Tree species versus regional controls on ecosystem properties and processes: an example using introduced *Pinus contorta* in Swedish boreal forests[1]

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Abstract: When species are introduced into new regions, there is great uncertainty whether the trait differences of the introduced species or regional factors, such as climate or edaphic properties, will serve as the dominant control of ecosystem properties or processes. In this study, we examined whether the introduction of *Pinus contorta* Douglas ex Loudon into Sweden has altered forest floor properties and processes or whether these properties are more strongly controlled by regional factors. We compared forest floor pH, potential N mineralization rates, bulk density, litter and forest floor depths, C and N concentrations and pool sizes, C:N ratios, and soil microbial communities using substrate-induced respiration and phospholipid fatty acid analysis among stands of introduced *P. contorta* (SwPc), native Swedish *Pinus sylvestris* L. (SwPs), and native Canadian *P. contorta* (CaPc). For most forest floor properties (pH, net NH_4^+ mineralization, bulk density, N mass, and the microbial phospholipid fatty acid community structure), SwPc sites were more similar to SwPs than to CaPc, whereas litter and forest floor depth were significantly higher in SwPc than the two other forest types. Our findings suggest that regional factors exerted a stronger control on most forest floor properties and processes than did species differences between the two *Pinus* species for the regions we studied.

Résumé : Lorsque des espèces sont introduites dans de nouvelles régions, il y a une grande incertitude quand à savoir si les propriétés et les processus de l'écosystème seront surtout déterminés par les différences de caractéristiques des espèces introduites ou par les facteurs régionaux, tels que le climat ou les propriétés du sol. Dans cette étude, nous examinons si l'introduction de *Pinus contorta* Douglas ex Loudon en Suède a modifié les processus et les propriétés de la couverture morte, ou si ces propriétés sont plus fortement déterminées par les facteurs régionaux. Nous avons comparé le pH, le taux potentiel de minéralisation du N, la densité apparente de la couverture morte, la profondeur de la litière et de la couverture morte, la concentration et la taille des réservoirs de N et de C, le rapport C:N et les communautés microbiennes du sol à l'aide de la respiration induite par le substrat et de l'analyse des acides gras phospholipidiques dans des peuplements de *P. contorta* introduit (SwPc), de *Pinus sylvestris* L. indigène (SwPs) et de *P. contorta* canadien (CaPc). Pour la plupart des propriétés de la couverture morte (pH, minéralisation nette de NH_4^+, densité apparente, masse de N et structure de la communauté microbienne basée sur les acides gras phospholipidiques), les stations de SwPc étaient plus semblables aux stations de SwPs qu'aux stations de CaPc, tandis que la litière et la couverture morte étaient plus profondes dans les stations SwPc que dans les deux autres types forestiers. Nos résultats indiquent que les facteurs régionaux exercent une plus forte influence sur les propriétés et les processus de la couverture morte que les différences entre les deux espèces de *Pinus* dans les régions que nous avons étudiées.

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Introduction

Humans frequently distribute species outside their native ranges, and sometimes these introductions adversely affect the composition and diversity of native communities; indeed, non-native species invasions are considered one of the greatest threats to biodiversity globally (Pejchar and Mooney 2009). One way that exotic species can adversely affect native communities is by altering critical ecosystem processes or properties (hereafter referred to as ecosystem-level change; Ehrenfeld 2003), which can in turn affect the performance of native species (Vitousek 1986). Introduced species can sometimes strongly affect the storage and release of soil C, N, and other elements and have been shown to be of equal or greater importance in controlling these properties than some other more frequently studied ecosystem drivers, such as plant species diversity or herbivore abundance (Ehrenfeld 2003). Despite the important effects that introduced species can have on native ecosystems, including through below-ground inter-

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actions with soil biota in the introduced ecosystem (Nuñez et al. 2009), relatively few studies have evaluated their impacts on below-ground properties or processes (Levine et al. 2003). Thus, an increased understanding of the below-ground ecosystem-level changes arising from non-native species introductions is needed.

Most studies evaluating ecosystem-level change following non-native species introductions suggest that observed changes are primarily due to invader abundance (Strayer et al. 2006) or functional differences between the introduced species and those of the native community (Vitousek 1990; Ehrenfeld 2003). For instance, if the introduced species is abundant and possesses different traits than the native species, such as differences in litter quality, these can lead to significant changes in ecosystem processes (e.g., decomposition and nutrient cycling rates) or ecosystem properties (e.g., soil C pool sizes) (Wardle et al. 2011). Even introduced species that are functionally similar to native species may drive changes in ecosystem properties and processes if they have different growth and C input rates in their introduced environments. Herein, we consider three possible outcomes for ecosystem change following a species introduction: (1) ecosystem change results from functional differences between the introduced species and the native community (e.g., Vitousek 1990), (2) there is no effect of the introduction because regional factors in the introduced range have stronger ecosystem-level effects than does the introduced species, and (3) despite functional similarity of the introduced species relative to the native species, ecosystem-level change occurs due to positive interactions between the introduced species and the biotic or abiotic attributes of the introduced ecosystem (e.g., increased growth of the introduced species relative to its native range or relative to native species in the introduced range, possibly due to escape from antagonistic biotic interactions of the introduced species within its native range). Which of these three outcomes occurs is likely to vary depending on the ecosystem property or process being measured, the species or introduced region evaluated, or time since introduction (Strayer et al. 2006). Few studies have been able to evaluate these alternative outcomes because they lack explicit comparisons of the introduced species in both native and introduced ranges (Hierro et al. 2005).

