Running head: Tree influence on litter decomposition

Home field advantage of litter decomposition in pure and mixed plantations under boreal climate

Mathilde Chomel[1,3] *, Marie Guittonny-Larchevêque[2], Annie DesRochers[3], Virginie Baldy[1]

[1]Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE) - Aix Marseille Université, UMR CNRS 7263, IRD, Avignon Université, 13331 Marseille Cedex 03, France (Present address of the corresponding author).

[2]Institut de recherche en mines et en environnement, Université du Québec en Abitibi-Temiscamingue, 341 rue principale Nord, Amos, Québec J9T 2L8, Canada.

[3]Université du Québec en Abitibi-Temiscamingue - Institut de Recherche sur les forêts, 341 rue principale Nord, Amos, Québec J9T 2L8, Canada.

* Corresponding author: mathilde.chomel@imbe.fr, phone number: +33413551233

Statement of authorship

AD and MGL were leaders of the global project. All authors participated to the design of the study. MC performed the present study and analyzed the data. All the authors contributed to the writing of the present manuscript.

Abstract

Tree species can affect the decomposition process by promoting decomposer communities adapted both to litter quality and to soil microclimatic conditions. Thus, plant litter could decompose faster when placed in the habitat from which it was derived than in a foreign habitat, which has been termed home field advantage (HFA) of litter decomposition. In mixed-plant species environments however, it is not known whether a specific decomposer community under one tree species is affected by the presence of another tree species in the vicinity. To address this question, we tested if spruce and poplar litters showed HFA in mono-specific and in mixed species plantations under each tree species by reciprocally transplanting litter in the two plantation types. Decomposition rates, as well as the composition and ability of decomposer communities to degrade the different types of litter, were monitored during two years. Only spruce litter exhibited a faster decomposition rate at home. This HFA could be explained by higher abundance of decomposers. Furthermore, cellulose was less decomposed in this environment, suggesting that soil communities of mono-specific spruce plantations were more able to decompose relatively recalcitrant litter, but they were less able to decomposing more "simple" substrates. In mixed plantations, there was no more HFA, but this "mixed environment" had synergistic effects on decomposition rates under poplar trees. These 'tree environment-specific' results highlighted the possible importance of spatial distribution of each litter on decomposition rates in mixed stands. Thus the influence of litter dispersal should be taken into account in future studies.

Keywords: litter decomposition, white spruce, hybrid poplar, cellulose, home field advantage, mites, collembola, microorganisms, reciprocal transplant, mixed plantation

Introduction

Litter decomposition is a key functional process in ecosystems, determined by the interaction between resource quality and decomposers, both controlled by the environment (climatic and soil conditions) (Hobbie et al., 2006). However, mechanisms underlying relationships between the composition of decomposer communities, that carry out specific decomposition functions, and plant species that provide specific quality of resources and microenvironmental conditions, remain poorly understood. Evidence is growing that litter tends to decompose more rapidly in the habitat from which it was derived (*i.e.*, home, under the plant species producing the litter) than in other habitats (*i.e.*, away, under another plant species), which has been termed the "home field advantage" (HFA) of litter decomposition (Hunt et al., 1988; Gholz et al., 2000; Ayres et al., 2006; Vivanco and Austin, 2008; Ayres et al., 2009a; Ayres et al., 2009b; Strickland et al., 2009; Veen et al., 2014). Therefore, the composition of soil decomposer communities should differ between areas that are dominated by different plant species due to adaptations, both to local microenvironments of the forest floor (habitat effect) and to the chemical composition of the litter (resource effect) (Wardle and van der Putten, 2002; Ayres et al., 2009b; Wang et al., 2013). Low-quality litters that contain highly recalcitrant (as lignin or tannins) or toxic compounds (as secondary metabolites, terpenoids, phenolics), might generate a larger HFA since fewer soil communities would include biota that are able to degrade these compounds, in contrast to higher quality litters (Ayres et al., 2009a; Strickland et al., 2009). However, a faster decomposition of litter in its "home" could also be due to an overall greater functional ability of organisms to decompose litter substrate rapidly, regardless of environment and substrates (Keiser et al., 2014).

Past studies measuring HFA did not estimate ability of decomposers and so did not disentangle HFA from other factors. Indeed, it is important to separate a real HFA, i.e. the adaptation of organisms to decompose litter at "home", and the ability of organisms to

68 decompose all types of litter. To study the habitat effect (environmental conditions) created
69 by a plant community on litter decomposition, the relative importance of these two
70 mechanisms should be addressed. The ability of organisms to decompose a certain litter type
71 in one tree community has been largely explored, but the results are contradictory depending
72 on trees species and quality of the litter (Ball et al., 2008; Vivanco and Austin, 2008).The
73 majority of studies have focused on HFA effect for single-species leaf litter in monospecific
74 forests or in neutral environments (*i.e.* common gardens). However, in mixed tree species
75 environments, it is not clear whether a specific decomposer community found under one tree
76 species in monospecific stand is similar or modified by the presence of another tree species in
77 the vicinity. Thus we do not know the relative effect of having more than one species in a
78 stand on HFA and plant-decomposers interactions. Moreover, the few studies that have
79 addressed the effect of mixing plant species on decomposition have used litterbags placed
80 equidistantly from one tree species to another (Chapman and Koch, 2007; Vivanco and
81 Austin, 2008; Wang et al., 2009; Berger and Berger, 2014), neglecting to consider the
82 possibly differing spatial influence of each tree species in the mixture. Thus, we do not know
83 how particular tree species (e.g. broadleaved *vs* conifers) may affect adaptation or sorting of
84 decomposer communities through differences in litter quality and/or microclimatic conditions.
85 Differences in litter quality among tree species can indeed lead to a spatial patterning of soil
86 organisms and processes (Saetre and Baath, 2000; Ettema and Wardle, 2002; De Deyn and
87 van der Putten, 2005). In order to advance our understanding in mechanisms underlying the
88 home field advantage (HFA), we used monospecific and mixed species plantations of poplar
89 and spruce and combine litter decomposition measurements with measures of microbial and
90 mesofauna community composition (including detritivorous and predators) and microbial
91 functioning. Furthermore, we applied the HFA approach in mixed forest stands by accounting
92 for the influence of each species in the mixture. We also calculated for the first time a net

93 effect of mixing tree species on decomposition (i.e., net effect of the plant community), rather
94 than net effect of mixing litters (Wardle et al., 1997; Gartner and Cardon, 2004;
95 Hättenschwiler et al., 2005), allowing us to measure if decomposition is different from that
96 expected from the additive decomposition of the species present in the mixture. If decomposer
97 communities from each monospecific tree environment were maintained under each tree
98 species in mixed stands (*i.e.* similar HFA in monospecific and mixed plantations), we should
99 observe non-additive effects of litter decomposition in mixed stands, positive under the
100 corresponding tree species, and negative under the other tree species. Conversely, if
101 decomposer communities are homogenized in mixed stands (i.e. no HFA) and decompose
102 each tree litter at a similar rate than the mean decomposition rate found in monospecific
103 stands, we should observe an additive effect of mixing tree species. This study deals with
104 reciprocal litter transplantation between monospecific and mixed-species plantations of poplar
105 and spruce established ten years ago in three replicate-sites side by side, thereby minimizing
106 differences in climatic and soil parameters (Prescott and Grayston, 2013). The main objective
107 of this study was to compare the effects that poplar and spruce trees exert on soil communities
108 (microorganisms and mesofauna) and on the litter decomposition process in monospecific and
109 mixed plantations. In addition to the HFA measurement for poplar and spruce litter, we
110 measured the overall decomposition 'ability' of soil communities with a "standard litter" (i.e.
111 cellulose) which was placed under and between trees in each plantation type. This substrate
112 was used to measure the decomposition potential of the substrates by soil communities and
113 avoid any home-field advantage (*sensu* Hunt et al., 1988)

114 The following hypotheses were addressed:
115 H1) There is a HFA for litter decomposition in spruce and poplar mono-specific plantations
116 due to the specialization of soil communities that decompose their "home" litter;

H2) HFA is more pronounced for the low-quality spruce litter compared to higher-quality poplar litter (Ayres et al., 2009b);

H3) HFA is maintained in mixed plantations for litter placed under its corresponding tree species. In this case, we should observe non-additive effect of mixing tree species, positive for the litter under its corresponding trees, and negative under the other tree species in mixed stands.

H4) Spruce and poplar litters, and a standard substrate (cellulose) decompose more rapidly in the mixed plantations since their decomposer communities are potentially more diverse

Methods

Site description

The study was located in the boreal region of Abitibi-Témiscamingue, Québec, Canada. Three sites were selected for the study: Amos (48°36'N, 78°04'W), Rivière Héva (48°11'N, 78°16'W), and Nédelec (47°45'N, 79°22'W). The Amos site was abandoned farmland with a heavy clay soil that was dominated by grasses and sparse patches of alder (*Alnus incana* [L.] Moench ssp. *rugosa* [Du Roi] R.T. Clausen), willow (*Salix* spp.), and trembling aspen (*Populus tremuloides* Michaux). Rivière Héva was an abandoned farmland site with heavy clay soil, which was also dominated by shrubs, including patches of alder, willow, and trembling aspen. Nédelec had been previously dominated by trembling aspen forest, which was commercially harvested in 2000. This last site was characterized by soils with a sandy loam texture. Based on the 30-year running climate average (1970-2000), Amos and Rivière Héva receive an annual mean 918 mm of precipitation (Amos station) and have a mean temperature of 1.2 °C, while Nédelec has mean precipitation of 916 mm $year^{-1}$ and a mean temperature of 1.9 °C (Remigny station, Environment Canada 2014). Site preparation was conducted in 2002, where tree stumps were removed and soils were ploughed to a depth of

about 30 cm. The plantations were established in 2003, using one hybrid poplar clone (*Populus maximowiczii* A.Henry x P. *balsamifera* L., clone MB915319), and an improved white spruce family (*Picea glauca* [Moench] Voss). These two species were planted in both mono-specific and mixed species plots under two spacings, i.e., 1 × 1 m and 3 × 3 m. For the mixed plantation, each row consisted of spruce alternating with poplar. Each experimental unit contained 36 trees (6 × 6 trees). The experiment was designed as a randomized block design with three blocks (replicates = sites), three plantation types (pure poplar, pure spruce and mixed), and two spacings (1 × 1 m and 3 × 3 m). Through this paper, we have divided mixed plantations into mixed-spruce (under spruce trees) and mixed-poplar (under poplar trees) plantations.

