SE) annual fine-root productivity and annual fine-root productivity response ratios based on functional diversity at the Cloquet site. Effect significance: $^+$ indicates $0.05 < p \leq 0.10$, * indicates $0.01 < p \leq 0.05$ and ** indicates $p \leq 0.01$.

productivity in species mixtures. Without species-level identifications, response ratios cannot be ascribed to a particular mechanism (Loreau and Hector 2001, Mommer et al. 2010). Furthermore, by separating roots by size instead of by order, our measurements of fine-root biomass do not necessarily reflect measurements of acquisitive-root biomass (McCormack et al. 2015) and therefore some effects of diversity may be obscured (Wambsganss et al. 2021). However, within this context, our findings of greater belowground overyielding in mixtures composed of less productive species, along with known patterns of fine-root allocation based on origin (Jacob et al. 2014) and phylogenetic group (Archambault et al. 2019) are consistent with belowground resource partitioning.

Angiosperms make better belowground neighbors than gymnosperms

By comparing SFRB and AFRP between combinations of angiosperms and gymnosperms in two common gardens, we were able to isolate differences in root growth between these two major phylogenetic groups of trees. Across both SFRB and AFRP, we observed positive response ratios in angiosperm mixtures and either neutral or negative response ratios in gymnosperm mixtures. These patterns of over- or under-yielding belowground are reflected aboveground as well. Across both the Auclair and Cloquet sites, aboveground production of angiosperm mixtures often overyield, whereas aboveground production of gymnosperm mixtures often underyield (Belluau et al. 2021, Williams et al. 2021). However, the strength and direction of the link between aboveground and belowground overyielding is unclear (Martin-Guay et al. 2020). Our results could be explained by angiosperm species increasing belowground production in mixture in order to meet increasing demand for soil resources brought on by aboveground overyielding. Alternatively, aboveground overyielding may be facilitated at least partially by elevated productivity and associated resource acquisition belowground. Yet, our data are unable to distinguish the direction of causation, and further investigation is needed to disentangle them.

Fundamental differences in the rooting structure may explain why angiosperms were much more likely to overyield compared gymnosperms. Angiosperm roots are highly diverse, displaying a wide range of root phenologies (Makoto et al. 2020) rooting depths (Lei et al. 2012), and structural traits (Archambault et al. 2019). In contrast, gymnosperms typically produce thicker fine roots (Reich et al. 1998) that are less efficient at exploiting soil resources (Eissenstat et al. 2000) compared to angiosperms, suggesting lower plasticity belowground amongst gymnosperms relative to angiosperms (Archambault et al. 2019). Therefore, angiosperm rooting strategy may be conducive to spatial or temporal resource partitioning moreso than that of gymnosperms, as supported by our findings of overyielding in angiosperm mixtures and underyielding in gymnosperm mixtures. A study of one of our species, *P. abies*, suggests that gymnosperms may also intensify competition (i.e. reduce resource partitioning) by concentrating roots in more shallow soils in response to increasing soil acidity (Godbold et al. 2003). Therefore, declining soil pH following planting of gymnosperm plots (Alfredsson et al. 1998) might have further restricted the capacity for resource partitioning within gymnosperm mixtures as those trees allocated more roots into less soil, contributing to the neutral-to-negative response ratios we routinely detected in mixtures containing only gymnosperm species.

Given that more functionally diverse mixtures have greater AFRP and are more likely to overyield in AFRP (Fig. 4), why were combined mixtures of angiosperms and gymnosperms less productive than mixtures that contained only angiosperms or gymnosperms? Although there are some important physiological differences between angiosperms and gymnosperms, mixtures including both angiosperms and gymnosperms did not always have greater functional diversity based on the aboveground traits used in our functional diversity index (Tobner et al. 2014). Instead, the mixtures with the greatest functional diversity could be found spread across all three phylogenetic mixture types. We cannot fully disentangle the effects of phylogeny and functional diversity since we did not include all possible combinations of species. Re-analyzing our data considering only gymnosperm species also shows a positive effect of functional diversity on AFRP. Therefore, we expect that an experiment that could disentangle the effects of phylogeny and functional diversity by planting all combinations of the species considered here would also support the general trend of functional diversity driving patterns of belowground productivity.

Species origin affects productivity and standing fine-root biomass differently

We hypothesized that differences in ecological histories would cause divergent patterns of productivity between North American species and European species in our experiments located in North America. Indeed, species origin strongly affected the presence of mixing effects in both SFRB and AFRP, although not in the same way. North American mixtures had a lower SFRB than European mixtures, and North American SFRB was less than expected based on monocultures on average. North American species also had a lower AFRP than European species, but North American AFRP overyielded. Although not statistically significant, there was a general trend of response ratios increasing over time, consistent with longer-term studies (Marquard et al. 2009, Zhang et al. 2012, Belluau et al. 2021). This was largely due to declines in expected values from monocultures, particularly for North American species, such that deviations from the expected value were more influential as AFRP declined in each successive year.

