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Progeny selection for enhanced forest growth alters soil communities and processes

John K. Senior[1] | **Michael J. Gundale**[2] | **Glenn R. Iason**[3] | **Thomas G. Whitham**[4] | **E. Petter Axelsson**[1]

[1]Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

[2]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

[3]The James Hutton Institute, Aberdeen, Scotland

[4]Center for Adaptable Western Landscapes, Northern Arizona University, Flagstaff, Arizona, USA

Correspondence
E. Petter Axelsson
Email: petter.axelsson@slu.se

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Abstract

Genetic enhancement of tree species is integral to global forest management practices with mass propagation of enhanced plant material being used to reforest whole landscapes. It is unclear, however, how genetic enhancement of basic traits such as tree growth may influence the function of life supporting soil ecosystems. We studied the potential cascading effects of genetic increases in growth of Norway spruce (*Picea abies*) on a range of soil chemical and biological properties. Because this species is a prime candidate for the genetic enhancement of boreal forest landscapes and it has been introduced around the world, its impacts on soil microbiomes are likely of importance both locally and globally. In a 40-year common garden, we assessed how genetic increases in growth generated through controlled crossing of high-quality "plus" trees from across the central boreal zone of Sweden influenced a range of soil properties beneath the canopies. Properties included pH, carbon, nitrogen, nitrate, ammonium, phosphate, respiration rate, and the composition of microbial communities assessed via phospholipid fatty acids (PLFAs). We found that Norway spruce family significantly affected each of the seven chemical properties assessed, with differences of up to 140% among families, and that three of the seven were significantly correlated with mean family growth rate. We also found that fungal PLFAs varied significantly across Norway spruce families, but these differences were not strongly related to mean family growth rate. This study, representing just one cycle of selective breeding, suggests that genetic increases in tree growth rates may also be inadvertently altering soil communities and ecosystem services. Such alterations across forest landscapes may have unexpected implications for the function of forest ecosystems (i.e., nutrient cycling) as well as processes of global significance (i.e., carbon sequestration).

KEYWORDS
common garden, condensed tannins, genetic legacy effects, growth, intraspecific variation, *Picea abies*, selective breeding, soil chemical and biological properties

INTRODUCTION

Human activities have resulted in large changes to the genetic identity of many forest regions around the world. These changes are occurring globally as a result of the over-exploitation, clearing, and fragmentation of forests (Geburek & Myking, 2018; Potter et al., 2017) as well as the direct and indirect effects of climate change (Alsos et al., 2012, Fettig et al., 2013, Six et al., 2018). However, changes to the genetic composition of forests are also occurring as a result of selective breeding programs (Aravanopoulos, 2018; Ratnam et al., 2014) and more recently through the direct genetic modification of trees (Chang et al., 2018). Only now are we beginning to understand how some of these genetic changes can influence ecological communities and ecosystem processes, such as the flow-on consequences of the genetic modification of trees (Axelsson et al., 2011; Hancock et al., 2007; Newhouse et al., 2018; Vauramo et al., 2006). Nevertheless, there is still a lack of research addressing how tree improvement through traditional methods may be influencing ecological communities and ecosystem function. Such studies are especially important since selective breeding is an integral part of forest management in many parts of the world.

As foundation species, trees have a central role in influencing soil communities and ecosystem processes (Whitham et al., 2012). This occurs through trees mediating the quantity and quality of organic matter entering soils, providing habitat for microorganisms, and influencing soil structure and chemistry (Ehrenfeld et al., 2005). It is well established that different tree species can have highly variable effects on soil ecosystems (Mueller et al., 2019; Russell et al., 2010; Wardle et al., 2008). For example, Russell et al. (2010) found that interspecific variation in traits such as growth rate, partitioning of C among biomass components, tissue turnover rates, and tissue chemistry determined carbon balances above- and belowground in tropical forests. Furthermore, sometimes trees leave a legacy that can last decades in the soil after tree death (Mueller et al., 2019; Wardle et al., 2008).

Trees also exhibit intraspecific genetic variation in a range of morphological, chemical, and phenological traits (Barbour et al., 2009; Des Roches et al., 2017; Orians et al., 2003; Osier & Lindroth, 2006). Selective breeding programs typically target this variation, where trees with desirable characteristics, or "plus" trees, are selected in natural populations and the open-pollinated or crossed seed of these trees are collected to establish progeny trials. Through this process, tree breeding has led to substantial increases in tree growth rates, and to a lesser extent, resistance to pests and pathogens (Pâques, 2013). For instance, in Sweden, 80% of harvested forest area is reforested with material that has been genetically improved in some way (Black-Samuelsson et al., 2017). The first round of selective breeding has been estimated to have increased stand volume per unit area by 10% (Rosvall et al., 2001), while the second round is estimated to result in gains of 10%–25%, compared to unimproved trees (Jansson et al., 2013). Thus, it is necessary to understand whether the large-scale replanting of selected and bred material that is currently occurring worldwide may be influencing soil communities, ecosystem processes, and potentially, future forest generations.

Intraspecific genetic variation not only influences tree growth, but also plays an important role in influencing soil properties and communities (Van Nuland et al., 2016; Whitham et al., 2012). For instance, intraspecific variation in various growth-related traits has been shown to affect mycorrhizal community composition as well as soil respiration, carbon decomposition, and C and N concentrations (Korkama et al., 2007; Mueller et al., 2017; Pregitzer et al., 2013). Furthermore, resistance to pests and pathogens can also be an important target in genetic improvement programs (Pâques, 2013) and is known to impact soil communities and ecosystem processes. Plant resistance often relates to underlying genetic variation in plant secondary metabolites (Agrawal & Weber, 2015), and many of these compounds have important "afterlife" effects following foliage senescence (Chomel et al., 2016; Whitham et al., 2012). For instance, Driebe and Whitham (2000) found that foliar tannin concentration decreased litter decomposition in both aquatic and terrestrial environments. Furthermore, intraspecific variation in litter condensed tannins has been shown to influence soil microbial communities and carbon (C) and nitrogen (N) cycling (Pregitzer et al., 2013; Schweitzer et al., 2008). Thus, growth and defense-related traits present prime candidates to understand how replanting with selected material might also affect soil communities and ecosystem processes.