In this study, we evaluated the effects of the introduction of the North American tree species *Pinus contorta* Douglas ex Loudon into northern Sweden on forest floor properties and processes. *Pinus contorta* is a commercially valuable timber species that has been shown to be a strong invader in many parts of the world where it has been introduced, particularly in Southern Hemisphere ecosystems (Ledgard 2001; Langdon et al. 2010) where it has been shown to alter community- and ecosystem-level properties (Simberloff et al. 2010). However, relatively little is known about the ecological consequences of its introduction into European forest ecosystems (Engelmark et al. 2001). Nearly 600 000 ha of *P. contorta* have been planted in Sweden, with its widespread introduction beginning approximately 50 years ago (Elfving et al. 2001). *Pinus contorta* produces approximately 36% more total volume relative to the phylogenetically similar native Swedish species *Pinus sylvestris* L., irrespective of site conditions (Elfving et al. 2001); further, it exhibits higher growth rates in Sweden relative to its native range (B. Elfving, personal communication). Thus, interactions between *P. contorta* and biotic or abiotic conditions in the introduced range may play an important role in determining its effects on forest floor properties or processes as compared with the native *P. sylvestris*.

Forest floor properties and processes are primarily influenced by litter inputs (i.e., quality and quantity of litter) and regional factors such as climate, site fertility, or pH that influence rates of decomposition (Fisher and Binkley 2000). Boreal forests are considered N limited, and differences in litter quality or quantity between *P. contorta* and *P. sylvestris* are likely to influence decomposition and N mineralization rates as well as the long-term accumulation of C and N in the forest floor. Studies have shown that *P. sylvestris* produces less litter, has higher initial litter decomposition rates, and has lower lignin concentrations compared with *P. contorta* in Swedish forests (Berg and Lundmark 1987; Norgren 1995; Ågren and Knecht 2001), suggesting that differences in forest floor properties between *P. contorta* and *P. sylvestris* may occur. Differences in litter properties may also alter soil microbial properties such as microbial biomass or community composition (Wolfe and Klironomos 2005). Whether or not forest floors are altered in response to *P. contorta* introduction should depend on the relative importance of species differences versus regional factors in controlling ecosystem properties or processes.

Using an explicit comparison of *P. contorta* in both its native and introduced ranges, we tested the following hypotheses: (1) we hypothesized that in these N-limited ecosystems, several forest floor properties relevant to N cycling, including N availability and potential mineralization rates, would be controlled to a greater extent by canopy species than by regional factors (i.e., regional abiotic or biotic controls), (2) we predicted that accumulation rates of forest floor organic matter, C, and N would be higher in Swedish *P. contorta* stands than in Canadian *P. contorta* or Swedish *P. sylvestris* due to the higher productivity that introduced *P. contorta* is reported to achieve (Elfving et al. 2001), and (3) we hypothesized that both *P. contorta* forest types would have different microbial communities than *P. sylvestris* stands and microbial biomass would be higher in the Swedish *P. contorta* stands due to their higher productivity and greater litter production. Collectively, these three hypotheses provide a rare evaluation of the potential outcomes for ecosystem-level change following the introduction of a non-native species.

Methods

Study area

We selected study sites consisting of *P. contorta* forest in Alberta, Canada (15–57 years), and two *Pinus* forest types in northern Sweden: similarly aged stands of *P. contorta* and *P. sylvestris* (17–47 years), which are representative of the age range of *P. contorta* in the boreal forest of northern Sweden (Table 1). For each forest type, we sampled eight replicate stands, yielding a total of 24 stands sampled (3 forest types × 8 replicates). Each stand was a minimum size 0.5 ha. We determined the age of each stand by evaluating stand records or by aging trees using increment cores, calculated basal area of each stand using a basal area factor prism for stands >3 m tall, and used a clinometer and tape to measure tree heights.

Table 1. Properties of the stands for each of the three forest types, Canadian *Pinus contorta* (CaPc), Swedish *Pinus contorta* (SwPc), and Swedish *Pinus sylvestris* (SwPs).

Forest type	Age (years)	Origin	Basal area ($m^2 \cdot ha^{-1}$)	Stand height (m)	Latitude	Longitude	Date collected (dd/mm/yyyy)[b]
CaPc	15	Natural	—[a]	3	53°20′58.9″N	116°52′03.8”W	07/10/2010
CaPc	30	Natural	34.4	8	53°12′59.1″N	116°47′09.5″W	07/10/2010
CaPc	47	Planted	26.4	14	53°10′48.8″N	117°27′21.2″W	14/10/2010
CaPc	19	Planted	—[a]	2.5	53°10′46.3″N	117°28′05.0″W	14/10/2010
CaPc	33	Natural	16.8	9	53°11′53.0″N	117°29′09.5″W	14/10/2010
CaPc	57	Natural	20.8	14	53°13′43.1″N	117°21′09.8″W	14/10/2010
CaPc	33	Natural	13.6	9	53°16′11.0″N	117°20′51.1″W	14/10/2010
CaPc	44	Planted	24.8	14	53°16′38.7″N	117°10′11.7″W	14/10/2010
SwPc	21	Planted	25.6	8	63°56′64.0″N	20°34′55.9″E	21/10/2010
SwPc	17	Planted	20.4	6	64°04′95.7″N	19°48′37.9″E	21/10/2010
SwPc	24	Planted	25.6	9	64°14′80.8″N	19°48′08.2″E	22/10/2010
SwPc	23	Planted	20.8	9	64°09′26.7″N	19°35′17.7″E	25/10/2010
SwPc	47	Planted	27.2	15	64°09′44.4″N	19°34′73.0″E	25/10/2010
SwPc	22	Planted	22	9	64°16′39.0″N	19°39′33.9″E	26/10/2010
SwPc	17	Planted	18.8	6	64°17′19.5″N	19°27′43.5″E	26/10/2010
SwPc	28	Planted	22.4	10	64°10′45.7″N	19°32′99.9″E	26/10/2010
SwPs	24	Planted	18.8	12	63°56′59.5″N	20°35′76.9″E	21/10/2010
SwPs	17	Planted	13.2	6.5	64°04′97.0″N	19°48′23.1″E	21/10/2010
SwPs	24	Planted	26	6	64°14′86.5″N	19°48′13.1″E	22/10/2010
SwPs	23	Planted	15.2	9	64°09′18.4″N	19°35′68.7″E	25/10/2010
SwPs	47	Planted	33.2	16	64°09′48.7″N	19°34′75.9″E	25/10/2010
SwPs	22	Planted	28.4	9	64°16′44.5″N	19°39′50.3″E	26/10/2010
SwPs	17	Planted	16.4	5	64°17′23.2″N	19°27′49.5″E	26/10/2010
SwPs	28	Planted	18.4	9	64°10′45.7″N	19°32′99.9″E	26/10/2010

[a]Basal area was not recorded for the two stands ≤3 m tall.

