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Leaf Litter Decomposition of Nonnative Shrub Species in Nonnative and Native Shrub Environments: A Field Experiment with Three Rosaceae Shrubs

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Invasion by nonnative plants may have ecosystem-wide effects, altering the decomposition rate of plant material via changes in litter quality or altered environment (abiotic conditions, associated biotic community), or both. Yet, the relative importance of these factors for decomposition rates is not clear. We studied decomposition using the leaves of related shrub species (nonnative *Sorbaria sorbifolia* and *Rosa rugosa*, native *Rubus idaeus*) with comparable physiognomy but different leaf characteristics and origin (alien vs. native) in patches formed by *S. sorbifolia* and *Rubus idaeus* in southwestern Finland. Decomposition of cellulose in the topsoils of the patches was also studied. Using litter bags, we found that *S. sorbifolia* leaf litter decomposed slowest and *Rosa rugosa* leaves fastest irrespective of patch type. Topsoils in *S. sorbifolia* patches were richer in carbon, nitrogen, and calcium than those of *Rubus idaeus*, but these differences did not affect decomposition rates. Very little decomposition appeared to happen during the winter but during the summer, microclimate had minor but significant effects on decomposition rates. Our results highlight the key role of litter source in the decomposition of plant material. Between-patch differences in abiotic conditions appear to play a minor role relative to litter quality.

Nomenclature: False spirea, *Sorbaria sorbifolia* (L.) A. Braun; rugosa rose, *Rosa rugosa* Thunb.; red raspberry, *Rubus idaeus* L.

Key words: Alien species, invasive plants, leaf decomposition, Rosaceae, shrub.

Invasive plants have become a pervasive problem throughout the world because they may threaten native plant species and alter ecosystem processes by altering trophic structure and changing resource availability (Boswell and Espie 1998; D'Antonio and Vitousek 1992; Ehrenfeld 2003; Hobbs and Mooney 1986; Kempel et al. 2013; Kourtev et al. 1998; Mack et al. 2000; Richardson and Rejmánek 2011; Skurski et al. 2013; Vilà et al. 2011). Plant invasion may greatly affect aboveground–belowground feedbacks, especially when the physiological traits of the invading species differ from the native flora (Wardle et al. 2004). For example, invasive nonnative species have been shown to alter decomposition rates and soil nutrient cycling in deciduous forests (Ashton et al. 2005). Decomposition of plant material is one of the major processes in the biogeochemical cycle of carbon and macronutrients (Morin 1999; Wild 1993); it has been estimated that the decomposition of plant material contributes approximately 70% to the total annual carbon flux (Raich and Schlesinger 1992). If invasive species alter the rate of decomposition, the invasion may have system-wide effects in the ecosystem. When an invading plant differs by its physiological traits from other plants in the invaded community, the quantity or chemical composition of litter is likely to change, which may affect the decomposition process. Leaf litter chemistry may affect soil biota, leading to changes in decomposition, nutrient cycling, or both (Coq et al. 2010). For example, chemicals that protect plant tissue against herbivory, or are used in interspecific competition (allelopathy; Inderjit et al. 2011), may also have an effect on soil organisms (Coq et al. 2010; Kotilainen et al. 2009; Martinson et al. 2008).

Recently, the accumulation of studies on changes in ecosystem responses to plant invasion has allowed a meta-analysis across various ecosystem types (Liao et al. 2008). Although the analysis revealed that invasive plants decompose on average faster than co-occurring native