Within a long-established common garden experiment at Sävar, Sweden, we tested how 10 full-sibling families with known variation in growth rates, varied in their influence on soil chemical and biological properties and whether this variation was influenced specifically by intraspecific variation in growth rate (measured as diameter at breast height; dbh) and litter condensed tannin concentrations. We examined soil pH, carbon (C) and nitrogen (N) concentrations, nitrate (NO_3^-), ammonium (NH_4^+) and phosphate (PO_4^-) availability, respiration rate, and the composition of phospholipid fatty acids (PLFAs) as a coarse measure of soil microbial community composition. We hypothesized that (1) families would differentially alter soil chemical and biological properties, and (2) variation in soil properties associated with different families would be related to dbh and litter condensed tannin concentrations. Thus, our study provides

important insight into the potential indirect consequences of genetic variation in growth and defense-related traits on soil ecosystems. This facilitates an understanding of the wider ecosystem consequences of natural and artificial selection on the growth rate of trees, particularly coniferous forest trees, which cover a significant proportion (30%) of world's total forested area.

MATERIALS AND METHODS

Tree species

Norway spruce (*Picea abies*) is one of the most economically important tree species in Europe, accounting for 38% of the total coniferous planted area (Pâques, 2013). The species is also of great ecological importance, given its wide distribution and dominance in the region (Axelsson et al., 2015). In Sweden, Norway spruce has a long history of genetic improvement dating back to the 1940s (Figure 1; Jansson et al., 2013), and it is currently estimated that 80% of harvested forest area is reforested with material that has been genetically improved in some way (Black-Samuelsson et al., 2017). For instance, it is expected that first round of selective breeding in Sweden has increased stand volume per unit area by 10% (Rosvall et al., 2001), while the second round is estimated to result in gains of 10%–25%, compared to unimproved trees (Jansson et al., 2013). Within a long-established common garden experiment at Sävar, Sweden, we previously tested for intraspecific variation in growth rates and a range of ecologically important traits among 10 full-sibling families (i.e., the progeny of a single controlled crossing) generated through the controlled crossing of high quality plus trees and four open-pollinated, non-improved populations of Norway spruce occurring across central Sweden (Senior et al., 2019). We found up to threefold genetic variation in the growth rates of Norway spruce families, with half of the controlled crossed progenies exhibiting greater growth rates than the open-pollinated progenies (on average 52%) and the other half performing more poorly. We also found significant variation among families in litter condensed tannin concentrations, an important group of defense compounds.

Field site

To test for family variation in soil chemical and biological properties, we utilized common garden trial established by the Forest Research Institute of Sweden located at Sävar, Sweden (63°53′5.02″N, 20°33′10.63″E). The experiment was established in 1977 on an abandoned agricultural field, and we expected pre-planting differences to be small due to a long history of cultivation. The first year after planting the experiment was weeded twice, in 1978 and 1979 to reduce competition with grasses. Later, in 1991, broadleaf regrowth was removed to reduce competition with woody vegetation. After that, the experiment was left to develop on its own. At the year of these studies in 2017, 40 years had passed since the experiment was established and the initial field layer of grasses had gone through a succession toward a field layer dominated by mosses. We used the same sub-set of 10 families and their respective replicates as selected in our previous study on genetic control over trait variation, including plant growth, litter, and fine root chemical and morphological traits. From this study, we identified growth rate and litter condensed tannins as being plant traits under genetic control, and hence, they would represent traits of prime importance for understanding genetic effects on soils (Senior et al., 2019). Briefly, the overall trial includes 115 full-sibling families that are the progeny of controlled crosses of "plus" trees within native populations originating from the mid-boreal zone of Sweden. The families are arranged in a

FIGURE 1 A 1941 photograph demonstrating early efforts to create a seed library of individuals with only desirable characteristics after thinning out poor-quality Norway spruce trees within a native forest stand in Skåne, Sweden. The original photograph can be found in Sylvén (1943). Permission to reproduce the photograph was granted by the publisher

randomized block design with 10 blocks, where within each block a single replicate for a given family consists of four trees planted together in a 2 × 2 tree plot with 1 m spacing between trees. Blocks consisted of 120 (30 × 4) plots orientated North–South that were divided by drainage dikes into three rows of 420 (10 × 42) plots orientated East–West. As all families were replicated across these three rows, we used row to account for spatial variation in the experiment. The diameter at breast height (130 cm) of all living individuals within the trial was measured, and 5–9 replicate plots (depending on survival) in each of 10 families were selected, ranging from the slowest to the fastest growing (see Senior et al., 2019, for details). We used dbh as a proxy for growth rate in this study since all trees within the trial were planted at the same time, meaning that their current dbh equates to a good predictor of their growth rate up until this point in time.