[b]Note that bulk density soil cores were collected in spring 2011 immediately after snowmelt.

The Canadian study sites (hereafter referred to as CaPc) were located in the Upper Foothills subregion of Alberta in *P. contorta* forests near Robb, Alberta (53°10′N to 53°20′N, 116°44′W to 117°29′W) (Table 1). The climate is continental subhumid (Dfc) under the Köppen classification system (The National Atlas of Canada 1974). The annual mean air temperature is 2 °C and the annual mean summer (June–August) temperature is 13.6 °C (1971–2000). Snow usually covers the frozen ground from the end of October to late April. Mean annual precipitation is approximately 560 mm (1971–2000), of which approximately 75% falls as rain. The underlying geology of the Upper Foothills is shale and sandstone overlain by medium-textured, weakly calcareous glacial till, with gray luvisol soils characteristic of the region. The Swedish study sites were located in Västerbotten County, Sweden (63°56′N to 64°17′N, 19°27′E to 20°35′E) (Table 1). The annual mean air temperature is 1 °C and the annual mean summer (June–August) temperature is 13.0 °C (1961–2010). Snow usually covers the frozen ground from early December to late April. Mean annual precipitation is approximately 600 mm (1980–1999), of which half falls as rain and half as snow. The underlying geology of the Swedish study area is fine- to medium-textured glacial till weathered from granitic bed rock, with brown podzols characteristic of the region. Swedish *P. contorta* stands consisted of different provenances derived from the Canadian Rocky Mountains. At each of the eight Swedish sites, we selected similarly aged paired stands of *P. contorta* and *P. sylvestris* (hereafter referred to as SwPc and SwPs, respectively) no greater than 1 km from each other (usually directly adjacent to each other) so that slope, aspect, elevation, and underlying geology were held constant between the paired stands (paired stands were identical in age, except for one site where the SwPs was 3 years older than the SwPc). The sites we chose were relatively flat and therefore did not have much variation in slope and aspect, and with our paired sampling design, moisture status was considered equal for paired Swedish stands. Our sample size was restricted to eight replicates because of the limited availability of Swedish *P. contorta* stands with adjacent similarly aged *P. sylvestris* stands.

Forest floor sampling and measurements

Within each of the 24 stands, we collected five forest floor subsamples (F and H horizons combined, each sample was ~10 g) for phospholipid fatty acid (PLFA) analysis using aseptic techniques and 10 intact forest floor cores (10 cm diameter) for characterization of other forest floor properties and processes. These were collected a minimum distance of 10 m from the stand edge and at random intervals of 5–10 m along transects, but if the sampling point fell next to a tree base, it was moved 50 cm away from the tree base. For five of the intact cores, we measured the depths of the litter layer and F-H organic layer and measured bulk density of the F-H layer. Forest floor subsamples and cores were kept in a cooler and transferred back to the laboratory. The samples collected for PLFA analysis were immediately placed in a sterile Whirlpak bag, stored in a freezer (–20 °C), and then freeze-dried prior to PLFA extraction. Five of the forest floor

cores were sieved (4 mm) and kept refrigerated (4 °C) in polyethylene bags for up to 5 weeks prior to several analyses requiring field-moist soil. To report forest floor response variables on a dry mass basis, we used a portion of the five sieved cores to measure the field-moist and oven-dried (48 h at 65 °C) mass, which allowed for calculation of soil moisture content. We also oven-dried (65 °C) the remaining unsieved five cores for three days, weighed them, and calculated bulk density as mass per core volume. The mass of these samples was also used to report total C and N data on an area basis.

The sieved forest floor cores were analyzed for pH, total C and N, extractable ammonia, potential N mineralization, and substrate-induced respiration (SIR) as a measure of active microbial biomass, as described below. Oven-dried samples (65 °C) were used to measure pH and total C and N content. Soil pH was measured potentiometrically in a saturated paste that was in equilibrium with a soil suspension of a 1:10 soil – 0.01mol·L^{-1} $CaCl_2$ liquid mixture. Total percent C and N were measured on ground samples using a NC Soil Analyzer (Thermo Electron Corporation, Thermo Fisher Scientific, Bremen, Germany).

Potential N mineralization rates were measured on each sieved core using an aerobic laboratory incubation (Hart et al. 1994; Gundale et al. 2005). Briefly, this method involves creating two parallel incubation tubes from each forest floor subsample, one that is extracted immediately and one that is dark-incubated (22 °C) and extracted 1 month later. Differences in inorganic N concentrations between the beginning and end of the incubation indicate net mineralization, which can be positive or negative (indicating net immobilization occurred). Each sample was prepared by placing 5 g of sieved forest floor (wet mass) into a 100 mL glass nalgene bottle. For incubated samples, the moisture content during the incubation period was maintained by checking weekly whether addition of water to maintain the initial jar and sample mass was needed. Inorganic N extraction was done on the two sets of samples by placing 50 mL of 1 mol·L^{-1} KCl in each bottle, shaking for 1 h, and then filtering through Whatman No. 42 filter paper. Extracts were used for determination of NH_4^+-N and NO_3^--N using standard colorimetric methods on an Auto-Analyzer III (Omni Process, Solna, Sweden). There was no detectable NO_3^--N measured in the majority of extractions; therefore, only NH_4^+ -N data are reported.