Litter decomposition experiment

In late September 2010, spruce needles and poplar leaves were collected from plantations surrounding the study sites. Abscission of needles or leaves in which senescence was complete was aided by shaking the trees, and the fallen needles/leaves were collected on a plastic sheet that was placed on the ground beneath the trees to prevent contamination with soil. Collected leaf material was homogenized and stored at room temperature prior to the experiment. A subsample of each species was oven-dried at 60 °C to establish the relationships between air-dried and oven-dried mass. Seven grams (air-dried) of either poplar or spruce litter were placed in 1-mm mesh litter bags (15 x 15 cm for poplar litter; 10 × 15 cm for spruce litter) to allow colonization by soil mesofauna and microbes, while excluding macrofauna (Swift et al., 1979). We used pairs of litterbags with one bag being used for chemical and microbial measurements and the other for mesofauna extraction. To prevent losses of spruce needles through the net mesh during handling and travel, a sheet of paper was inserted into each litterbag with spruce needles. These paper sheets were removed just before closing the litterbags and placing them on the soil surface. Dimensions of the litterbags

containing spruce needles were smaller than those for poplar leaves, to create similar litter incubation conditions among litter types and to prevent needle losses.

To optimize the influence of trees on the decomposition process, this experiment was performed in the 1 x 1 m spacing plantations. In November 2010, 12 pairs of litterbags filled with poplar litter and 12 pairs of litterbags filled with spruce litter were randomly deposited around 12 trees in each mono-specific plantation (pure poplar and pure spruce). In mixed plantations, 24 pairs of litterbags of each litter were placed, half under poplar trees and half under spruce trees (Figure 1). The litter bags were placed equidistantly one from each other around trees approximately 15 – 25 cm away from the stem but under the overlapping of tree crowns on the ground where soil accumulation of litter was maximum. This was repeated at the 3 sites (replicates), resulting in a total of 576 litterbags (12 pairs x 2 litter bags x 2 litter species x 4 plantations types x 3 sites). Litterbags were placed on the experimental sites on 9–10 November 2010. Freshly fallen litter was removed from the surface of the forest floor prior to placing the litterbags on the ground surface, and then replaced over the litterbags. Litterbags were fixed with one galvanized nail to prevent movement by animals or wind. After 7, 11, 18 and 24 months, 3 pairs (pseudo-replicates) of litterbags were retrieved from around three randomly chosen trees at each site. Sampling dates corresponded to snowmelt and anticipated snowpack development, generally mid-May and early or mid-October, respectively.

Litter bag processing

The first litterbag of each pair was used for mesofauna extraction, after which it was oven-dried at 60°C for 3 days. An aliquot of fresh material from the second litterbag was used for microbial analysis and the remainder of the sample were freeze-dried (Lyovac GT2®) for chemical analysis. To prevent soil contamination of litter, we wiped needles/leaves

thoroughly before analysis. At t_0, 26 samples of each litter type (7 g air-dried) were used to determine initial litter quality.

Mesofaunal extraction

Mesofauna were extracted from fresh litter using the dry funnel method (Berlese, 1905). Animals were stored in 90 % alcohol, counted using a binocular scope, and identified to family for Collembola (Gisin, 1960) and to order for Acari (Gamasida, Acaridida, Actinedida, Oribatida; (Coineau, 1974). Other invertebrates were separated according to taxa (e.g., Arachnida, Diplopoda, Chilopoda, Araneae, Hymenoptera, etc.).

Fungal biomass

Fungal biomass was determined by quantifying ergosterol, a fungal membrane constituent and good indicator of living fungal biomass (Gessner and Chauvet, 1993; Ruzicka et al., 2000). Samples were frozen and lyophilized to enable more efficient extraction of ergosterol (Gessner and Schmitt, 1996). Ergosterol was extracted from 50 mg of needles/leaves with 5 mL of an alcohol base (KOH/methanol 8 g L^{-1}) for 30 min, and purified by solid-phase extraction on a Waters® (Milford, MA, USA) Oasis HLB cartridge (Gessner and Schmitt, 1996). The extract that was produced was purified and quantified by high-performance liquid chromatography (HPLC) on a Hewlett Packard series 1050 system running with HPLC-grade methanol at a flow rate of 1.5 mL min^{-1}. Detection was performed at 282 nm, and the ergosterol peak was identified based on the retention time of an ergosterol standard.

Catabolic profiles of microorganisms

Microbial (fungal and bacterial) catabolic profiles were assessed using Biolog® EcoPlates (Biolog Inc., Hayward, CA, USA) for all sampling dates using a procedure adapted from Garland and Mills (1991). To have enough fresh material, the three pseudo-replicates in each plantation were pooled, with the three sites remaining as replicates. Briefly, 2 g (dry mass

214 equiv.) of ground litter were stirred in 100 mL of a sterile 0.1% tetra-sodium pyrophosphate
215 solution for 1 h to suspend microbial communities. Each 96-well plate contained 3 replicate
216 blocks of a water blank and 31 of the most useful carbon sources for soil community analysis
217 (for details, see Annexe 1), nine of which are considered as constituents of plant root exudates
218 (Preston-Mafham et al., 2002). A 125 µL aliquot of extract solution, diluted 1:110, was added
219 to all 96 wells in each EcoPlate. The plates were incubated at 30 °C for 7 days, and
220 absorbance was measured at 595 nm on a microplate spectrophotometer (Multiskan GO,
221 Thermo Fisher Scientific). Different microbial communities can exhibit different patterns of
222 substrate use, as revealed by the ensuing colorimetric reactions.

223 *Soil temperature and moisture content*

224 At each litterbag sampling date, soil temperature and volumetric water content (VWC) under
225 6 randomly chosen trees per plantation type and at each site were measured respectively with
226 an Acorn series meter with K probe (Oakton Instruments, Vernon Hills, IL, USA), and a Field
227 Scout TDR 100 with 12 cm-long probe (Spectrum Technologies Inc., Plainfield, IL, USA).

228 *Standard substrate decomposition*

229 Cellulose decay rates were measured at each plot using Whatman no. 5 filter papers as
230 standard substrates. Two filters (corresponding to 2.44 g dry mass) were enclosed in the same
231 size of litterbags that were used for poplar litter (15 x 15 cm, 1mm mesh). To study the area of
232 tree influence on the decomposition process, these litterbags were placed in 3 x 3m
233 plantations. In October 2011, 4 litterbags were randomly placed beneath 4 trees, and 4 more
234 litterbags were placed between the trees in the mono-specific plantations (poplar and spruce
235 plantations). For mixed plantations, 8 litterbags were placed, half under poplar trees and half
236 under spruce trees, and 4 more litterbags were placed between the trees, equidistantly from
237 spruce and poplar (Figure 1). Since there were 3 replicate sites, this resulted in a total of 84
238 litterbags (3 sites x 28 litterbags = 84). Freshly fallen litter was removed from the forest floor

surface prior to placing the litterbag on the ground. Litterbags were fixed with one galvanized nail to prevent movement by animals or wind. As decomposition rate of cellulose is relatively rapid, all litterbags were removed after one year. Remaining dry mass was determined after oven-drying the litter at 60 °C for 3 days. Mass loss was expressed as the percentage of total initial dry mass.

Data analyses

Mass loss was expressed as the percentage of total initial dry mass for the full set of litterbags (leaves/needles and cellulose). Litter decomposition rates were determined from poplar and spruce litterbags, by fitting needle/leaf mass loss data to a simple negative exponential model $m_t = m_0.e^{-kt}$, where m_t is needle mass remaining (g) at time t (years), m_0 is initial needle mass (g), and k (year^{-1}) is the exponential decomposition rate coefficient (Olson, 1963). To compare litter decomposition rates between plantation and litter types, we log-transformed remaining mass data, and compared slopes of the fitted lines by using the comparison of regression lines analysis (Statgraphics plus 5.1). In order to separate overall ability of organisms to decompose different litter types and a real HFA, we performed the regression approach proposed by Keiser et al. (2014). This statistical approach is based on a least squares regression that explicitly estimates the influence of relative litter quality and soil communities' ability on decomposition, as well as the HFA of each home combination (Keiser et al., 2014). The following model was used:

$$Y_i = \alpha + \sum_{l=1}^{N} \beta_l \; Litter_{li} + \sum_{s=1}^{M} \gamma_{ls} \; Litter_{si} \; + \sum_{h=1}^{k} \eta_h \; Litter_{hi} + \varepsilon_i$$

where Y_i is the decomposition for observation i, β_l is the ability of litter species l (from species *1* to *N*), γ_s is the ability of the soil community s (from community *1* to *M*), and η_h is

261 the HFA of *h* (from home combinations *1* to *K*) (see Keiser et al, 2014 for more details). This
262 statistical analysis was done with SAS 9.3 software.

263 To determine whether interactions occurred in mixed compared to pure plantations, predicted
264 mass loss in mixed plantation was calculated based on observed mass losses of the component
265 species in monoculture, which assumes that there are no diversity effects, i.e., the
266 decomposition in mixed species plantations are the additive sums of mass loss in the two
267 mono-specific plantations. According to Wardle et al. (1997), a relative mixture effect can be
268 calculated as the ratio: [(observed - predicted) / predicted]*100. If this ratio differs from zero,
269 it would indicate non-additive effects of mixing tree species on decomposition rate. To test if
270 the observed *vs* predicted ratios of litter decomposition in mixed plantations differed
271 significantly from zero, we used one-sample Student's *t*-tests, and associated 95 % confidence
272 intervals.