Soil sampling and analyses

In August 2017, soil cores were taken within each plot to examine soil pH, C and N concentrations, and the composition of PLFAs. Within each replicate plot, three evenly positioned soil cores (4 cm diameter) were taken to a depth of 10 cm and pooled. When returned to the laboratory, the pooled soils from each plot were homogenized and large root fragments and stones were removed using a 2-mm sieve. One portion of the resulting homogenized soil per plot was stored at −20°C for C, N, and PLFA analysis, while another was bench-dried for the determination of pH. The portion intended for C, N, and PLFA analysis was freeze-dried and finely ground on a roller mill. All equipment was cleaned with 10% bleach solution and rinsed with distilled water between samples originating from different plots in order to limit the cross-contamination of PLFAs. The pH of each soil sample was measured by creating a 1:5 slurry of dried soil sample and 0.01 M $CaCl_2$ solution. After combining with the 0.01 M $CaCl_2$ solution, samples were mixed and left to equilibrate for 1 h before measuring pH. Microbial PLFAs were extracted (Bligh & Dyer, 1959), and their composition was measured using the methods of White et al. (1979) on a gas chromatograph (PerkinElmer, Shelton, CT, USA) coupled to a FID detector and an Elite-5MS column (L 30 m ID 0.25 DF 0.25). Different PLFAs represent different subsets of the soil microbial community, where the PLFAs i:14, 14:00, i-15:0, α-15:0, 15:00, i-16:0, 16:1ω9, 16:1ω7c, 16:1ω7t, 16:00, br17:0, 10:me16a, 10:me16b, i-17:0, α17:0, 17:1ω8, cy17:00, 17:00, br18:0, 10me17:0, 18:1ω7, 18:01, 18:00, 19:1α, 10me18:0, and cy19:0 were classified as bacteria and 16:1ω5, 18:2ω6, and 18:1ω9 were classified as fungi—based on a recent review of PLFA biomarkers by Willers et al. (2015). Soil C and N concentrations were measured using an isotope ratio mass spectrometer (DeltaV, Thermo Fisher Scientific, Bremen, Germany) coupled with an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific) as described by Werner et al. (1999).

We measured soil respiration for each plot over five separate measurement events in the autumn of 2017 between August and October, with 3 weeks between each measurement event. Respiration rate measurements were made within the headspace of a single cylindrical 250-mm diameter PVC collar installed within the center of each plot (Gundale et al., 2016). The collars were inserted into the soil at a depth of 2 cm, and all aboveground vegetation within and 5 cm around each collar was removed. The collars were allowed to equilibrate for 3 weeks prior to the first measurement. After this period, the height of each collar was measured from the surface of the soil to the rim at four evenly spaced positions around the collar and the headspace volume was calculated. Soil respiration rate was measured between 8:00 AM and 4:00 PM over a single day during each measurement event by sealing the collar with a lid fitted with a portable infrared gas analyzer (CARBOCAP model GMP 343, Vaisala, Finland). For all collars, CO_2 concentrations were recorded every 15 s over a duration of 3 min. Soil respiration rate was calculated by regressing CO_2 measurements against time, with the slope of the linear regression indicating respiration rate. The resulting respiration rate values were then corrected for headspace volume and reported in units of micromoles of CO_2 per square meter per second. Data from the five separate measurement were ultimately averaged prior to statistical analyses to provide a single estimate of soil respiration rate for each plot.

The relative availability of NO_3^-, NH_4^+, and PO_4^- within the soil of each plot was assayed using ionic bed resin capsules (PST1 capsule, Unibest, Kennewick, WA, USA). In July 2017, a single resin capsule was buried 25 cm from the base of each of two randomly selected trees within each plot. The resin capsules were inserted beneath the humus layer to a depth of 5 cm and at a 45° angle (Gundale et al., 2016). After 3 months, the resin capsules were recovered and extracted with three consecutive rinsings of 10 ml of 1 M KCl solution (Gundale et al., 2016). The concentrations of NO_3^-, NH_4^+, and PO_4^- within extracts were then measured using standard colorimetric techniques on an Autoanalyzer III (Omni Process, Solna, SE). The concentrations of NO_3^-, NH_4^+, and PO_4^- extracted from each of the two capsules per plot were averaged and reported as average milligram per capsule.

Statistical analyses

All univariate analyses were conducted in the statistical package R (R Core Team, 2018), while multivariate

analyses were conducted using the software PRIMER v.6.1.11 with the PERMANOVA+ add on (Plymouth Marine Laboratory, Plymouth, United Kingdom). To address the hypotheses that (1) families would differentially alter soil chemical and biological traits and (2) variation in soil properties associated with different families would be related to their dbh and litter condensed tannin concentrations, linear mixed effects models were fitted analyzing for the effects of family, dbh, and litter condensed tannin concentrations on each soil trait using the lme function from the nlme package (Pinheiro et al., 2016). Row was included as a random intercept to account for spatial variation in the trial. However, in cases where row did not significantly influence the fit of the model ($p > 0.05$), as determined by a likelihood ratio test using the package *stats* (R Core Team, 2018), it was removed. Data were checked for the assumptions of normality and homogeneity of variances using the function qqnorm from the package *stats* (R Core Team, 2018) and the function plot from the package graphics (R Core Team, 2018), respectively. Soil pH and NH_4^+ met all model assumptions. While C, N, C:N, NO_3^-, and PO_4^- data were normally distributed, residual variance was dependent on family leading to heteroscedasticity in the model residuals. This issue was resolved by fitting a variance function to allow a different residual variance for each family using the lme varIdent argument. This was also necessary for all soil biological properties, except the concentration of actinomycete PLFAs. The significance testing of main effects was conducted using marginal sums of squares, and model partial R^2 values were returned for fixed effects using the r2beta function from the package r2glmm (Jaeger, 2017).