Field-moist sieved cores were also used to measure SIR, which is a measure of the relative active microbial biomass responsible for regulating the supply of plant-available nutrients from the soil (Anderson and Domsch 1978). SIR was measured by placing 5 g (dry mass equivalent) from each subsample into a 100 mL glass bottle and then adjusting the moisture content to 250% (dry mass basis). After adjusting the water content, samples were placed in a dark incubator (25 °C) for 24 h to equilibrate. The following day, 2.5 mL of glucose solution (40 g·L^{-1}) was pipetted into each bottle, which increased the water content of the soil to 275%, and added a quantity of glucose C equivalent to 2% soil dry mass. The jar was then sealed and we determined evolution of CO_2 between 1 and 4 h following glucose addition by injecting 0.2 mL subsamples of headspace gas into an infrared gas analyzer, which allowed for estimation of SIR. Forest floor samples too wet after moisture content adjustment to allow for meaningful SIR readings (23 of 120 samples) were excluded from analysis; the numbers of excluded samples was evenly distributed among forest types and thus should not bias our results.

Soil microbial community structure was analyzed using PLFA analysis. PLFA profiles were analyzed for each subsample by freeze-drying and extracting each forest floor sample (0.3 g) using a modified Bligh and Dyer method, which included extraction with a single-phase chloroform mixture, lipid fractionation on a solid-phase-extraction Si column, followed by a mild methanolysis (Bligh and Dyer 1959; King et al. 1977; White et al. 1979; Kates 1986; Frostegård et al. 1991). The fatty acid methyl esters were then analyzed by capillary gas chromatography (Perkin Elmer Clarus 500GC; Waltham, Massachusetts) and chromatograms interpreted using Perkin Elmer Total Chrome peak identification software. A total of 27 individual fatty acids were detected. Excluding the internal standard (19:0) and one peak that was only present in a few PLFA samples, 25 PLFAs were included in the analysis of total PLFA biomass. Fatty acids were designated *X*:*Y*ω*Z*, where *X* represents the number of C atoms, *Y* represents the number of double bonds, and *Z* indicates the position of the first double bond from the aliphatic (ω) end of the molecule. Total PLFAs were quantified as nanomoles per gram of forest floor. In addition, PLFAs used as biomarkers for functional groups (i.e., fungi, bacteria, gram-positive bacteria, gram-negative bacteria, actinomycetes, and arbuscular mycorrhizae) were quantified on a mol percent basis. The fungal PLFA 18:2ω6 was used to estimate the contribution of fungi (Frostegård and Bååth 1996), while 16:1ω5 was used to estimate arbuscular mycorrhizae (Frostegård and Bååth 1996; Olsson 1999). Bacterial PLFAs included 14:0, i14:0, 15:0, a15:0, i15:0, i16:0, 16:1ω9, 16:1ω7t, i17:0, a17:0, 17:0, cy17:0, 18:1ω7, and cy19:0 (Bååth et al. 1992; Frostegård and Bååth 1996; Myers et al. 2001). The ratio of 18:2ω6 to the bacterial PLFAs was used to estimate the relative contributions of fungi and bacteria. The 10-methyl branched fatty acids (10me16:0, 10me17:0, and 10me18:0) were used to measure actinomycetes (Kroppenstedt 1985; Brennan 1988).

Statistical analyses

We first determined whether each variable met the assumptions for analysis of variance (ANOVA) and transformed response variables when necessary. One-way ANOVAs were used to test for significant ($\alpha = 0.05$) differences in the response of individual variables among the three forest types (i.e., CaPc, SwPc, and SwPs) (Proc Mixed). For data that could not be transformed to meet the assumptions, nonparametric Kruskal–Wallis tests were used (Proc Npar1-way). When significant differences were detected, we used post hoc linear contrasts with Bonferroni-adjusted *P* values (family-wise $\alpha = 0.05$) to identify significant pairwise differences for ANOVAs (Proc Mixed) and we used a permutation test to do pairwise comparisons after Kruskal–Wallis tests (Proc Multtest). SAS software (version 9.2; SAS Institute Inc., Cary, North Carolina. Copyright 2000) was used for ANOVA, Kruskal–Wallis tests, permutations, and linear contrasts.

Multivariate patterns of microbial community structure using individual forest floor PLFAs (mol percent) among forest

types were examined using nonmetric multidimensional scaling (NMS) ordination (McCune and Grace 2002). We used PC-ORD (version 5; MjM Software Design, Gleneden Beach, Oregon), with Sørenson as the distance measure, and completed 100 runs with real data and 100 Monte Carlo randomized runs, starting with a six-dimensional solution and stepping down to a one-dimensional solution. We determined the number of dimensions of our final solution by evaluating the scree plot and the reduction in stress with step-down in dimensionality of the preliminary runs (McCune and Grace 2002). Stability of the solution (stability criterion = 0.00005) was assessed by plotting stress versus iteration for each of our iterations. After checking the optimal number of dimensions and best solution from the preliminary runs, we ran a final NMS with the number of dimensions determined from the preliminary runs ($n = 2$) using the starting configuration that worked best in our preliminary runs and omitting the Monte Carlo test. We then calculated the Pearson correlation coefficients for stand and forest floor descriptive variables (e.g., PLFA functional groups, bulk density, and total C and N) with the NMS ordination axes. We used the multiresponse permutation procedure (MRPP) to test for statistically significant differences in PLFA community profiles among the three forest types. MRPP is a nonparametric multivariate procedure for testing the null hypothesis of no difference between two or more groups of entities (Zimmerman et al. 1985). The initial MRPP comparing the three forest types was followed up by pairwise comparisons among forest types; P values were Bonferroni-adjusted so the family-wise Type I error rate remained 0.05.

Results

For several of the measured forest floor properties and processes, we found that SwPc was similar to SwPs and both were different from CaPc. There were significant differences in pH among forest types, with the pH of CaPc significantly higher than for both Swedish forest types (Table 2). Although the Kruskal–Wallis test indicated that there were significant differences in initial NH_4^+-N concentrations ($P = 0.03$) among the three, none of the pairwise comparisons were significant (Fig. 1). NH_4^+ -N concentrations for samples incubated for 1 month were not significantly different among forest types (ANOVA, $P = 0.12$) (Fig. 1); however, potential net mineralization rates during the 1-month incubation were similar for both SwPc and SwPs but significantly higher compared with the CaPc stands, which showed net immobilization (Kruskal–Wallis, $P = 0.0009$) (Fig. 1). The bulk density of the forest floor in the CaPc stands was significantly higher than for both Swedish forest types (ANOVA, $P = 0.004$) (Fig. 2). Both litter and forest floor depths were significantly deeper in SwPc than in both CaPc and SwPs stands (Kruskal–Wallis tests: litter, $P = 0.0002$; forest floor, $P < 0.0001$) (Fig. 2). The CaPc stands had significantly higher N mass in the forest floor than the Swedish forest types, although there were no significant differences in C mass or the C and N concentrations (Table 2). Forest floor C:N ratios did not significantly differ among the stand types (Table 2).