273 All other statistical analyses were performed using R version 3.1.0 (R Development Core
274 Team 2008). To determine bacterial catabolic diversity and mesofauna community diversity,
275 Shannon indices were calculated. Mean values (soil temperature and humidity, ergosterol,
276 mesofauna abundance, mesofauna diversity and catabolic diversity) were compared among
277 decomposition times and plantation types for each litter type using hierarchical linear mixed-
278 effects models using the *lme* function in the *nlme* package (Pinheiro et al., 2014). Site
279 replicates were treated as random effects, and plantation type was nested within site replicates
280 to reflect the structure of our data set. If the effect of treatment was significant, the different
281 treatments were compared with pre-planned linear contrasts (differences are noted in the
282 manuscript as a < b < c). To compare catabolic profiles of microbial communities among
283 samples, non-metric multidimensional scaling (NMDS) was performed to find the best low-
284 dimensional representation of the distance matrix (function *metaMDS* of R *Vegan* package,
285 (Oksanen et al., 2012). For catabolic profiles of microorganisms, the data were first

normalized. A data matrix of pairwise comparisons among samples was then calculated using Euclidean distance. To evaluate how well (or poorly) the particular configuration produced the observed distance matrix, a stress value was given. The best solution to the dimensional reduction of the data set minimized the stress value associated with the NMDS solution, the smaller the stress value, the better the fit of the reproduced distance matrix to the observed distance matrix. Permutation-based Multivariate Analysis of Variance (PERMANOVA) was used to test differences in patterns of the catabolic profiles and those of the mesofaunal community composition among plantations and between litter types, based on 999 permutations of the data (function *adonis* of R package *vegan*). For mesofaunal abundances, the data were subjected to Wisconsin double standardization, with pairwise dissimilarities calculated among samples using Bray-Curtis indices (Bray and Curtis, 1957). When plantation types were significantly different, SIMPER (similarity percentage) was used to identify the species/compounds that were responsible for dissimilarities between plantations. For all statistical analyses, the significance threshold was set at $\alpha = 0.05$.

Results

Soil temperature and humidity

Across all sampling dates, soil temperature was greater in poplar mono-specific plantations and lower in spruce mono-specific plantations with differences of 1.5, 0.6, 1.9, 0.5 °C at each respective sampling date (Table 1, linear contrasts, $P < 0.05$). Soil temperature had intermediate values in mixed plantations, regardless of tree species. Soil volumetric water content was not significantly different between plantation types (*lme*, $F_{3,6} = 1.38$, $P = 0.34$).

Decomposition rate, home field advantage and ability

On average, 53 % of poplar and 40 % spruce litter was lost after 2 years. Decomposition rates of spruce litter were significantly greater in mono-specific spruce plantations (0.29 $year^{-1}$)

310 compared to rates found in mono-specific poplar (0.21 $year^{-1}$), mixed-spruce (0.22 $year^{-1}$), or
311 mixed-poplar plantations (0.23 $year^{-1}$; comparison of slopes, $F_3 = 12$. $P < 0.001$). Poplar litter
312 decomposition rates were similar ($P > 0.05$) among the four plantation types (Fig.3), with
313 0.35 $year^{-1}$ in spruce, 0.33 $year^{-1}$ in poplar, 0.34 $year^{-1}$ in mixed-spruce and 0.36 $year^{-1}$ in
314 mixed-poplar plantations, respectively.

315 The HFA model indicated that the litter quality index of poplar litter was the highest and
316 spruce litter the lowest, indicating that poplar litter decomposed the fastest and spruce litter
317 the slowest, across all soil communities, while cellulose had an intermediate value (Fig 2).
318 Concerning the ability of soil organisms to decompose all litter types, the HFA model also
319 showed that spruce soil communities (in monospecific or mixed plantations) had less ability
320 to decompose all litter types than soil communities under poplar in monospecific or mixed
321 stands. Parameter estimates and statistical significance of HFA by the model indicated that
322 spruce monospecific soil communities showed greater HFA ($P < 0.0001$) followed by spruce
323 soil communities in mixed plantations ($P = 0.0007$) (Fig 2). Conversely, poplar soil
324 communities (in monospecific or mixed stands) showed negative HFA ($P < 0.0001$; $P =$
325 0.0013 respectively).

326 *Ergosterol*

327 Regardless of plantation type, ergosterol concentrations were greater in poplar litter than in
328 spruce litter at 11 (330 vs 269 µg g^{-1}, respectively; *lme*, $F_{1,57} = 13.2$ $P < 0.001$) and 18 months
329 (417 *vs* 348 µg g^{-1}, respectively; *lme*, $F_{1,56} = 11.2$ $P < 0.01$) of decomposition (Fig. 3). Before
330 18 months of decomposition had elapsed for spruce litter and 11 months for poplar litter,
331 ergosterol concentrations were the same under each plantation type. For spruce litter, fungal
332 biomass was greater at home than in poplar plantations after 18 and 24 months of
333 decomposition (Fig. 3, linear contrasts, $P < 0.05$). For poplar litter after 24 months of
334 decomposition, fungal biomass was greater away than at home (Fig. 3, linear contrasts, $P <$

0.05). Fungal biomass in mixed-spruce and mixed-poplar plantations reached similar values during the experiment, except at 18 months of decomposition for spruce litter and at 11 months of decomposition for poplar litter, where values were higher under poplar than under spruce in mixed plantations. After 24 months of decomposition, ergosterol concentrations in mixed plantation were intermediate between poplar and spruce mono-specific plantation values (Fig. 3, linear contrasts, $P < 0.05$). Ergosterol dynamics in the different plantation types suggested that fungal biomass was still increasing in mono-specific spruce plantations for the two litter types after 24 months of decomposition, whereas fungal biomass reached a plateau from 11 months of decomposition onward in mono-specific poplar plantations. In mixed plantations, a decrease of fungal biomass was observed between 18 and 24 months of decomposition (except for spruce litter under spruce trees) (Fig.3, linear contrasts, $P < 0.05$).

Biologs

Ordination (NMDS) of the different catabolic profiles that was based on Euclidean distance is presented in Fig. 4. At 7, 11 and 18 months, NMDS globally showed that catabolic profiles of poplar litter communities were more similar than communities associated with spruce litter. NMDS also revealed temporal differences among plantation types, as confirmed by PERMANOVA, which was performed on the spruce and poplar litter datasets separately. Catabolic profiles of microbial communities that were present in spruce litter significantly varied among plantation types at 7 and 11 months of decomposition (Permanova on spruce litter data among plantation type at 7 and 11 months, $F_3 = 2.2$, $P = 0.037$, and $F_3 = 1.33$, $P = 0.015$, respectively), but catabolic profiles for poplar litter remained different among plantation types throughout the experiment (Permanova on poplar litter data among plantation type, $F_3 = 1.68$, $P = 0.014$). Catabolic diversity of microbial communities, as measured by the Shannon index, was similar in all plantation types (Table 2, *lme*, $F = 2.01$, $P = 0.21$). However, microorganisms colonizing spruce litter had lower catabolic diversity (mean of 17

360 compounds used) compared to those colonizing poplar litter (mean of 28 compounds used),
361 after 7, 11 and 18 months of decomposition (linear contrast, $P < 0.001$). Microbial catabolic
362 diversity was constant among dates for poplar litter, whereas catabolic diversity increased
363 with time during spruce litter decay (Table 2, *lme*, $F = 12$, $P = 0.0015$).

364 *Mesofauna*

365 During two years of litter decomposition, the composition of mesofauna communities differed
366 among plantation types for spruce and poplar litters (Permanova on spruce and poplar litter
367 data among plantation type, $F_3 = 0.03$, $P = 0.02$; and $F_3 = 1.76$, $P = 0.001$, respectively).
368 These differences were mainly due to a greater abundance of oribatids in spruce plantations,
369 Coleoptera larvae in poplar plantations, and Symphypleona and Araneae in mixed plantations.
370 As mesofaunal diversity was not different among plantation types, the results are not shown.
371 Abundance of main groups (detritivorous mites, springtails and predators) of mesofauna are
372 summarized in Fig. 4. Statistical analysis (*Lme)* showed no significant interactions between
373 the three factors, i.e., time, litter and plantation types for mites and predators. Of the two litter
374 types, mites were significantly more abundant in spruce than in poplar and mixed-spruce
375 plantations throughout the experiment, with mixed-poplar plantations having intermediate
376 abundances relative to the 3 other plantation types (lme, $F = 20.1$, $P = 0.002$). Springtails
377 abundance were significantly different between plantation types only at 24 months of
378 decomposition, with greater abundance under spruce in each plantation type compared to
379 poplar mono-specific plantation (lme, $F_{3,6} = 6.02$, $P = 0.03$). Predator abundance was similar
380 among plantation types (lme, $F_{3,6} = 0.68$, $P = 0.6$, respectively). For these three groups,
381 abundance varied with decomposition time, reaching maxima of 34, 17, and 3 individuals per
382 g of litter after 24 months of decomposition for detritivorous mites, springtails and predators,
383 respectively (linear contrasts, $P < 0.05$).

384 *Decomposition rate of cellulose and litterbag positioning*

385 When the litterbags were placed under the trees, the lowest cellulose decomposition rate was
386 measured under spruce in mono-specific plantations (mean of 20 % of mass loss), while the
387 highest decay rate was found under poplar trees, regardless of plantation type (mean 55 %
388 mass loss, lme, $P < 0.01$, Table 3). However, when litterbags were placed between the trees,
389 plantation type influenced cellulose decomposition rates; decomposition rates decreased from
390 pure poplar to mixed plantations (linear mixed model, $P < 0.05$), reaching minimum values
391 similar to those found under spruce in mixed plantations. In pure plantations, cellulose was
392 more rapidly decomposed between than beneath trees (lme, $F_{1,42} = 5.17$, $P = 0.028$).