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Management Implications

Decomposition of plant material is crucial for nutrient cycling. Invasive woody species may alter decomposition rates by altering litter quality and by altering the environmental conditions below the plants. We compared the leaf decomposition of a native and two nonnative shrubs in environments created by the native and one of the nonnative shrubs to estimate the relative importance of leaf source (species identity) and environment (microclimatic conditions, soil nutrient levels) for leaf decomposition rates. All shrubs belonged to the same family (Rosaceae) and had comparable physiognomy and leaf biomass production, which helped to minimize the influence of confounding factors. Our results demonstrate how the decomposition rate of leaves depends on species-specific differences in the quality of leaves rather than on the minor differences in the environments created by the patch-forming shrubs. The predominant importance of leaf source has been stressed also in some previous studies, suggesting that our conclusions can be generalized to a wider group of woody species. Although our conclusions can be regarded as preliminary rather than conclusive due to the small number of studied species, our results suggest that evaluations based solely on changes in leaf litter quality (and quantity) may capture the essential changes in leaf decomposition rates after an invasion of a nonindigenous plant. However, our results also indicate that species-specific differences in leaf quality prevent generalizations across all species, so the consequences of plant invasions for decomposition rates should be evaluated at the level of plant species.

species, the review of Ehrenfeld (2010) listed studies demonstrating contrarily slower rates of litter decay of exotic species. The conclusions of the reviews may, however, be affected by an overrepresentation of studies focusing on plants with the most obvious effects on ecosystems, such as nitrogen-fixing invaders in ecosystems where low soil nitrogen level is limiting plant growth and possibly also decomposition. Another factor affecting the conclusions of the reviews is that the impact of invasive nonnative species on decomposition rates are linked to the amount of litter produced; competitively superior invasive species often have a higher biomass production than the plant species that they replace (Ehrenfeld 2010; Liao et al. 2008). The reviews also emphasized the fact that decomposition in an invaded system depends on many factors, including differences in litter quality and abiotic conditions (Dehlin et al. 2008; Heneghan et al. 2006; Hunt and Wall 2002; Weidenhamer and Callaway 2010) and soil biotic communities (Hunt and Wall 2002; Inderjit and van der Putten 2010). Invasion of an exotic species is likely to cause changes in the associated biotic community and often also alters the physico-chemical environment, such as humidity or soil nutrient contents (Ehrenfeld 2010). Litter quality is evidently among the key factors affecting decomposition of plant material but the relative role of changes in the other factors—abiotic conditions and associated biotic communities—is less obvious.

In this study, we report results of decomposition experiments focusing on the relative importance of litter source (reflecting the quality of leaf material) and the altered environment on decomposition. We compared decomposition of native and nonnative litter in patches formed by native and nonnative shrubs. The nonnative Rosaceae shrubs selected for this experiment were well-defended invasive species that experienced very little or no leaf herbivory because of toxic compounds [*Sorbaria sorbifolia* (L.) A. Braun] or a combination of chemistry and leaf structure (*Rosa rugosa* Thunb.). The unpalatability of the leaves to herbivores indicated that the quality of the leaves of these nonnative species deviated from the quality of native plants and also indicated that the leaves provide a challenge to consumers. The nonnative plants were compared to a phylogenetically related native shrub, *Rubus idaeus* L. This plant, considered as a reference species, occurs at the same habitats and forms patches of similar physiognomy and biomass production (Lanta et al. 2013). The allocation of growth to leaves (relative biomass values) were comparable between study species, suggesting that the quantity of leaf litter produced annually would be comparable among the shrub patches (Lanta et al. 2013). Also, the amount of photosynthetically active radiation at the ground level was comparable between the *S. sorbifolia* and *Rubus idaeus* patches (Lanta et al. 2013). Decomposition of cellulose in topsoil was also studied. We focused on the following questions: (1) Does the decomposition rate of leaf litter depend on the species of the patch-forming shrub? (2) What is the relative importance of leaf origin (shrub species) vs. abiotic conditions (temperature, humidity, soil nutrient content) for the decomposition rate? (3) Does the decomposition rate of cellulose in the topsoil correspond to the decomposition rate of leaf litter on soil?

Materials and Methods

Model System. The study was conducted in southwestern Finland ($60^\circ27'$N to $60^\circ23'$N, $22^\circ16'$E to $23^\circ07'$E), in close vicinity of three towns: Turku, Paimio (12 km [7.5 mi] east of Turku) and Salo (50 km east of Turku). The landscape consists of a mosaic of inhabited areas, forests, and agricultural fields along a main road connecting Scandinavia with Russia (European route E18).