There was no significant difference in active microbial biomass as measured by SIR among the forest types (Table 2) or in total PLFA biomass among the forest types (Table 2). There was also no significant difference in PLFA mol percent for any of the PLFA functional groups among the three forest types (Table 2). The fungi to bacteria ratio did not significantly differ among the forest types (Table 2).

The NMS two-dimensional solution (final stress = 7.62 after 36 iterations) explained 96.1% of the variation in the data set (Fig. 3). MRPP analysis of PLFA profiles showed significant differences among the three forest types (A = 0.14, $P = 0.0002$); the CaPc stands were different from the Swedish forest types, whereas the Swedish forest types did not significantly differ from each other (CaPc versus SwPc: A = 0.15, $P = 0.002$; CaPc versus SwPs: A = 0.16, $P = 0.002$; SwPc versus SwPs: A = –0.02, $P = 1.0$). Overlaying the other stand and forest floor descriptive variables on the NMS ordination of individual PLFAs showed correlations of several variables with the two ordination axes (Fig. 3). CaPc stands were located towards the lower end of axis 1 and widespread across axis 2 and based on their relative locations in the plot were correlated with higher values for pH (axis 1: $r = –0.86$, axis 2: $r = 0.24$), mole percent of fungal PLFAs (axis 1: $r = –0.63$, axis 2: $r = –0.87$), and time zero ammonia (axis 1: $r = –0.40$, axis 2: $r = 0.48$). PLFA profiles for the two Swedish forest types were overlapping, both loaded toward the upper end of axis 1 with spread across axis 2. Their relative locations on the ordination were positively correlated with the greater depth of forest floor (axis 1: $r = 0.46$, axis 2: $r = 0.00$), bacteria to fungi ratio (axis 1: $r = 0.47$, axis 2: $r = 0.92$), bacteria (axis 1: $r = 0.16$, axis 2: $r = 0.93$), gram-positive bacteria (axis 1: $r = 0.45$, axis 2: $r = 0.53$), gram-negative bacteria (axis 1: $r = 0.04$, axis 2: $r = 0.89$), C:N ratio (axis 1: $r = 0.15$, axis 2: $r = –0.49$), and arbuscular mycorrhizae (axis 1: $r = 0.13$, axis 2: $r = 0.73$). Correlations for other variables (e.g., stand age, total N, total C, and net mineralization) with the ordination axes were low (axis 1: R^2 ranged from 0.0 to 0.16, axis 2: R^2 ranged from 0 to 0.17) and thus were not considered in further detail.

Discussion

This study provides a rare evaluation of whether species differences versus regional factors control ecosystem processes and properties following the introduction of a non-native species. The differences among the Canadian and Swedish forest types that we observed suggest that regional factors that differ between the native and introduced range appear to exert a stronger influence on most forest floor properties and processes than do species differences, whereas some forest floor properties, notably litter and forest floor depth, appear to be driven by a positive interaction between *P. contorta* and its introduced location. Contradicting our first hypothesis, that canopy species would exert a stronger control than regional factors on N cycling attributes, we alternatively found significantly lower potential net mineralization rates for CaPc than for SwPc and SwPs, and SwPc and SwPs did not differ. This analysis showed that CaPc stands exhibited net immobilization, whereas both Swedish forest types exhibited positive net mineralization rates. Nitrogen mineralization from decomposing plant litter is a major source of N for forest trees (Fisher and Binkley 2000). Typical of most

Table 2. Means, SEs, and *P* values for one-way ANOVA and nonparametric Kruskal–Wallis tests to test for significant differences in the response of variables among the three forest types, Canadian *Pinus contorta* (CaPc), Swedish *Pinus contorta* (SwPc), and Swedish *Pinus sylvestris* (SwPs).