393 *Net effect of mixed plantations*

394 Net effects (NE) of habitat on litter decomposition represent the difference between litter
395 decomposition rates that were expected (mean of the decomposition rates measured in the two
396 mono-specific plantations) and the litter decomposition rate that was measured in mixed
397 plantations, under each tree species. We observed significant synergistic NE for poplar litter
398 and cellulose decomposition under poplar trees in mixed plantations (12 %, $t = 2.15$, $df = 17$,
399 $P = 0.046$, and 53 %, and $t = 2.21$, $df = 11$, $P = 0.049$, respectively). However, antagonistic
400 NAE was significant for spruce litter decomposition under poplar in mixed plantations (-16%,
401 $t = -2.78$, $df = 16$, $P = 0.013$). Mean NE for cellulose decomposition between trees
402 represented a decrease of 36 % in mixed plantations compared to predicted values ($t = -2.66$,
403 $df = 11$, $P = 0.022$) (Figure 4).

404 **Discussion**

405 The feedbacks between above- and below-ground biota are major ecological drivers in
406 terrestrial ecosystems (Wardle and van der Putten, 2002) but are still not completely
407 understood. Our study is among the first to observe the home field advantage (HFA) of two

408 tree species in mono-specific and pluri-specific “environments”, while separating the
409 influence of each tree species in mixed plantations. By performing litter transplants, we were
410 able to tease apart the mechanisms that contribute to HFA among three distinct levels of the
411 soil food web (microorganisms,  itivorous microarthropods and predators), as well as to
412 discriminate the influence of HFA and ability of decomposer communities on the litter
413 decomposition process.

414 **1. Home field advantage and decomposer ability depending on litter type**

415 In monospecific plantations, home field advantage was only found for spruce litter with an
416 increase of 10 % in mass loss of spruce litter at home versus away, in support of our
417 hypothesis that HFA should be greater for recalcitrant litter types than for more labile litters
418 (Ayres et al., 2009b; Strickland et al., 2009). Coniferous species are recognized as having
419 lower quality litter compared to broadleaf species (Perez-Harguindeguy et al., 2000; Cornwell
420 et al., 2008) and our estimate of litter quality index confirmed this statement with a lower
421 quality index for spruce than for poplar litter. The compounds found in labile litters can
422 probably be degraded by many decomposer organisms, whereas the complex compounds
423 found in recalcitrant litters likely require specialized enzymes in order to be decomposed
424 (Wallenstein et al., 2013). Accordingly, cellulose (least recalcitrant litter) decomposition was
425 35 % lower in spruce compared to poplar plantations. Furthermore, the spruce soil community
426 showed the lowest, and poplar soil community the highest ability to decompose all litter
427 types. These results confirmed that HFA found for spruce litter in its environment was really
428 due to an adaptation of soil organisms, rather than an overall ability of spruce soil
429 communities to decompose litter (Keiser et al., 2014).

2. Decomposer communities: drivers of the HFA

Globally, microorganisms colonizing spruce litter had lower catabolic diversity compared to those colonizing poplar litter. This result indicates that microbial communities colonizing poplar litter were able to decompose a greater number of compounds, and would be more opportunistic than microbes that were colonizing spruce litter, which were more specialized. In a recent study, HFA effects for recalcitrant litter was mainly explained by specialization of organisms in this "recalcitrant litter environment" to degrade lignin dimers (Wallenstein et al., 2013). The greater fungal biomass that was found in spruce plantations could then partially explain HFA for spruce litter in its environment since fungi are better adapted to decompose recalcitrant materials (lignin, cellulose, hemi-cellulose) through their enzymatic activities and given their hyphal growth form (Meidute et al., 2008; Paterson et al., 2008).

Moreover, the greater fungal biomass found in spruce monospecific plantations could also explain why mites and springtails were more abundant under mono-specific spruce cover, regardless of litter type. Indeed, among the litter mesofauna taxa, oribatid mites and springtails were typically among the most important fungal feeders (Scheu, 2002; Schneider et al., 2005). This is in accordance with Wardle's (2002) statement that conifers should favour soil communities that are dominated by fungi and fungivorous microarthropods, compared to broadleaved species. Furthermore, fungivores and microbivores (such as mites and springtails) have important indirect regulatory controls on microorganisms through their grazing activities and often stimulate hyphal growth if the grazing is at low intensity (Crowther et al., 2011). Thus, mites, springtails and fungal abundance in mono-specific spruce plantations could be reciprocally linked by a positive feedback that could promote HFA through increased lignin degradation (Wallenstein et al., 2013).

This greater abundance of decomposers in spruce monospecific plantations could be attributed to changes in temperature and moisture conditions instead of a real effect of tree species

habitat (Prescott and Grayston, 2013). In our study, moisture conditions were similar among plantation types; however, temperatures were higher in poplar compared to spruce plantations, with mean differences of 1.7 °C in May and 0.6 °C in October, respectively. Higher soil temperatures in the boreal region should promote greater abundance and activity of soil organisms. However, in poplar plantations, we observed the lowest abundance of fungi and mites. This result suggested that the differences observed in soil communities were mainly due to the effects of tree species and litter chemistry and not due to changes in environmental heterogeneity.

3. Home field advantage and decomposer ability changes in mixed plantations

Relative HFA and ability of organisms measured by the HFA regression model in mixed plantations were in the same trend but at a lower level than in monospecific plantations. Although spruce litter was not decomposed faster under spruce than poplar in mixed plantations, the relative HFA for spruce litter under spruce indicated that other litters (mainly cellulose and to a less extend poplar litter) were less decomposed under spruce than poplar in mixed stands. This result indicates that HFA is sensitive to accompanying plant communities, but the influence of tree habitat persists in mixed stands. In other words, mixing tree species with different canopy covers promotes spatial separation of specific resources, and associated spatial separation of diverse organisms (Ettema and Wardle, 2002). Concomitantly, we did not find support for our hypothesis that litter would decompose more rapidly in mixed compared to pure plantations, since decomposition rates of the three litter types was not greater in mixed plantations. Therefore, our results do not support the hypothesis that activity and diversity of decomposer communities are stimulated by mixing tree species (McTiernan et al., 1997; Hansen, 2000; Ettema and Wardle, 2002; Wardle, 2006). Under poplar trees in mixed plantations we observed non-additive effects of mixing tree species (positive effects for cellulose and poplar litter, and negative effect for spruce litter), whereas under spruce trees

480 additive effects were observed for the three litter types. These results indicate that
481 decomposition rates in mixed plantations under spruce corresponded to the mean
482 decomposition rate in the two mono-specific plantations, whereas decomposition rates under
483 poplar were different from this mean. These 'tree environment-specific' results suggests that
484 in mixed plantations poplar presence influenced the habitat under spruce while spruce
485 presence had little influence on the habitat under poplar.

486 **4. Litter dispersal as a possible driver of the observed changes between mono- and mixed**
487 **plantations**

488 Poplar has high litter dispersal ability, given that it is tall and its leaves have high specific leaf
489 area (SLA), in contrast to spruce height and SLA of needles. During the experiment, poplar
490 litter was collected in litter traps that were placed beneath spruces, whereas the opposite was
491 not observed (Chomel et al., 2014). These observations highlight that within mixed stands, a
492 tree species may have an effect on the forest floor only in a localized way through the spatial
493 distribution of its litter (Saetre et al., 1999; Saetre and Baath, 2000; Aubert et al., 2006).
494 Indeed, litter cover is not homogenous, with spruce litter being restricted to being under
495 spruce whereas poplar litter is more widely spread. In mixed plantations, both litters may be
496 present under the spruce canopy, which could explain the additive effect under spruce trees,
497 whereas the lack of spruce litter under poplar trees induced non additive effects
498 (decomposition rates similar to what was observed in poplar mono-specific plantations).
499 Under our experimental conditions, decomposer communities that were present under spruce
500 in mono-specific plantations were consequently more likely to have been in contact with
501 poplar litter than the reverse. It has been recently demonstrated that soil communities are
502 driven by historical exposure of tree species and the resource history of the soil microbial
503 community appears to influence contemporary functions (Strickland et al., 2009; Keiser et al.,
504 2013).Spruce decomposer communities could thus have "learned" to decompose poplar litter.

505 We could emit the hypothesis that the intensity of home field advantage would be partially
506 controlled by litter dispersal capacity: the greater the litter dispersal, the less intense home
507 field advantage would be. Dispersal ability of litter would thus be an important trait to
508 consider in decomposition studies of mixed species.

509 Concerning the area of influence of a tree on the decomposition process, there was a net
510 effect of cellulose litter bag positioning both under and between the trees. Cellulose was
511 decomposed rapidly in poplar mono-specific plantations, under and between the trees.
512 However, in spruce mono-specific plantations, cellulose was poorly decomposed under spruce
513 trees (20 % mass loss), but rapidly decomposed between the spruce trees (45 % mass loss),
514 showing an important negative effect of spruce canopy on decomposition rates. In mixed
515 plantations, a high decomposition rate was maintained beneath the poplar trees (53 % mass
516 loss), but between the trees cellulose was less decomposed (19 % less mass loss). These
517 results show that the tree canopy has an important effect on the decomposition process. For
518 example, Saetre and Baath (2000) found ranges of 1–3 m for changes in microbial
519 communities in a *Picea abies–Betula pubescens* forest. Therefore, the positioning of litter
520 bags appears to be rather important when studying the effects of diversity of plant
521 communities on soil processes and should be carefully considered.