Prior to multivariate analysis, the abundance of all soil microbial PLFAs was natural logarithm plus one transformed and standardized by the total abundance of PLFAs detected in their respective sample. Data were then converted into a Bray–Curtis similarity matrix, and permutational multivariate analysis of variance (PERMAVOVA) was used to test whether families differentially altered soil microbial PLFA composition in PRIMER and PERMANOVA+. The model included family as a fixed effect, dbh, and litter condensed tannins as covariates (Type III SS) and row as a random effect ($p < 0.05$), and was run for 999 permutations. The effects of family on soil microbial PLFA composition were visualized in a constrained canonical analyses of principal coordinates (CAP). Distance-based linear models were used to test for significant relationships between the soil microbial PLFA composition of families and both mean plot dbh and litter condensed tannin concentrations (Type III SS) in PRIMER and PERMANOVA+. Diameter at breast height and litter condensed tannin (acid butanol assay) data was sampled on the same year as soil variables and was obtained from a previous study using the same families and replicates (Senior et al., 2019).

RESULTS

The effect of genetic variation in Norway spruce on soil chemical and biological properties

Norway spruce family had a significant effect on all of the soil chemical properties assessed (Table 1). However,

TABLE 1 The effects of Norway spruce family, growth rate, and litter condensed tannin concentrations on soil chemical properties

Variable	Mean	Family range	Family			Growth rate				Condensed tannins			
			F_{df}	p	R^2	Est.	F_{df}	p	R^2	Est.	F_{df}	p	R^2
pH	3.6	3.5–3.7	$2.9_{9,44}$	**0.008**	0.08	<0.01	$3.5_{1,44}$	0.069	0.09	−0.03	$1.1_{1,44}$	0.302	0.02
Carbon (% DM)	4.9	3.5–4.9	$3.9_{9,42}$	**<0.001**	0.17	−0.02	$6.7_{1,42}$	**0.030**	0.03	0.80	$10.5_{1,42}$	**0.002**	0.05
Nitrogen (% DM)	0.21	0.17–0.27	$3.4_{1,42}$	**0.003**	0.09	<−0.01	4.0	**0.054**	0.03	0.04	$11.8_{1,42}$	**0.001**	0.07
C/N ratio	22.9	21.1–25.8	$3.7_{9,42}$	**0.002**	0.18	<0.01	$0.5_{1,42}$	0.497	<0.01	0.81	$3.1_{1,42}$	0.085	0.02
NO_3^- (mg/capsule)	0.04	0.03–0.51	$2.2_{9,35}$	**0.045**	0.19	<0.01	$0.4_{1,35}$	0.533	<0.01	<−0.01	$1.2_{1,35}$	0.284	0.01
NH_4^+ (mg/capsule)	1.74	1.36–2.22	$2.4_{9,37}$	**0.029**	0.18	<0.01	$0_{1,37}$	0.895	<0.01	−0.11	$0.8_{1,37}$	0.367	0.02
PO_4^- (mg/capsule)	1.13	0.32–2.41	$4.5_{9,35}$	**<0.001**	0.31	0.01	$33.5_{1,35}$	**<0.001**	0.03	−0.02	$0_{1,35}$	0.892	<0.01

Note: The mean and range of values among families as well as the results of linear models analyzing for the effects of family (family), dbh (growth rate), and litter condensed tannin concentrations (condensed tannins). For each model parameter, its estimate (Est.), F (numerator and denominator degrees of freedom), probability, and partial R^2 values are reported. The significance of main effects was evaluated using marginal sums of squares, where bold values indicate statistical significance at $\alpha = 0.05$.