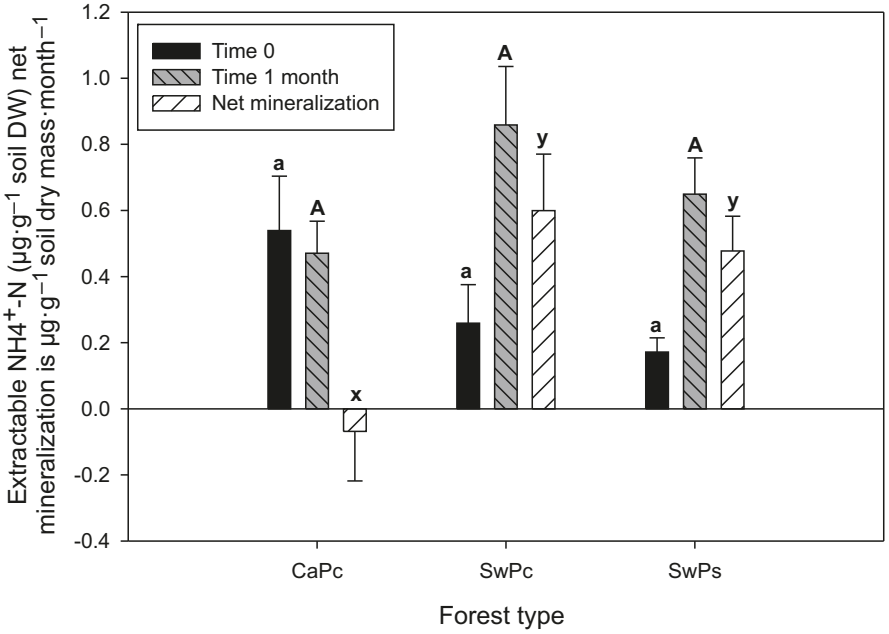
	CaPc		SwPc		SwPs		
Variable	Mean	SE	Mean	SE	Mean	SE	*P*
pH	4.03a	0.10	3.14b	0.06	3.20b	0.07	**0.0007**[a]
Total N mass ($kg \cdot ha^{-1}$)	1.75a	0.31	1.01b	0.09	1.03b	0.09	**0.009**[a]
Total C mass ($tons \cdot ha^{-1}$)	14.00	3.33	15.51	1.65	10.68	1.31	0.17[b]
%C	34.34	1.67	36.37	1.57	34.36	1.71	0.68[b]
%N	0.95	0.05	1.08	0.05	0.98	0.05	0.48[a]
C:N ratio	36.62	1.21	33.89	0.80	35.46	0.94	0.52[b]
Substrate-induced respiration ($\mu g\ CO_2 \cdot g^{-1} \cdot h^{-1}$)	0.11	0.01	0.14	0.01	0.11	0.01	0.15[a]
Phospholipid fatty acids biomass ($nmol\ g^{-1}$)	827	44	823	50	940	46	0.37[a]
Fungi to bacteria ratio	55.7	4.3	46.6	3.4	45.7	3.0	0.21[a]
Phospholipid fatty acids (mol%)							
Bacteria	47.1	1.1	47.0	0.9	47.1	0.9	1.0[a]
Gram-positive bacteria	11.1	0.4	11.7	0.2	11.5	0.3	0.67[a]
Gram-negative bacteria	34.2	1.0	33.2	0.8	33.8	0.7	0.75[a]
Actinomycetes	1.3	0.1	1.2	0.1	1.1	0.1	0.45[a]
Fungi	24.5	1.3	20.8	1.1	20.6	1.0	0.11[a]
Arbuscular mycorrhizae	3.4	0.2	3.4	0.2	3.7	0.2	0.54[a]

Note: Significant pairwise contrasts are highlighted with the *P* value bolded. Significant differences in means between forest types are indicated by letters.

[a]One-way ANOVA, df = 2,21.

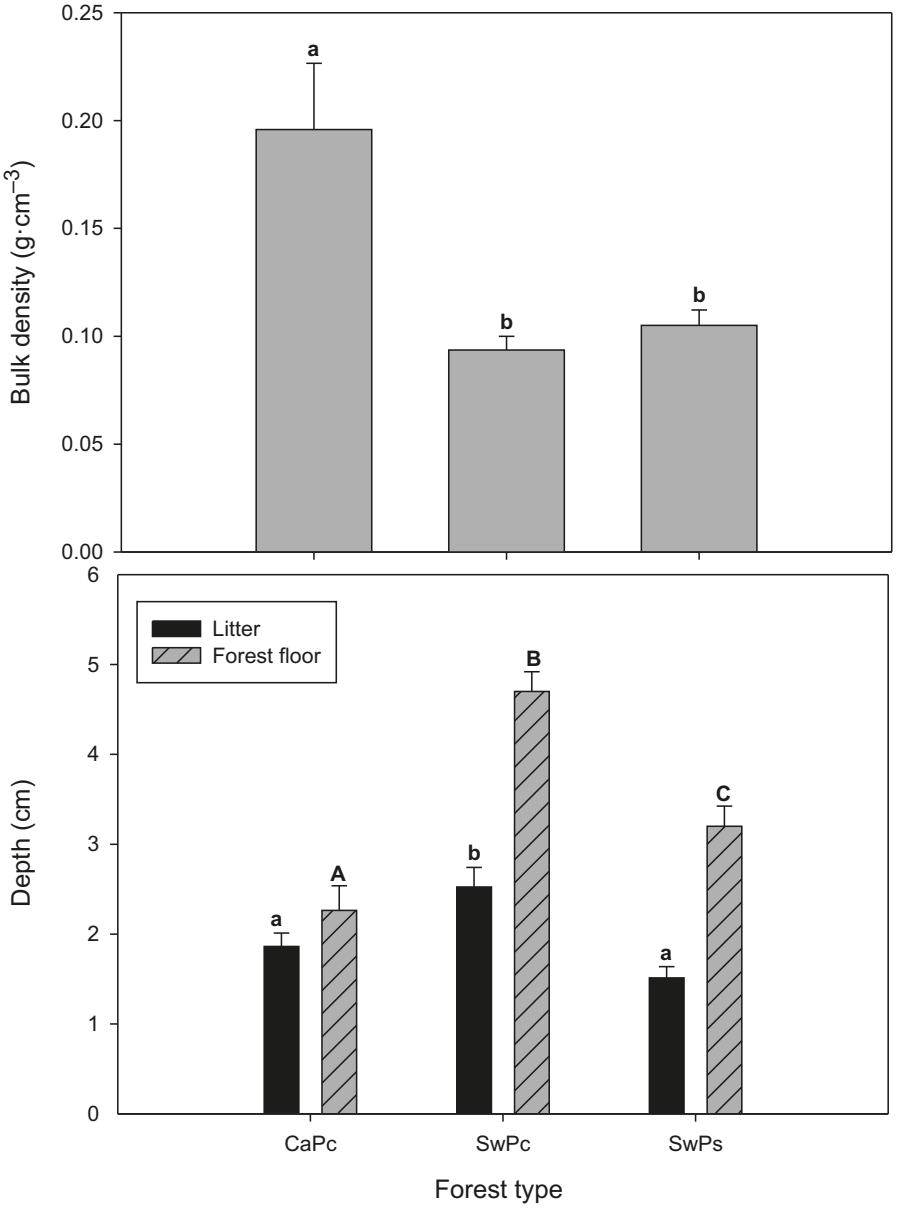
[b]Kruskal–Wallis.