522

523 **Conclusion**

524 Our study showed a home field advantage only for spruce litter in spruce mono-specific
525 plantations, whereas poplar litter was decomposed at a similar rate under all tree species and
526 plantation types. This HFA could be partially explained by greater abundance of fungi,
527 detritivorous mites and springtails, possibly due to positive reciprocal interactions between
528 fungi and fungivorous which stimulates each other. This, in turn, affects positively the spruce

litter decomposition. Furthermore, cellulose was less decomposed in spruce plantations, indicating that soil communities of spruce mono-specific plantations were more capable of decomposing relatively recalcitrant litter, while they were less efficient in decomposing more "simple" substrates. We suppose that the intensity of the home field advantage would be partially controlled by litter dispersal capacity: the greater the litter dispersal, the less intense home field advantage would be. Activity and diversity of decomposer communities and, thus, litter decomposition rates, were not stimulated in mixed compared to mono-specific plantations. However, the "mixed environment" had a synergistic effect on decomposition rates (compared to what was predicted from the two mono-specific plantations), but only under poplar trees. These 'tree environment-specific' results may indicate that within mixed stands, spruce trees affected the forest floor but only in a localized way through the limited spatial distribution of their needle litter. This knowledge contributes to our understanding of how mixing tree species influences soil processes, and why differences in litter dispersal must be taken into account in future studies.

Acknowledgments

We thank Line Blackburn for field assistance, Caroline Lecareux and Germain Bougnou for chemical analyses, and W.F.J. Parsons of the Centre for Forest Research (CEF) for English language correction and for his comments on the manuscript. This study was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC-CRSNG) through a Collaborative and Research Development grant awarded to Annie DesRochers. We also thank the CRSNG-UQAT-UQAM Industrial Chair in Sustainable Forest Management, the Quebec Intensive Silviculture Network and the CEF for additional support.

References

552 Aubert M, Margerie P, Ernoult A, Decaens T, Bureau F. 2006. Variability and heterogeneity of
553 humus forms at stand level: Comparison between pure beech and mixed beech-hornbeam
554 forest. Annals of Forest Science 63: 177-188.
555 Ayres E, Dromph KM, Bardgett RD. 2006. Do plant species encourage soil biota that specialise
556 in the rapid decomposition of their litter? Soil Biology & Biochemistry 38: 183-186.
557 Ayres E, Steltzer H, Berg S, Wall DH. 2009a. Soil biota accelerate decomposition in high-
558 elevation forests by specializing in the breakdown of litter produced by the plant species
559 above them. Journal of Ecology 97: 901-912.
560 Ayres E, Steltzer H, Simmons BL, Simpson RT, Steinweg JM, Wallenstein MD, Mellor N,
561 Parton WJ, Moore JC, Wall DH. 2009b. Home-field advantage accelerates leaf litter
562 decomposition in forests. Soil Biology & Biochemistry 41: 606-610.
563 Ball BA, Hunter MD, Kominoski JS, Swan CM, Bradford MA. 2008. Consequences of non-
564 random species loss for decomposition dynamics: experimental evidence for additive and
565 non-additive effects. Journal of Ecology 96: 303-313.
566 Berger TW, Berger P. 2014. Does mixing of beech (Fagus sylvatica) and spruce (Picea abies)
567 litter hasten decomposition? Plant and Soil 377: 217-234.
568 Berlese A. 1905. Appariccchio per raccogliere presto ed in gran numero di piccoli artropodi.
569 Redia 2: 85-89.
570 Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of Southern
571 Wisconsin. Ecological Monographs 27: 325 – 349.
572 Chapman SK, Koch GW. 2007. What type of diversity yields synergy during mixed litter
573 decomposition in a natural forest ecosystem? Plant and Soil 299: 153-162.
574 Chomel M, DesRochers A, Baldy V, Larchevêque M, Gauquelin T. 2014. Non-additive effects
575 of mixing hybrid poplar and white spruce on aboveground and soil carbon storage in boreal
576 plantations. Forest Ecology and Management 328: 292-299.
577 Coineau Y. 1974. Introduction à l'étude des microarthropodes du sol et ses annexes. 118p.
578 Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie
579 SE, Hoorens B, Kurokawa H, Perez-Harguindeguy N, Quested HM, Santiago LS, Wardle
580 DA, Wright IJ, Aerts R, Allison SD, van Bodegom P, Brovkin V, Chatain A, Callaghan
581 TV, Diaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J, Reich PB,
582 Soudzilovskaia NA, Vaieretti MV, Westoby M. 2008. Plant species traits are the
583 predominant control on litter decomposition rates within biomes worldwide. Ecology
584 Letters 11: 1065-1071.

585 Crowther TW, Boddy L, Jones TH. 2011. Species-specific effects of soil fauna on fungal
586 foraging and decomposition. Oecologia 167: 535-545.
587 De Deyn GB, van der Putten WH. 2005. Linking aboveground and belowground diversity.
588 Trends in Ecology & Evolution 20: 625-633.
589 Ettema CH, Wardle DA. 2002. Spatial soil ecology. Trends in Ecology & Evolution 17: 177-
590 183.
591 Garland JL, Mills AL. 1991. Classification and characterization of heterotrophic microbial
592 communities on the basis of patterns of community-level sole-carbon-source utilization.
593 Applied and Environmental Microbiology 57: 2351-2359.
594 Gartner TB, Cardon ZG. 2004. Decomposition dynamics in mixed-species leaf litter. Oikos
595 104: 230-246.
596 Gessner MO, Chauvet E. 1993. Ergosterol-to-biomass conversion factors for aquatic
597 hyphomycetes Applied and Environmental Microbiology 59: 502-507.
598 Gessner MO, Schmitt AL. 1996. Use of solid-phase extraction to determine ergosterol
599 concentrations in plant tissue colonized by fungi. Applied & Environmental Microbiology
600 62: 415-419.
601 Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ. 2000. Long-term dynamics
602 of pine and hardwood litter in contrasting environments: toward a global model of
603 decomposition. Global Change Biology 6: 751-765.
604 Gisin H. 1960. Collembolen fauna Europas.: *Museum d'Histoire naturelle*, Genève.
605 Hansen RA. 2000. Effects of habitat complexity and composition on a diverse litter
606 microarthropod assemblage. Ecology 81: 1120-1132.
607 Hättenschwiler S, Tiunov A, Scheu S. 2005. Biodiversity and litter decomposition in terrestrial
608 ecosystems. Annual Review of Ecology, Evolution, & Systematics 36: 191-218.
609 Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowiak R, Hale C, Karolewski P. 2006. Tree
610 species effects on decomposition and forest floor dynamics in a common garden. Ecology
611 87: 2288-2297.
612 Hunt HW, Ingham ER, Coleman DC, Elliott ET, Reid CPP. 1988. Nitrogen limitation of
613 production and decomposition in prairie, montain meadow, and pine forest. Ecology 69:
614 1009-1016.
615 Keiser AD, Keiser DA, Strickland MS, Bradford MA. 2014. Disentangling the mechanisms
616 underlying functional differences among decomposer communities. Journal of Ecology
617 102: 603-609.

618 Keiser AD, Knoepp JD, Bradford MA. 2013. Microbial communities may modify how litter
619 quality affects potential decomposition rates as tree species migrate. Plant and Soil 372:
620 167-176.
621 McTiernan KB, Ineson P, Coward PA. 1997. Respiration and nutrient release from tree leaf
622 litter mixtures. Oikos 78: 527-538.
623 Meidute S, Demoling F, Baath E. 2008. Antagonistic and synergistic effects of fungal and
624 bacterial growth in soil after adding different carbon and nitrogen sources. Soil Biology &
625 Biochemistry 40: 2334-2343.
626 Oksanen J, Blanchet GF, Kindt R, Legendre P, Minchin PR, O'Hara B. 2012. Vegan:
627 Community Ecology Package. R version 2.0-3. Available at: http://vegan.r-forge.r-
628 project.org/.
629 Olson JS. 1963. Energy storage and balance of producers and decomposers in ecological
630 systems. Ecology 44: 322-&.
631 Paterson E, Osler G, Dawson LA, Gebbing T, Sim A, Ord B. 2008. Labile and recalcitrant plant
632 fractions are utilised by distinct microbial communities in soil: Independent of the presence
633 of roots and mycorrhizal fungi. Soil Biology & Biochemistry 40: 1103-1113.
634 Perez-Harguindeguy N, Diaz S, Cornelissen JHC, Vendramini F, Cabido M, Castellanos A.
635 2000. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum
636 of functional types and taxa in central Argentina. Plant and Soil 218: 21-30.
637 Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Core team. 2014. nlme: Linear and Nonlinear
638 Mixed Effects Models. R package version 3.1-115, http://CRAN.R-
639 project.org/package=nlme.
640 Prescott CE, Grayston SJ. 2013. Tree species influence on microbial communities in litter and
641 soil: Current knowledge and research needs. Forest Ecology and Management 309: 19-27.
642 Preston-Mafham J, Boddy L, Randerson PF. 2002. Analysis of microbial community functional
643 diversity using sole-carbon-source utilisation profiles - a critique. Fems Microbiology
644 Ecology 42: 1-14.
645 Ruzicka S, Edgerton D, Norman M, Hill T. 2000. The utility of ergosterol as a bioindicator of
646 fungi in temperate soils. Soil Biology & Biochemistry 32: 989-1005.
647 Saetre P, Baath E. 2000. Spatial variation and patterns of soil microbial community structure in
648 a mixed spruce-birch stand. Soil Biology & Biochemistry 32: 909-917.
649 Saetre P, Brandtberg PO, Lundkvist H, Bengtsson J. 1999. Soil organisms and carbon, nitrogen
650 and phosphorus mineralisation in Norway spruce and mixed Norway spruce-birch stands.
651 Biology and Fertility of Soils 28: 382-388.