There are many potential causes of the AFRP overyielding we observed in North American mixtures. It may be that differences in belowground resource acquisition strategies among North American species are more complementary than those differences among European species (Kawaletz et al. 2013). However, our data are limited and preclude such investigations. It may also be that the higher AFRP of European mixtures may have led to increased filling of the soil column by European species and greater competition for soil resources, potentially drawing down soil resources and limiting additional fine-root growth (Jacob et al. 2014). Increased production of fine roots by European species could have also facilitated accumulation of soil pathogens that limited fine-root growth (Zak et al. 2003, Khlifa et al. 2017). In contrast, North American mixtures were less productive than European species belowground and likely created less competitive soil environments that allowed for species to occupy different soil strata (Kawaletz et al. 2014, Jo et al. 2015, Caplan et al. 2019) or for more advantageous soil microbial communities.

The dichotomy of overyielding in AFRP in North American mixtures and underyielding in AFRP in European mixtures contrasts recent aboveground findings of the same experiments by Belluau et al. (2021). European mixtures were found to increase aboveground productivity in response to mixing over time, whereas mixtures of North American species were consistently insensitive to mixing (Belluau et al. 2021). These aboveground and belowground results combine to suggest alternative growth strategies between North American and European species such that overyielding occurs either aboveground or belowground, but not both – at least for these species. Our findings also reinforce observations of aboveground overyielding being at least partially offset by lower production belowground, such that total biomass responses to mixing are over-estimated by aboveground measurements alone (Martin-Guay et al. 2020). It may be that European species, faced with greater competition belowground, shift allocation aboveground where there is potential for greater gains. Conversely, North American species may shift growth allocation belowground where there is less competition – suggesting our results may be more a result of resource allocation within groups of species and less of a result of gross changes in productivity. Yet, to what extent these trends are generalizable across North American and European taxa or how they might shift in response to conducting our experiments in Europe instead of North America is unclear and warrants further study.

If North American mixtures' AFRP overyielded, why did North American mixtures' SFRB underyield? It is intuitive that more productive mixtures would also result in larger SFRB and that overyielding AFRP would also be reflected in SFRB (as we observed in angiosperm mixtures). However, this may not be true if mixtures create conditions that significantly alter root longevity or decomposition rates. SFRB is comprised of new growth (captured in AFRP) as well as remnant roots from previous growing seasons, meaning that even highly productive mixtures can have low SFRB if root turnover is sufficiently high (Jacob et al. 2014, Sun et al. 2016). Indeed, previous work on the effects of species origin (Lemma et al. 2007) and diversity (Jacob et al. 2014) on forest root turnover rates suggests that North American mixtures might have had higher root turnover rates than the European mixtures in our experiment. Thus, although we were unable to adequately quantify root turnover rates in our experiment (Hertel and Leuschner 2002, Andreasson et al. 2016), our data suggest that higher root turnover rates likely contributed to lower than expected SFRB of North American mixtures despite those mixtures overyielding AFRP (Jacobs et al. 2018).

Conclusion

Our results suggest that fine-root productivity is stimulated by more functionally diverse forest communities, and highlights how diversity effects can manifest differently between measurements of standing fine-root biomass and annual fine-root production. In particular, we observed a tradeoff between species-level monoculture root productivity and overyielding belowground in the young, artificially assembled forest communities of our experiment. Within those communities, we found that mixtures of angiosperms had a greater propensity for overyielding in AFRP and SFRB compared to mixtures of gymnosperms, and that while diversity effects also promoted overyielding in AFRP of North American mixtures, those mixtures likely enhanced fine-root turnover rates to result in lower SFRB than European mixtures. Our findings demonstrate the key influence of both species geographic origin and phylogeny in regulating belowground overyielding, such that either facet of species identity may have larger impacts on forest belowground productivity than species richness or diversity alone.

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Author contributions

Michael J. Schuster: Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Laura J. Williams**: Investigation (equal); Writing – review and editing (equal). **Artur Stefanski**: Investigation (equal); Project administration (equal); Writing – review and editing (equal). **Raimundo Bermudez**: Investigation (equal); Writing – review and editing (equal). **Michaël Belluau**: Investigation (equal); Project administration (equal); Writing – review and editing (equal). **Christian Messier**: Conceptualization (equal); Project administration (equal); Writing – review and editing (equal). **Alain Paquette**: Conceptualization (equal); Project administration (equal); Writing – review and editing (equal). **Dominique Gravel**: Conceptualization (equal); Investigation (equal); Project administration (equal); Writing – review and editing (equal). **Peter B. Reich**: Conceptualization (equal); Project administration (equal); Writing – review and editing (equal).

Data availability statement

Data are available from: https://hdl.handle.net/11299/226614 (Schuster et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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