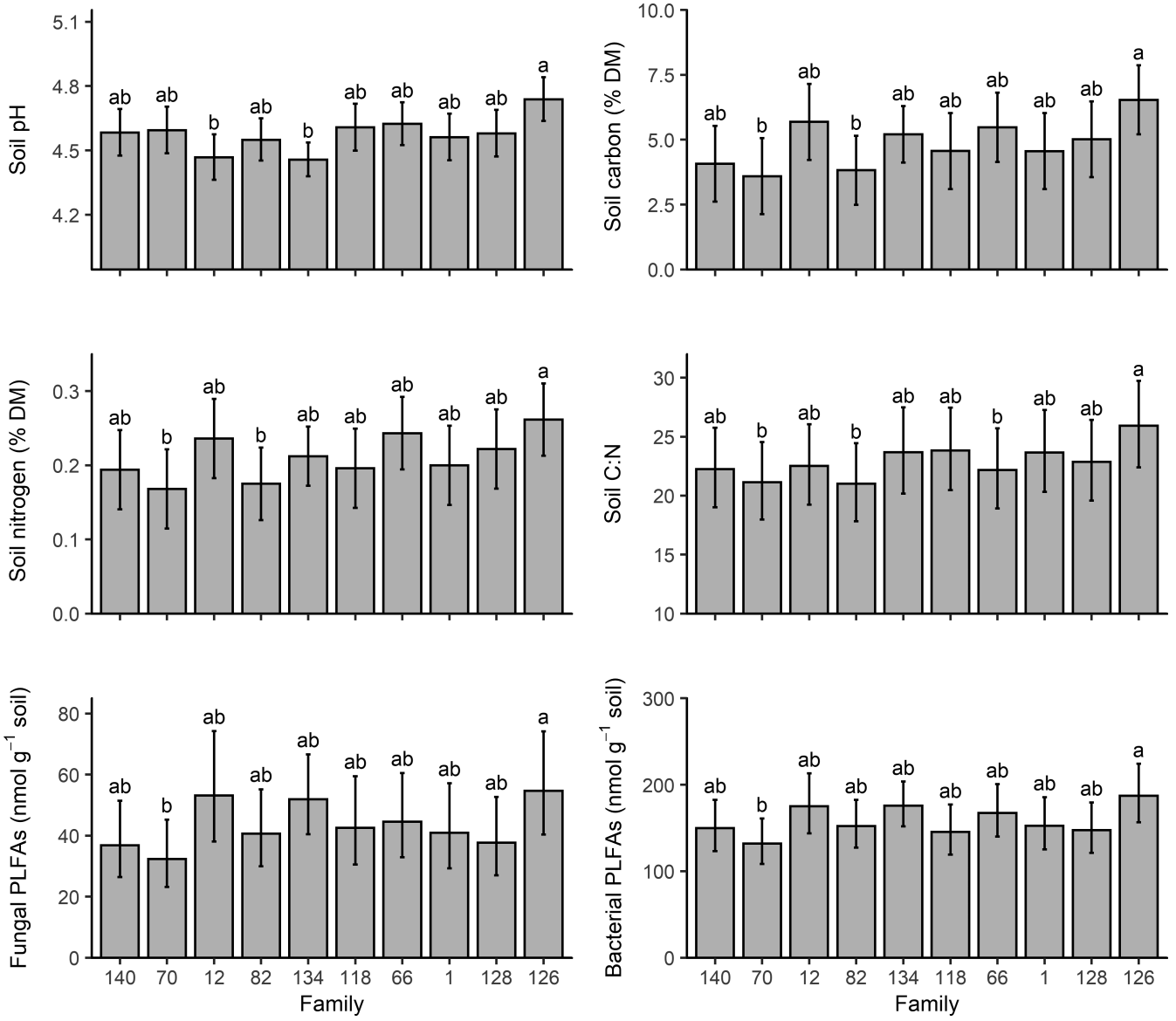

FIGURE 2 Among-family variation in soil chemical and biological properties. Least squares means and standard error of trait values are presented for each family. Families are arranged in ascending order of dbh. Letters that differ indicate significant differences ($\alpha = 0.05$ after Tukey-Kramer adjustment for multiple comparisons)

only soil C, N, C to N ratio, and NH_4^+ showed significant pair-wise differences among families after adjusting for false discovery rate (Figure 2). The significant main effect of family on soil C was driven by several pair-wise differences. Specifically, soils collected from families 126 and 66 had a twofold and 70% higher soil C concentrations, respectively, than family 70, while family 126 also had a twofold higher soil C concentrations than family 82. The main effect of family on soil N was driven by two significant pair-wise differences, where family 126 had a 65 and 75% greater soil N concentration than families 70 and 82, respectively. Many significant pair-wise differences contributed to the main effect of family on soil C to N ratio, where family 126 had a 22% greater value than both families 70 and 82 and both families 118 and 134 had a 12% greater values than family 70. Lastly, the effect of family on NH_4^+ was driven by a single pair-wise difference, where soils from family 134 had a 63% higher concentration than family 70.

We found evidence of family effects on microbial communities in both the univariate and multivariate data. Norway spruce family had a significant effect on three of the nine soil biological properties assessed (Table 2). For fungal PLFAs, the main effect of family was driven by a single pair-wise difference (Figure 2). Specifically, soils collected from family 126 had a twofold higher concentration of fungal PLFAs than family 70. There was also a significant effect of family on soil fungal

TABLE 2 The effects of Norway spruce family, growth rate and litter condensed tannins on soil biological properties

Variable	Mean	Family range	Family			Growth rate				Condensed tannins			
			F_{df}	p	R^2	Est.	F_{df}	p	R^2	Est.	F_{df}	p	R^2
Respiration rate (μmol CO_2 m^{-2} s^{-1})	0.8	0.60–1.12	$1.2_{9,42}$	0.297	0.13	<0.01	$0.6_{1,42}$	0.461	0.01	0.13	$5.5_{1,42}$	**0.024**	0.03
Fungi PLFAs (nmol/g soil)	47.1	32.1–66.9	$2.9_{9,42}$	**0.009**	0.16	−0.16	$29.7_{1,42}$	**<0.001**	0.02	1.49	$0.4_{1,42}$	0.535	<0.01
Bacteria PLFAs (nmol/g soil)	163	132–202	$1.9_{9,42}$	0.078	0.19	−0.23	$1.9_{1,42}$	0.176	0.01	11.3	$2.9_{1,42}$	0.096	0.02
Fungal to bacterial ratio	0.28	0.25–0.32	$3.5_{9,42}$	**0.003**	0.14	<−0.01	$2.9_{1,42}$	0.099	0.01	0.02	$3.5_{1,42}$	0.068	0.02
Actinomycetes (nmol/g soil)	25.0	21.7–27.7	$1.7_{9,42}$	0.119	0.11	−0.01	$0.2_{1,42}$	0.688	<0.01	1.29	$1.6_{1,42}$	0.208	0.01
AMF (nmol/g soil)	4.6	3.7–5.4	$2.0_{9,42}$	0.060	0.11	−0.02	$5.2_{1,42}$	**0.027**	0.03	0.51	$4.3_{1,42}$	**0.043**	0.02
Gram-positive bacteria (nmol/g soil)	35.6	30.2–43.5	$1.6_{9,42}$	0.147	0.18	−0.03	$0.7_{1,42}$	0.409	0.01	2.9	$4.4_{1,42}$	**0.042**	0.03
Gram-negative bacteria (nmol/g soil)	89.1	70.6–112.1	$2.2_{9,42}$	**0.045**	0.18	−0.17	$3.4_{1,42}$	0.070	0.02	2.8	$0.4_{1,42}$	0.509	<0.01

Note: The mean and range of values among families as well as the results of linear models analyzing for the effects of family (family), dbh (growth rate), and litter condensed tannin concentrations (condensed tannins). For each model parameter, its estimate (Est.), F (numerator and denominator degrees of freedom), probability, and partial R^2 values are reported. The significance of main effects was evaluated using marginal sums of squares, where bold values indicate statistical significance at $\alpha = 0.05$.