652 Scheu S. 2002. The soil food web: structure and perspectives. European Journal of Soil Biology
653 38: 11-20.
654 Schneider K, Renker C, Maraun M. 2005. Oribatid mite (Acari, Oribatida) feeding on
655 ectomycorrhizal fungi. Mycorrhiza 16: 67-72.
656 Strickland MS, Osburn E, Lauber C, Fierer N, Bradford MA. 2009. Litter quality is in the eye
657 of the beholder: initial decomposition rates as a function of inoculum characteristics.
658 Functional Ecology 23: 627-636.
659 Swift MJ, Heal OW, Anderson JM. 1979. Decomposition in Terrestrial Ecosystems. Oxford,
660 UK,: Blackwell Scientific. 509p.
661 Veen GF, Freschet GT, Ordonez A, Wardle DA. 2014. Litter quality and environmental controls
662 of home-field advantage effects on litter decomposition. Oikos: n/a-n/a.
663 Vivanco L, Austin AT. 2008. Tree species identity alters forest litter decomposition through
664 long-term plant and soil interactions in Patagonia, Argentina. Journal of Ecology 96: 727-
665 736.
666 Wallenstein MD, Haddix ML, Ayres E, Steltzer H, Magrini-Bair KA, Paul EA. 2013. Litter
667 chemistry changes more rapidly when decomposed at home but converges during
668 decomposition-transformation. Soil Biology & Biochemistry 57: 311-319.
669 Wang QK, Wang SL, Huang Y. 2009. Leaf litter decomposition in the pure and mixed
670 plantations of Cunninghamia lanceolata and Michelia macclurei in subtropical China.
671 Biology and Fertility of Soils 45: 371-377.
672 Wang QK, Zhong MC, He TX. 2013. Home-field advantage of litter decomposition and
673 nitrogen release in forest ecosystems. Biology and Fertility of Soils 49: 427-434.
674 Wardle DA. 2002. Communities and ecosystems: linking the aboveground and belowground
675 components. Princeton: Princeton University Press.
676 Wardle DA. 2006. The influence of biotic interactions on soil biodiversity. Ecology Letters 9:
677 870-886.
678 Wardle DA, Bonner KI, Nicholson KS. 1997. Biodiversity and plant litter: Experimental
679 evidence which does not support the view that enhanced species richness improves
680 ecosystem function. Oikos 79: 247-258.
681 Wardle DA, van der Putten WH. 2002. Biodiversity, ecosystem functioning and above-ground-
682 below-ground linkages. Loreau M, Naeem S, Inchausti P editors. Biodiversity and
683 Ecosystem Functioning: Synthesis and Perspectives. New York: Oxford University Press,
684 p155-168.

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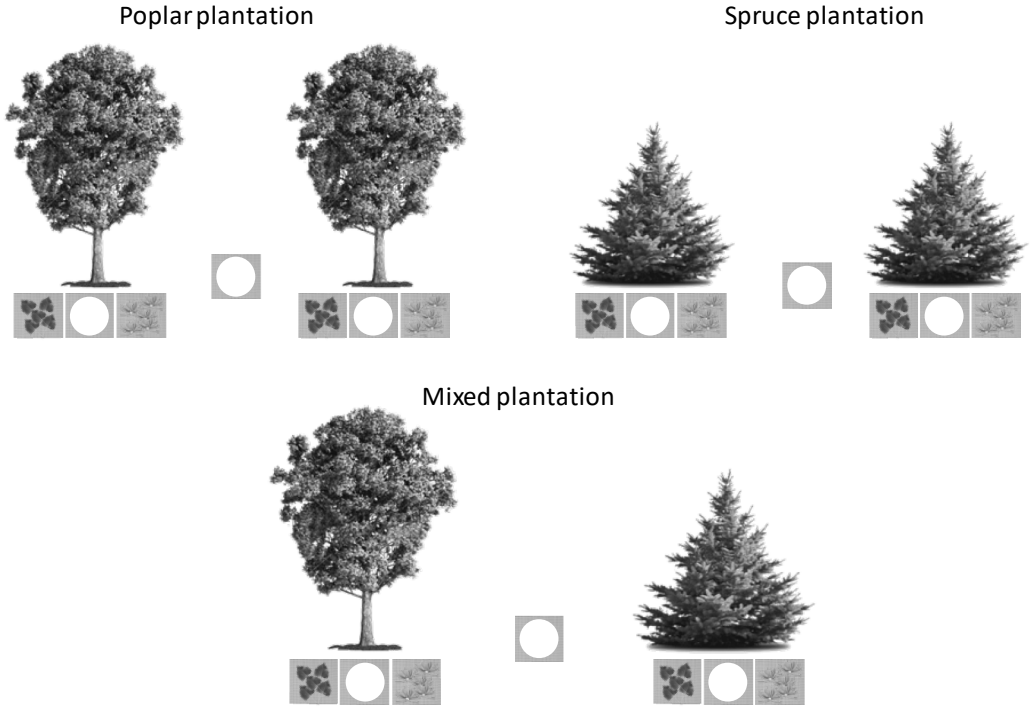
687 Figure 1



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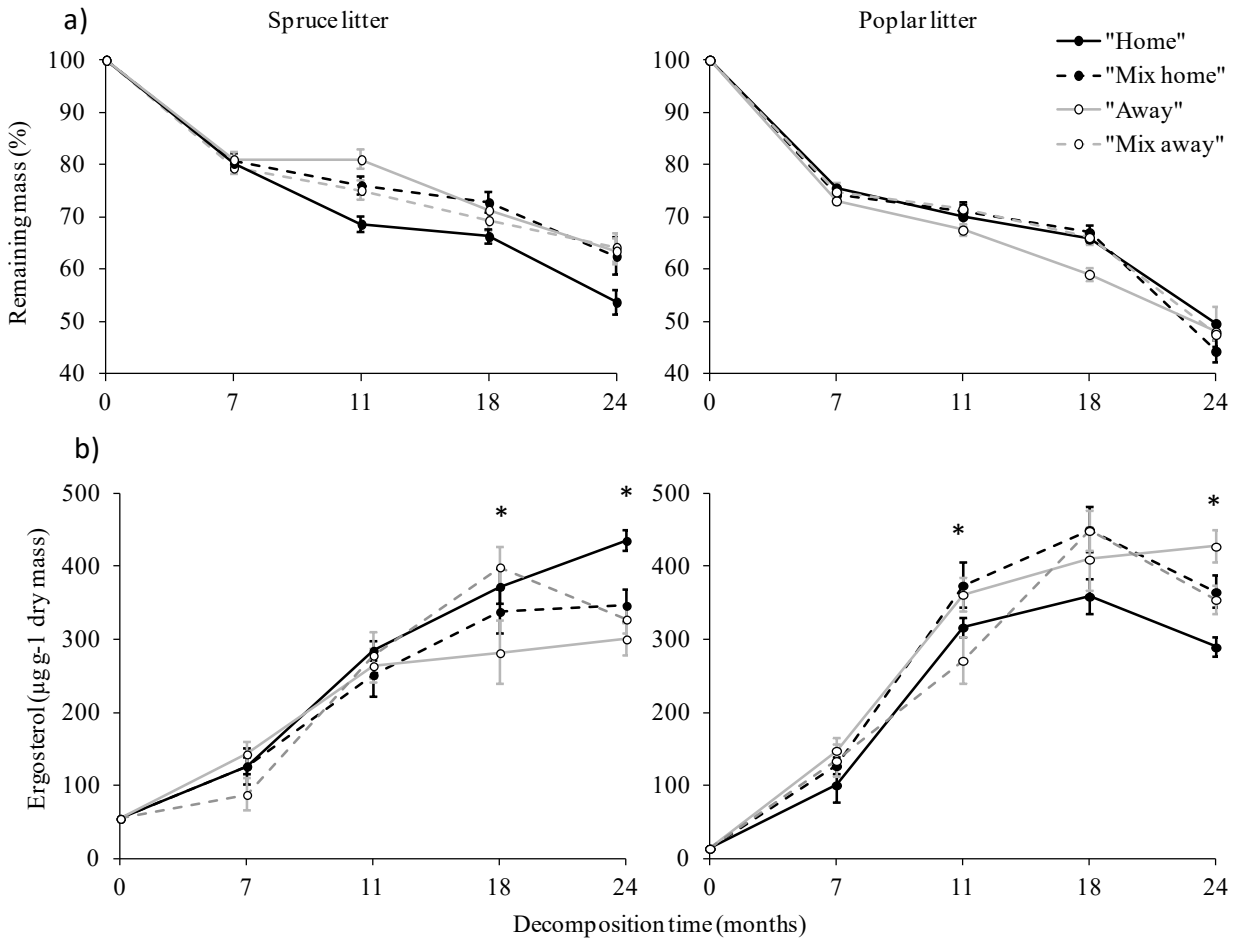
689 Figure 2



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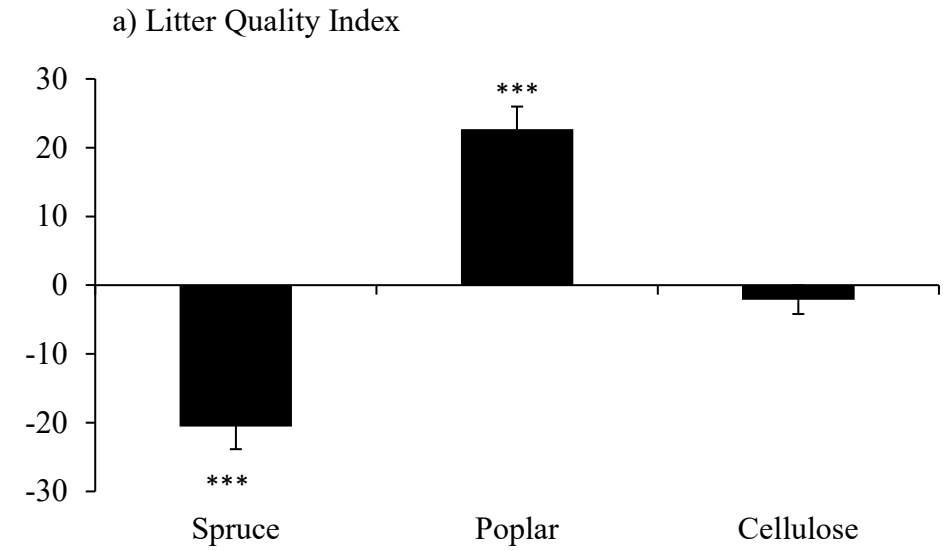