Fig. 1. Comparison of ammonia at time zero, after a month of incubation, and net mineralization rates among the three forest types (mean ± SE, $n = 8$), Canadian *Pinus contorta* (CaPc), Swedish *Pinus contorta* (SwPc), and Swedish *Pinus sylvestris* (SwPs). Within a time (bar pattern), bars with different letters (x, y) indicate significant differences based on pairwise comparisons.



boreal forests, all three forest types had relatively high forest floor C:N ratios, which generally stimulates net immobilization. One factor that might explain the differences in mineralization that we saw among regions is that in situ decomposition rates may be faster for CaPc than for the Swedish forest types. If decomposition rates were higher for CaPc, then we would expect initial NH_4^+-N concentrations to be higher and lower concentrations of labile organic N left to mineralize (i.e., because it has already mineralized), leading to very small changes in NH_4^+-N concentrations during the controlled incubation. Although we did not directly measure decomposition rates, our findings of higher bulk density levels in the CaPc stands than in both Swedish forest types and a shallower F-H layer in the CaPc forest floor relative to the

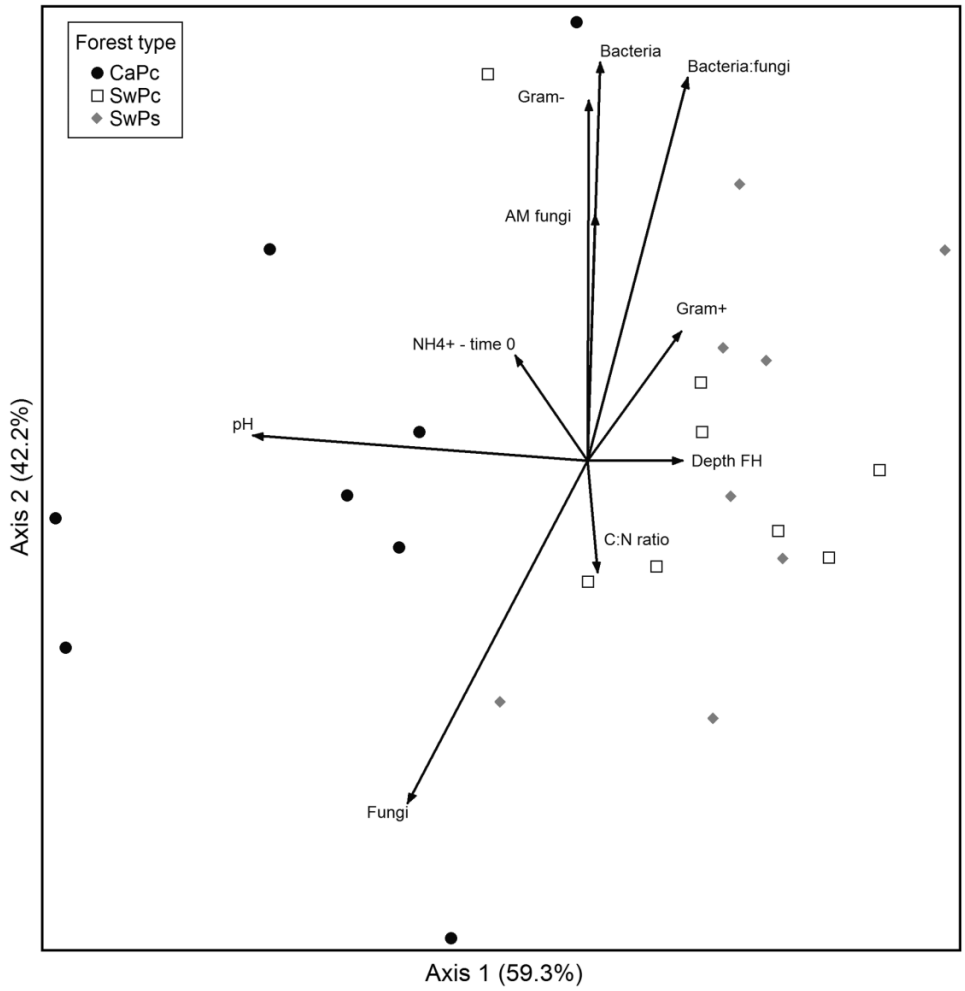
Fig. 2. Bulk density and depths of the litter and forest floor (F and H layers) for the three forest types (mean ± SE, $n = 8$), Canadian *Pinus contorta* (CaPc), Swedish *Pinus contorta* (SwPc), and Swedish *Pinus sylvestris* (SwPs). For each bar pattern, different letters (a, b or A, B, C) indicate significant differences based on pairwise comparisons.



Swedish forest floors further suggest that decomposition rates are higher in CaPc compared with the Swedish forest types. The Swedish *Pinus* forests are likely to have a poorer decomposition environment than the Canadian stands due to their colder summer temperatures and the significantly more acidic forest floor. These conditions likely result in lower in situ decomposition rates, resulting in a greater accumulation of labile organic N in the forest floor, which would likely produce lower initial NH_4^+-N concentrations and larger increases under the ideal conditions of the controlled incubation. The more acidic forest floors of the Swedish *Pinus* forest floors compared with CaPc described above is likely a function of the underlying geology of the two study areas; in the Swedish stands, the underlying geology is granite, which typically weathers into low-pH soils, whereas the underlying geology of the Alberta foothills is shale and sandstone overlain by medium-textured, weakly calcareous glacial till, which weathers into less acidic soils. The assertion that abiotic regional factors are affecting pH more than species differences is further supported by a study that compared 27-year-old Swedish stands of *P. contorta* and *P. sylvestris* and found no significant difference in soil pH, despite observing differences in the leaf chemistry for these two species (Alriksson and Eriksson 1998).