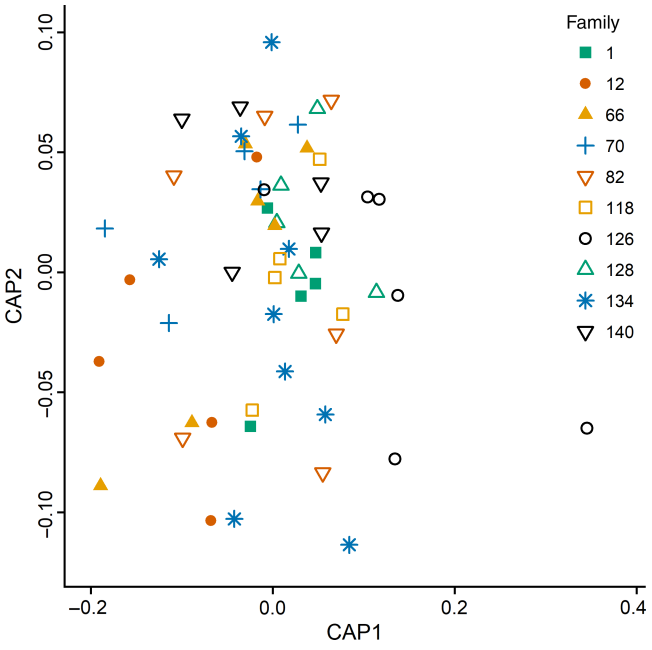

FIGURE 3 Norway spruce families support distinct soil communities. Constrained canonical analyses of principal coordinates (CAP) plot illustrating the effects of family on the composition of soil phospholipid fatty acids

to bacterial PLFA ratio, where families 118 and 126 had a 24% and 28% higher ratio value than family 70, respectively. Thus, the composition of PLFAs within soils was also significantly influenced by family (PERMANOVA; pseudo-$F_{9,56} = 1.9$, $p = 0.012$). Further, canonical analysis of principal coordinates (CAP) successfully separated soil microbial PLFAs by families (Figure 3). Specifically, families 70 and 12 separated from families 126, 128, and 118.

The effects of growth rate and condensed tannins on soil chemical and biological properties

Mean family dbh and litter condensed tannin concentrations exhibited significant and positive relationships with mean family variation in soil C and N (Figure 4). Specifically, genotypic and phenotypic variation in plot growth rate explained 7% and 20% of variation in soil C and N, respectively. At the family mean level, the percentage of C and N in soils increased by 51% and 33% from the slowest to fastest growing family, respectively. Genotypic and phenotypic variation in plot litter condensed tannin concentrations explained 5% and 7% of variation in soil C and N, respectively. The percentage of C and N in soils increased by 40% and 33% from the family with the lowest to highest concentration of litter condensed tannins, respectively. The composition of soil microbial PLFAs also exhibited a significant relationship with dbh and litter condensed tannins when fitted in the same model under marginal sums of squares. Mean plot growth rate explained 9% of variation in the soil microbial PLFA composition of plots (distance-based linear model; pseudo-$F_{1,8} = 5.1$, $p = 0.002$), while litter condensed tannin concentrations explained 5% of variation in mean soil microbial PLFA composition among plots (distance-based linear model; pseudo-$F_{1,8} = 3.0$, $p = 0.016$).