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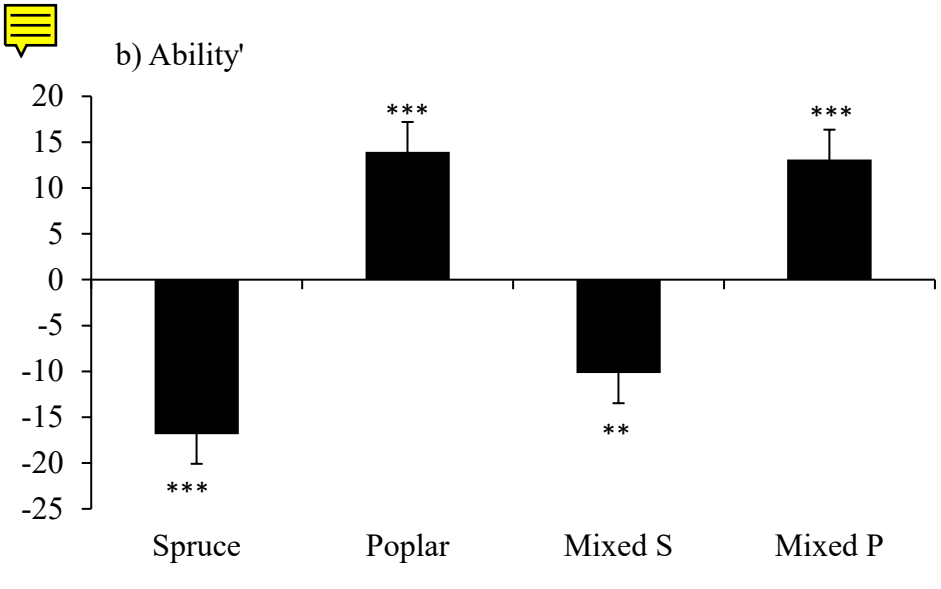

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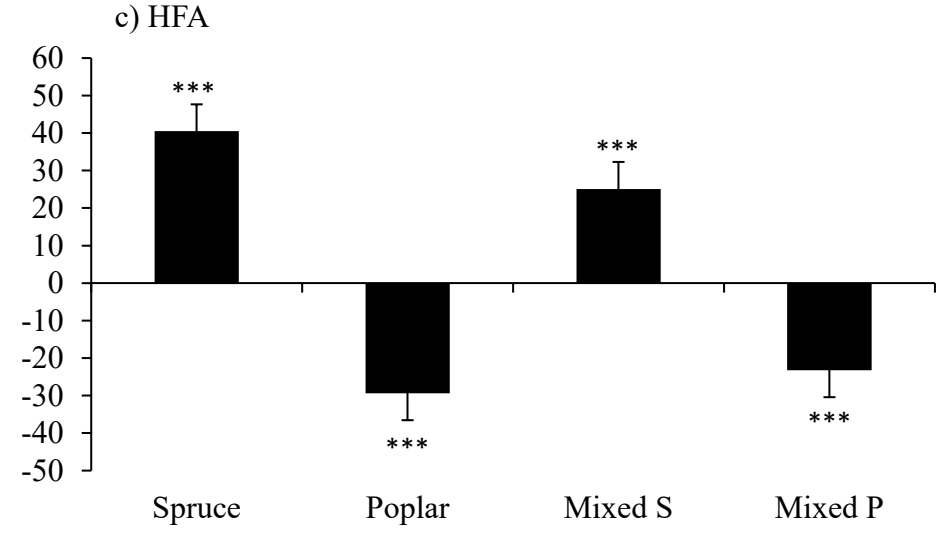

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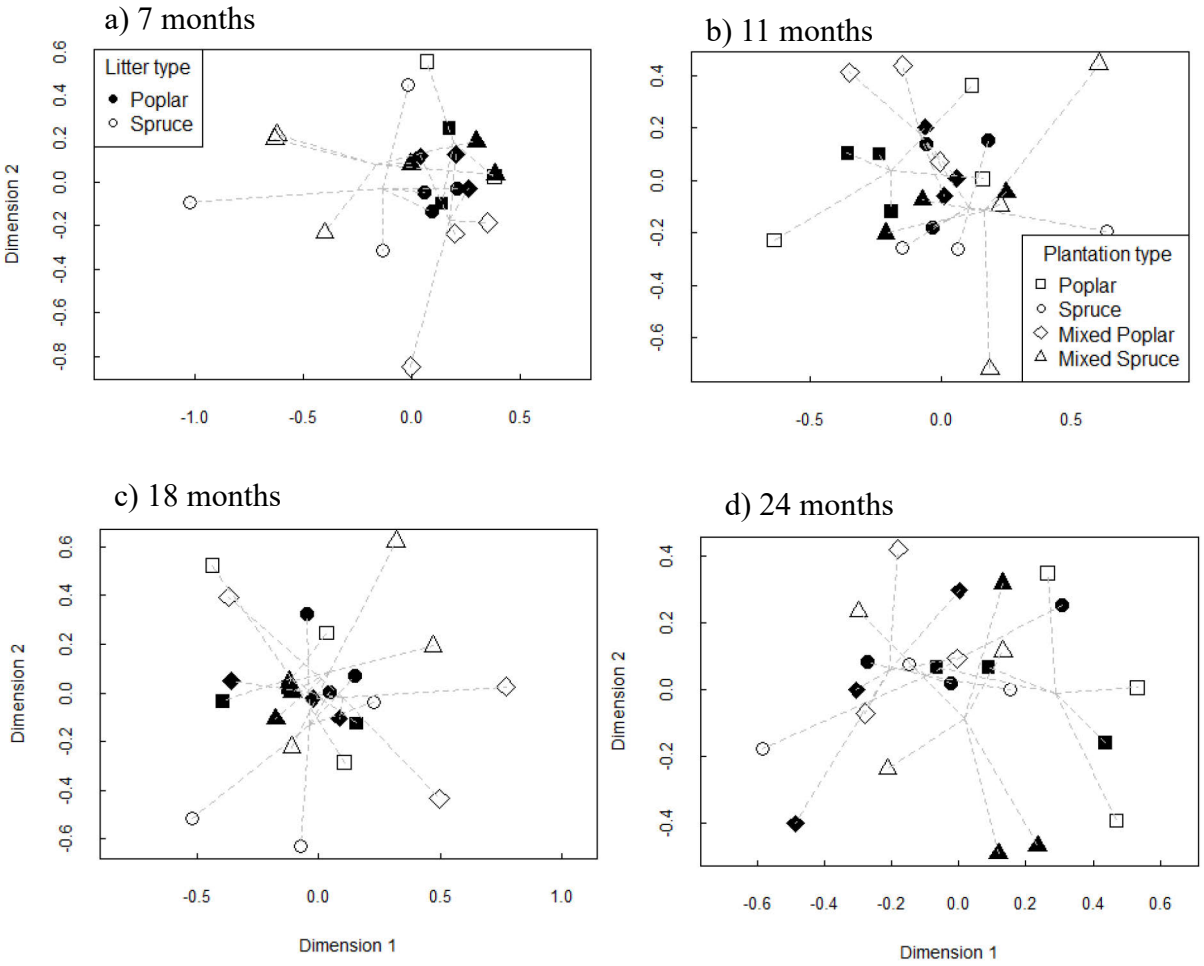

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699 Figure 5

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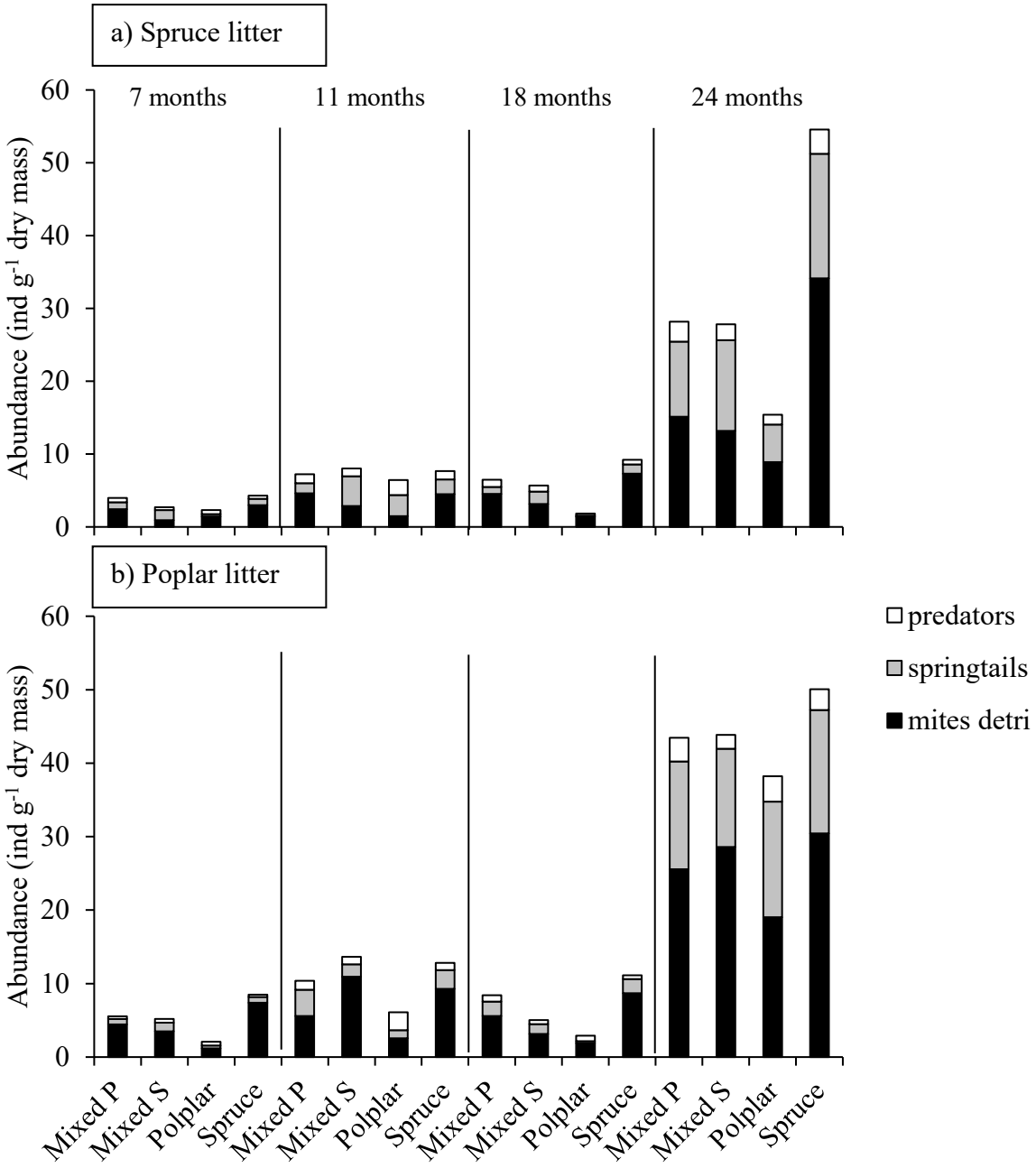