Our second hypothesis was that SwPc would cause organic matter to accumulate faster relative to SwPs and CaPc due to its higher productivity in Sweden than in Canada and relative to SwPs, which would in turn lead to higher accumulation rates of C and N. In support of this hypothesis, our results showed significantly higher litter and forest floor depths for SwPc, which is consistent with other studies that found that *P. sylvestris* has a lower production of litter than *P. contorta*

Fig. 3. Results of nonmetric multidimensional scaling ordination for the forest floor phospholipid fatty acid profiles delineated by forest type, Canadian *Pinus contorta* (CaPc), Swedish *Pinus contorta* (SwPc), and Swedish *Pinus sylvestris* (SwPs). The amount of variation explained by each axis is included in parentheses. The angles and lengths of the vectors indicate direction and strength of relationships of the variables with the ordination axes (cutoff for displayed variables was $R^2 > 0.2$).



in Swedish forests (Berg and Lundmark 1987; Ågren and Knecht 2001). Our higher litter depth for the SwPc stands is also consistent with Nilsson et al. (2008), who found that *P. contorta* had more than three times greater ground litter cover percentage compared with *P. sylvestris* stands. However, inconsistent with our second hypothesis, for soil N mass, we found differences only between CaPc and the Swedish forest types and we did not find differences in total mass per hectare of C or percent C or N among any of the forest types. Regional factors contributing to N mass differences between Canada and Sweden could include the warmer summer conditions in the Canadian stands, potentially causing N-fixation rates to be higher (Gundale et al. 2011, 2012). Berg (2000) examined litter from *P. sylvestris* and *P. contorta* across a large geographical region (i.e., across Scandinavia) and found that the species formed distinct groups with respect to their litter chemical composition; *P. sylvestris* needle litter was characterized by relatively low concentrations of both lignin and N, while *P. contorta* also showed relatively low N but higher lignin concentrations. Despite these differences, Ågren and Knecht (2001), using modeled relationships examining future storage potential of C, N, and other soil nutrients for Swedish *P. contorta* and *P. sylvestris,* found it unlikely that the small interspecific differences in litter concentrations of elements would lead to any major changes in soil stores of N. Likewise, in a study of pine forests (eight species, primarily focused on *P. sylvestris* and excluding *P. contorta*) from 31°N to 71°N, Berg et al. (1993) showed that climate (annual actual evapotranspiration) was the dominant rate-regulating factor for litter mass loss, while none of the species substrate quality factors were significant, which is consistent with our findings of regional similarities in N mass properties for SwPc and SwPs. One reason for the similarity among all forest types for C mass and percent C and N could be that these stands are all relatively young, so perhaps differences in soil C pools have not yet had time to emerge. Forest floor C in these boreal stands could be largely residual C from prior to stand establishment. Therefore, the litter of these relatively young stands may be only a minor contribution to the total forest floor C pool at this successional stage. However, the thicker litter and F and H horizons of the SwPc stands that we measured could indicate that the forest floor C properties are starting to diverge, as evidenced by the lower (albeit nonsignificant) C mass of SwPs compared with SwPc.

With our third hypothesis, we predicted that differences in both forest floor chemical composition and total quantity of litter inputs among the two *Pinus* species would cause greater differences in the microbial biomass and community structure compared with regional factors; however, our findings were inconsistent with this prediction. With respect to the active total microbial biomass, the lack of difference in SIR or of PLFA biomass among all three forest types suggests that the total pool of microbes regulating the supply of plant-available nutrients from the soil does not differ among forest types. Carbon is generally the primary control of soil microbial biomass, so the lack of difference in percent or mass of C among the forest types likely explains the lack of difference in microbial biomass among the forest types. In contrast, our data showed significant differences in microbial community structure among the three forest types, with different microbial community composition occurring in CaPc relative to both Swedish forest types. Given the reported differences in C quality between the two pine species (Berg and Lundmark 1987; Berg 2000), we expected soil microbial communities to differ beneath the two pine species. However, from the pattern of individual stands in the NMS ordination and the highly correlated vectors overlaid on the ordination, it is clear that non-species factors had a much greater influence on soil microbial community composition than did any differences between the two tree species. As shown in the ordination plot, the differentiation between CaPc and the Swedish forest types appears to be most strongly associated with pH, which may be associated with other regionally driven factors that we did not measure in this study, such as precipitation, age of soil development, or underlying parent materials. Additionally, regional differences in understory plant species composition may also contribute to the regional differences in soil pH or in the quality of C inputs, especially given that understory litterfall can make a large contribution (up to 50% of total) to total litterfall in *Pinus* forests (e.g., Stendahl et al. 2010).

Pinus contorta is an ideal species to investigate the relative control of species traits versus regional factors on ecosystem properties and processes following introduction because of its controlled and documented introduction in Sweden during the last half century and its growth in monocultures in both its native and introduced ranges. Based on a survey of existing literature, Ehrenfeld (2003) found that when a new species is introduced, its impacts on nutrient cycling depends on how different it is from the constellation of traits present within the existing plant community. While a number of studies have found that soil properties change in response to the introduction of new traits and new functional groups, few studies have explicitly compared the effect of these traits in both the native and introduced ranges of species (Hierro et al. 2005). Similarities in Swedish forest floor properties and processes among stands of the functionally and phylogenetically similar *Pinus* species evaluated in this study, contrasting with numerous significant differences in the properties of *P. contorta* stands between Canada and Sweden, signal that forest floor properties appear to be more driven by regional ecosystem factors than by species-specific properties for these species and regions. Our findings of limited differences between native and introduced Swedish *Pinus* species indicate that changes in forest floor properties may be minor relative to the major changes associated with *P. contorta* introduction and invasion documented in other parts of the world where *P. contorta* has vastly different litter properties than the native vegetation (Simberloff et al. 2010).

Understanding the ecosystem-level consequences of introduced and invasive organisms has great societal importance. Our study provides a rare evaluation of the effect of non-native species on ecosystem-level properties by comparing a species' effects on ecosystem properties and processes in both its native and introduced ranges and by making comparisons with the comparable native species in the region of introduction. Our results suggest that the impact of species introductions on ecosystem processes will be functions of regional influences and ecological differences between the introduced and comparable native species. An introduced species that is functionally similar to a native species may have minor ecosystem-level effects, but we currently lack an understanding of how functionally different an introduced species must be to cause ecosystem-level change. These concepts could be explored in the future by studying the impacts following introduction of a species into a range of ecosystem types and regions. Further, the regional influence by species interaction could be explored through studies involving reciprocal introductions of comparable species between regions.

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