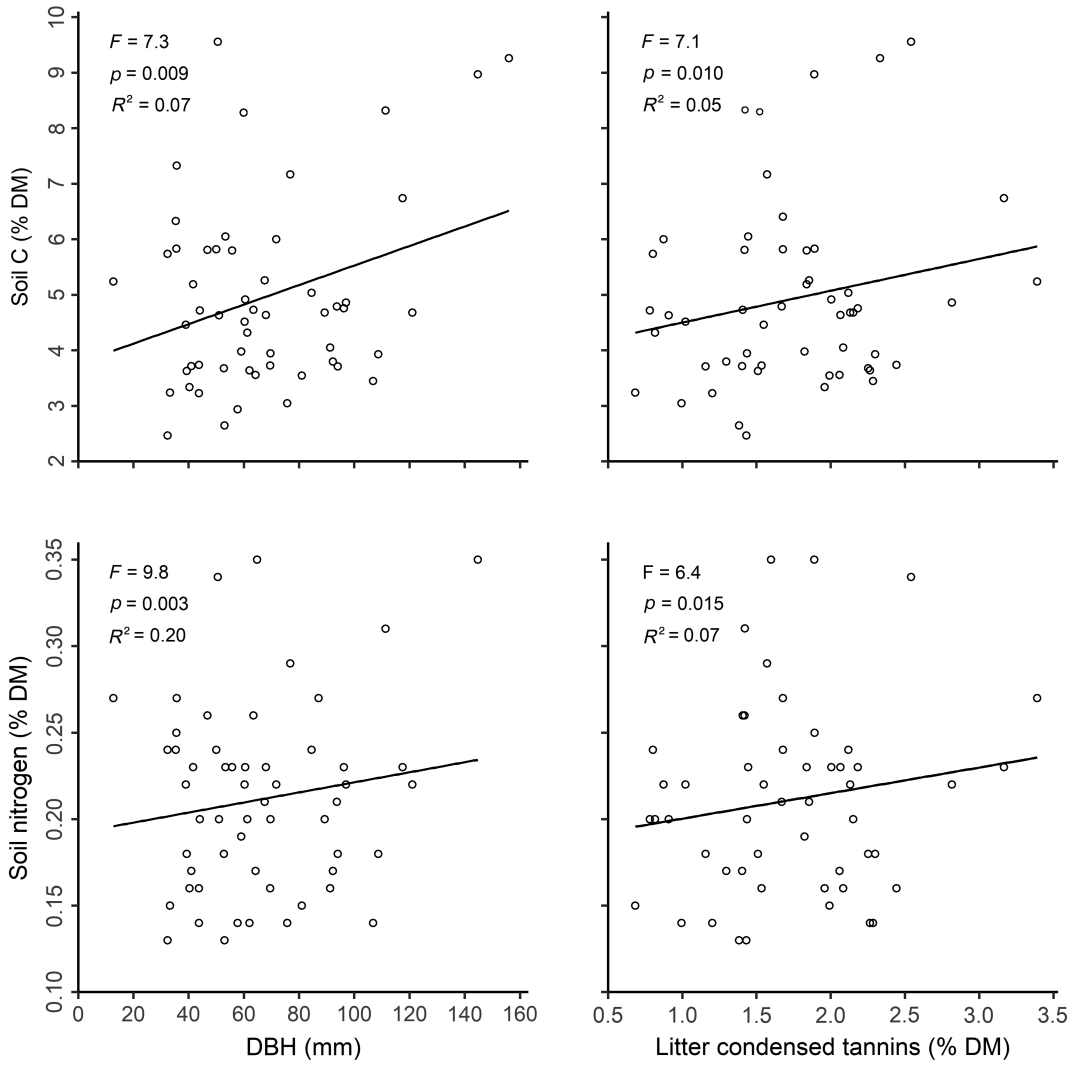

FIGURE 4 Growth rate and litter condensed tannin concentrations explain variation in soil chemical properties. The results of linear regressions between soil C and N and dbh and litter condensed tannin concentrations are presented, where data points represent mean plot values

DISCUSSION

The aim of this study was to assess whether genetic changes occurring from directional selection for tree growth in forest trees could influence soil ecosystems. To accomplish this, we tested how progeny from "plus" trees, which is a common selection strategy to enhance forest growth, differently alters soil communities and processes beneath trees in a 40-year-old common garden. Two key findings emerged from this study. First, Norway spruce families differently modified most of the chemical and biological soil properties assessed, with differences of up to 140% among families. While the importance of intraspecific variation in foundation tree species for aboveground communities has been demonstrated across numerous species and ecological contexts (Whitham et al., 2012) including Norway spruce (Axelsson et al., 2015; Axelsson & Senior, 2018), relatively few studies have investigated the impacts of intraspecific genetic variation on soil communities and processes (reviewed in Fischer et al., 2014). Our second key point is that growth rate and litter condensed tannins concentrations were in part dictating the extended genetic effects of Norway spruce on soil chemical and biological properties. Using the same trees as in Senior et al. (2019) demonstrating significant genetic variation in growth rates and litter condensed tannin concentrations, that is, two major characteristics by which trees may affect soils (Mueller et al., 2017; Pregitzer et al., 2013; Schweitzer, Madritch, et al., 2008), we found that mean family growth rate explained variation in five of 15 of the soil properties assessed. These findings suggest that there is potentially an underappreciation of the potential effects of selective outcrossing for increased growth rates on the soil ecosystems beneath the trees.

Our findings support the ecological significance of intraspecific variation in mediating plant–soil interactions as established in a number of studies with other tree species (Lamit et al., 2015; Mueller et al., 2017; Pregitzer et al., 2013; Schweitzer et al., 2008). While earlier studies on Norway spruce demonstrate variation in ectomycorrhizal community composition among different Norway spruce clones (Korkama et al., 2006; Korkama, Pakkanen, & Pennanen, 2007; Velmala et al., 2013; Velmala et al., 2014), our study shows that genetic variation within this species also influences the broader soil microbial community and soil processes including C and N cycling. Further, we show that the effects of tree genetics on soil ecosystems are not limited to clonal variation but can also occur in open-pollinated systems such as ours (see also Gehring et al., 2017). This is of fundamental importance since Norway spruce represents a prime candidate for genetic improvement for increased forest growth in the boreal forests. For instance, in Sweden, 80% of harvested forest area is reforested with material that has been genetically improved in some way (Black-Samuelsson et al., 2017).

We present evidence that genetic variation generated through selective outcrossing for tree improvement can impact soil chemical and biological properties and that some of these effects can be explained by genetic variation in growth and litter condensed tannins. While intraspecific genetic variation has often been shown to influence soil communities and processes (Fischer et al., 2014; Lamit et al., 2015; Mueller et al., 2017; Pregitzer et al., 2013; Schweitzer, Bailey, et al., 2008), these extended genetic effects are often demonstrated from genotypic variation. We are one of the first, to our knowledge, to assess the extended consequences of selective breeding for increased growth rates and defense in an open-pollinated species, for soil chemical and biological properties, but see Gehring et al. (2017) for a case with another open-pollinated tree species. Hence, we are providing the first evidence that selective outcrossing for increased growth in forest trees may have extended consequences for the broader ecosystem. We found significant family effects on a range of soil properties and that five of these properties were related to family variation in growth rates. Thus, while the selected families vary considerably in growth rate, they vary also in size and, thus, their potential effect on soils during the 40 years (i.e., family mean dbh ranged 35–110 mm). The predominant mechanism by which genetic variation in tree growth influenced soils was most likely the quantity and quality of organic matter inputs to soils. In the absence of a significant relationship with litter condensed tannin concentrations, soil fungal communities were likely influenced by the amount of organic matter entering soils, at least the heterotrophic component which uses these inputs as an energy source. On the other hand, soil C and N were likely influenced by not just the quantity, but also the quality of organic inputs to soils. Both growth rate and litter condensed tannins showed a significant relationship with these variables, and interestingly, increasing litter condensed tannin concentrations were associated with increasing soil C and N concentrations. This may indicate that condensed tannins are decreasing the palatability of soil organic matter for soil organisms or perhaps binding soil N (Pregitzer et al., 2013; Schweitzer, Madritch, et al., 2008). It is important to note that growth rate may be particularly important in an expanding young forest after planting when variation in growth may influence organic matter input and root expansion in the available soil column.