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704 Figure 6

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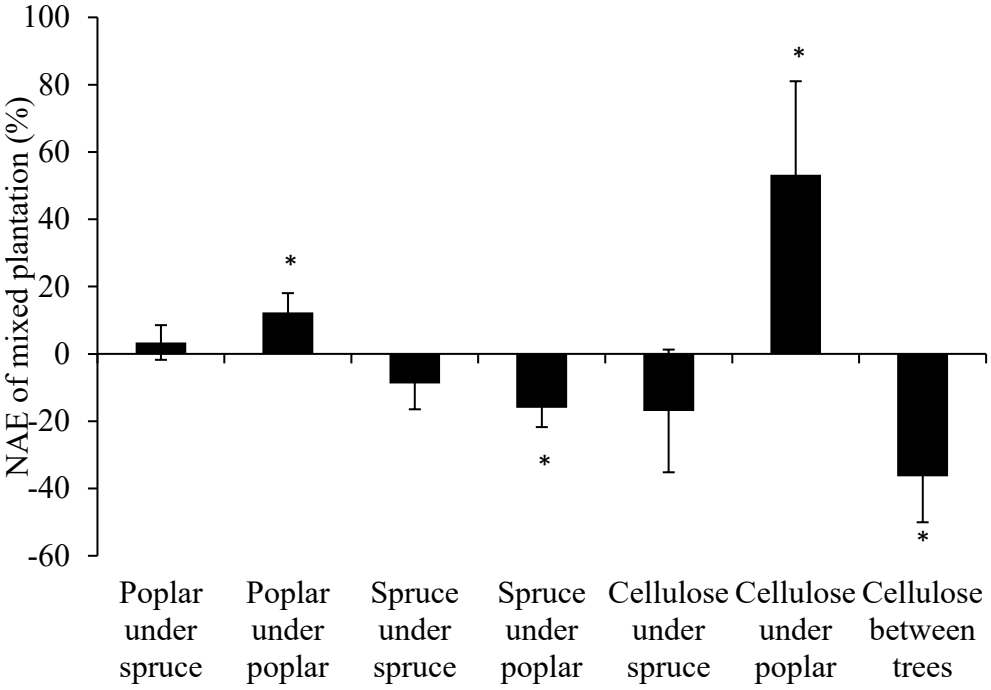

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Figure captions

Figure 1. Scheme of the experimental design of litterbag disposition within poplar and spruce monospecific and mixed plantations. Litterbags of poplar are symbolised by poplar leaves, litterbags of spruce are symbolised by spruce needles and litterbags of cellulose with a white circle.

Figure 2. a) Litter mass remaining (mean ± SE) expressed as a relative fraction of initial mass, and b) ergosterol content for spruce litter (left side) and poplar litter (right side) incubated in litter bags at "home" (black line) or "away" (gray line) in mono-specific plantations (solid line) or mixed-species plantations (dashed line) during decomposition. Significant differences between plantation type according to linear contrasts are indicated by *.

Figure 3. Parameter estimates (mean ± SE) calculated for (a) litter quality index, (b) ability and (c) HFA. Estimates that differ significantly from zero are indicated by * ($P < 0.05$).

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of catabolic profiles of microbial communities of both litter type and plantation type based on Euclidean distance at 7 (a), 11 (b), 18 (c) and 24 (d) months of decomposition. Stress = 0.15, 0.21, 0.21 and 0.19, respectively. Samples are grouped (dashed lines) by plantation type and the centroid of each group is indicated.

730 Figure 5. Abundance dynamics of mesofauna functional groups in spruce litter (a) and poplar
731 litter (b) in the different plantations.

732

733 Figure 6. Net effects (mean ± SE) of mixed plantations on decomposition of cellulose, poplar
734 and spruce litter under spruce or poplar trees. NAE (Non-additive effect) that are significantly
735 different from zero, according to one-sample Student's *t*-tests, are indicated by * ($P < 0.05$).

736

737 Table 1. Soil moisture and soil temperature.

Sampling dates	Variables	Plantation types			
		Poplar	Spruce	mixP	mixS
May 2011	Temp	11.6 ± 0.1 (c)	10.1 ± 0.1 (a)	10.4 ± 0.1 (b)	10.8 ± 0.2 (b)
	VWC	15.1 ± 0.6 (ns)	13.0 ± 0.4 (ns)	15.3 ± 0.9 (ns)	15.5 ± 0.9 (ns)
October 2011	Temp	11.9 ± 0.1 (b)	11.3 ± 0.1 (a)	11.5 ± 0.1 (a)	11.8 ± 0.2 (b)
	VWC	9.7 ± 0.5 (ns)	7.7 ± 0.3 (ns)	9.2 ± 0.6 (ns)	8.0 ± 0.8 (ns)
May 2012	Temp	8.9 ± 0.2 (c)	7.0 ± 0.2 (a)	8.2 ± 0.1 (b)	8.0 ± 0.1 (b)
	VWC	18.8 ± 1.1 (ns)	14.1 ± 0.7 (ns)	17.6 ± 0.5 (ns)	17.4 ± 1.1 (ns)
October 2012	Temp	8.1 ± 0.1 (b)	7.7 ± 0.1 (a)	8.0 ± 0.1 (ab)	7.8 ± 0.1 (ab)
	VWC	18.7 ± 1.0 (ns)	16.2 ± 1.3 (ns)	18.8 ± 0.7 (ns)	15.7 ± 0.8 (ns)

738 Note: mixP= mixed-poplar plantation, mixS= mixed-spruce plantation,

739

740 Table 2. Microbial catabolic diversity associated to litter.

Litter type	Plantation type	Decomposition time (months)			
		7	11	18	24
Spruce	Spruce	1.47 ± 0.25	2.36 ± 0.31	1.64 ± 0.55	2.88 ± 0.06
	Mixed-spruce	0.90 ± 0.17	1.68 ± 0.60	1.58 ± 0.41	2.73 0.08
	Mixed-poplar	1.59 ± 0.68	2.50 ± 0.17	1.76 ± 0.28	2.73 ± 0.12
	Poplar	2.45 ± 0.26	2.45 ± 0.33	1.72 ± 0.23	2.69 ± 0.05
Poplar	Spruce	2.8 ± 0.02	2.95 ± 0.05	2.58 ± 0.27	2.89 ± 0.08
	Mixed-spruce	2.61 ± 0.08	2.77 ± 0.01	2.58 ± 0.10	2.72 ± 0.01
	Mixed-poplar	2.64 ± 0.04	2.79 ± 0.07	2.57 ± 0.05	2.80 ± 0.05
	Poplar	2.75 ± 0.07	2.84 ± 0.06	2.56 ± 0.09	2.83 ± 0.02

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742

743 Table 3. Mass loss of cellulose beneath or between the trees.

744

Plantation	Species	Under	Between
Pure	Poplar	55.2 ± 9.1 b	62.6 ± 8.3 b
	Spruce	19.7 ± 3.5 a	44.7 ± 8.3 ab
Mixed	Poplar	54.1 ± 7.5 b	35.2 ± 7.6 a
	Spruce	35.9 ± 10.4 ab	

745

746

747 **Table captions**

748 Table 1. Soil moisture expressed as volumetric water content (VWC, %) and soil temperature
749 (Temp, °C). Mean ± SE from May 2011 to October 2012 for each plantation type. Significant
750 differences (pairwise contrasts) between plantation types within each row are presented with
751 different letter.

752

753 Table 2. Catabolic diversity (Shannon index, mean ± SE) of microorganisms colonizing
754 different litter and plantation types along decomposition time.

755

756 Table 3. Mass loss of cellulose (%, mean ± SE) beneath or between the trees (poplar or spruce)
757 in pure or mixed plantations. Across litterbag positioning, different letters within each
758 plantation type represent a significant difference between means according to linear contrast.

759

760 Annexe 1

Familly	Carbon source
Amides	phenyl ethylamine
	Putrescine
Amino acids	L-Arginine
	L-Asparagine
	L-Phenylalanine
	L-Serine
	L-Threonine
	Glycyl-Lglutamic acid
Carboxylic acids	D-Galactonic acid y-lactone
	D-Galacturonic acid
	Pyruvic Acid methyl ester
	γ-Hydroxybutyric acid
	D-Glucosaminic acid
	Itaconic Acid
	α-ketobutyric acid
	D-Malic acid
Carbohydrates	β-Methyl-DGlucoside
	D-Xylose
	i-Erythritol
	D-Mannitol
	N-Acetyl-DGlucosamine
	Glucose-1-phosphate
	D,L α-glycerol phosphate
	D-cellobiose
	a-D-Lactose
Phenolic compounds	2-Hydroxy Benzoic acid
	4-Hydroxy Benzoic acid
Polymers	Tween 40
	Tween 80
	α-Cyclodextrin
	Glycogen

761