Norway spruce families generated through selective outcrossing can vary in the amount of C that they can accumulate within soils. As our data show that soil C concentrations varied significantly among families, but soil respiration rate did not, there might be a genetic effect in Norway spruce on C accumulation in soils. While not yet widely considered in forestry, in future such variation could potentially be exploited to increase soil C sequestration in managed forests. However, future studies would need to distinguish between the heterotrophic and autotrophic part of soil respiration to interpret gross soil respiration. Furthermore, such assessment would also benefit from assessing bulk densities and C concentrations in the mineral soils in addition to topsoil C. We also found evidence that selectively crossed Norway spruce families can shape distinct soil microbial communities. That is, we detected significant family effects on fungal PLFAs, fungal to bacterial ratio, and gram-negative bacteria, and close to significant effects on bacterial PLFAs and AMF. We also found a significant effect of growth rate on fungal PLFAs, together suggesting that biological properties at least, in part, can be influenced by genetics via variation in growth rate. These communities may have been influenced by the large degree of variation in soil C and N concentrations among families (Fierer, 2017), but could also have been shaped by processes that influence soil conditions including decomposition and hence C and N turnover. Thus, different Norway spruce families could leave a "genetic legacy" effect on soils, potentially influencing the performance of subsequent forest generations.

Variation among, as well as within, plant species in effects on soil chemical properties and microbial community composition has often been shown to influence the performance of the individual tree, plant communities, and subsequent tree generations (Ehrenfeld

et al., 2005; Van der Putten et al., 2013; Van Nuland et al., 2016). These effects can be positive, where plant performance is increased on soils previously modified by mature trees (e.g., symbioses with mycorrhizae or increases in soil organic matter), or negative, where plant performance is reduced (e.g., a build-up of pathogens or nutrient depletion). While these plant–soil feedback are typically documented to vary among species, there is also some evidence to suggest that they can operate on an intraspecific level (Van Nuland et al., 2019). As plant-driven changes to soil C and N as well as soil microbial communities are often key mechanisms driving plant–soil feedback (Ehrenfeld et al., 2005, Van der Putten et al., 2013, Van Nuland et al., 2016), our data suggest that the variable effects of Norway spruce families on soil chemical and biological properties may result in plant–soil feedbacks. However, further studies are required to determine whether these distinct effects of different families on soil properties persist after tree death and whether they are strong enough to affect the performance of future forest generations. Such studies would be useful in informing management strategies and provide insight into whether the variable effects of tree genotypes on soils may have evolutionary consequences (Schweitzer et al., 2018).

Large genetic gains in growth rates are likely to have extended consequences for ecosystem function in replanted forests (But see Bélanger et al., 2004). We found that genetic variation in growth rates tended to be the predominant mechanism driving the effects of spruce genetics on soil chemical and biological properties. Increasing family dbh led to considerable increases in soil C and N concentrations. The observed increases in soil C are most certainly a consequence of increased inputs of litter and fine roots. Further, with greater inputs of C, soil N concentrations are likely to increase. We also found that variation in growth rate among families explained a large proportion of variation in soil microbial community composition. This is in agreement with Korkama et al. (2007), who found that fast- and slow-growing Norway spruce clones tended to shape distinct soil microbial communities. Similar to findings within other systems (Pregitzer et al., 2013; Schweitzer, Madritch, et al., 2008), we found that intraspecific variation in litter condensed tannin concentrations also could predict soil chemical and biological traits. In our case, we found that litter condensed tannin concentrations significantly influenced soil C and N concentrations but no biological properties. Thus, variation in growth rate was a much stronger predictor of among-family variation in soil chemical and biological properties within the Norway spruce families studied. Our findings suggest that active replanting with faster growing genetic material may not cause a nutrient depletion effect. However, it will likely influence soil C accumulation and the composition of microbial communities. This suggests that tree improvement for enhanced growth rates may have yet unforeseen effects on ecosystem function and the performance of future generations of forest trees.

CONCLUSIONS

We show that intraspecific genetic variation generated through selective breeding for increased growth impacts soil communities and processes. Soils collected from beneath different Norway spruce families significantly varied in a range of important soil characteristics related to plant performance and the structure of soil microbial communities. This indicates that the performance of future forest generations could vary depending on the genetic origin of the trees previously modifying that soil. However, whether trees leave behind a genetic legacy after death and whether these effects are strong enough to affect the performance of future forest generations requires further investigation. We also found that among-family variation in growth rate was the best predictor of intraspecific variation in soil chemical and biological characteristics. This suggests that the introduction of faster growing trees into forests through active replanting is likely to influence soil chemical and biological properties. The findings of our study highlight a need for research addressing how tree improvement through traditional methods, which are an integral part of forest management worldwide, may be influencing ecological communities, ecosystem function, and potentially, the performance of future forest generations.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

All authors were involved in the conception and design of the experiment. JKS, EPA, and GRI collected the data. JKS analyzed and interpreted the data, and all authors contributed to the writing of the manuscript.

DATA AVAILABILITY STATEMENT

Data are publicly available at figshare under the DOI: https://doi.org/10.6084/m9.figshare.16963897.v1. (Senior, J. & E.P. Axelsson 2021)

ORCID

John K. Senior https://orcid.org/0000-0002-6033-9239
E. Petter Axelsson https://orcid.org/0000-0002-0906-8365

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