The study area is situated within the hemiboreal zone. Average temperature in January is −4.4 C (24 F) and in July, 17.5 C. The snowy period with below-zero average temperatures lasts from December to March; average snow depth in mid-March is 24 cm (9.4 in). Growing season lasts from late April to October.

Our study system consisted of eight patches of the nonnative shrub species *S. sorbifolia* that had been planted as decorative patches along roads and eight patches of a

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native shrub occurring in the same habitats, the raspberry *Rubus idaeus*. *Sorbaria sorbifolia* is recognized as a potentially or locally harmful alien species in Finland because it is able to spread locally and threaten indigenous flora (Finland's National Strategy on Invasive Alien Species 2012). As the third study species we used *Rosa rugosa*, which is recognized as a harmful alien species in Finland; *Rosa rugosa* was only used as a source of leaves. We monitored 10, 2, and 4 shrub patches in the Turku, Paimio, and Salo regions, respectively. The distances between the patches varied from about 0.7 to 10.7 km, 0.5 km, and 0.3 to 3.5 km within the Turku, Paimio, and Salo regions, respectively. All patches (i.e., continuous stands formed by a single shrub species) represented a bush environment characterized by mature shrubs and dense canopy; available information on the history of the roads and study sites suggest that the patches were at least 15 yr old. The average size of a patch was ca 140 m^2 (167 yd^2); there were no differences in patch size or in the distance from the nearest roads between the shrub species (ANOVA; F = 1.01 to 3.05; P > 0.103). The between-species distances of *S. sorbifolia* and *Rubus idaeus* patches were between 16.1 and 52.6 m.

To get background information on leaf litter cover and the number of plant species within the patches a vegetation survey was conducted inside of the study patches in June 2011 ($n = 5$ patches per bush species; 0.5 by 0.5–m squares in five randomly chosen spots in every patch).

Litter Bag Experiment. We used leaves of the three plant species, *S. sorbifolia*, *Rosa rugosa*, and *Rubus idaeus*, in a decomposition experiment. Nonnative *Rosa rugosa* was included to the comparison because it possesses leaf characteristics that differ from those of the two other species. In *Rosa rugosa* leaves, the epidermal cells form a thick cuticle including volatile organic compounds (Tabuchi et al. 2010). The leaves also contain high amounts of phenols (Nagai et al. 2007). These leaf characteristics make the leaves less palatable and less attacked by insect herbivores (Bruun 2005) than most other wild species.

Leaf litter of the three species was collected from sun-exposed microsites within a 10-km radius around Turku (nine haphazardly chosen sites at Turku, distance ca. 0.7 to 8 km from each other). Thus, all leaves had been exposed to similar climatic conditions, which facilitated interspecies comparison of litter weight losses. At the end of September 2011, freshly senesced leaves that had lost their green color and were functionally disconnected from the plant were collected from nine shrub patches (i.e., nine samples of ca. 200 leaves per species, mixed together). Petioles were considered as a part of a leaf.

The litter collections were cleaned and air-dried in open paper bags (at 60 C) for 3 d. Samples of dry leaf material (3.0 ± 0.01 g) were weighed, then sealed into pillow-shaped litter bags made of nylon net (1.0 mm mesh size). The net retained leaf particles and allowed free movement of microorganisms and smallest invertebrates, but restricted the movement of larger invertebrates, such as earthworms (*Lumbricus* spp.). When flattened, the size of litter bags ($n = 288$) was 10 cm by 20 cm.

Incubation was initiated after the peak of natural senescence; leaf bags were placed on November 4, 2011. The leaf bags were placed in groups of three bags containing, respectively, the leaves of *S. sorbifolia*, *Rosa rugosa*, and *Rubus idaeus*. The original leaf litter layer covering the surface (ca. 0.5 cm thick) was removed from the spots where the bags were positioned. Leaf bags were placed on the soil surface close to the center and edge (0.5-m-wide edge zone within the patch) of each bush patch, so that the distance of the bag groups (referred hereafter as interior vs. edge) within a patch were 1.5 to 5 m, depending on the shape of the patch. The number of such triplets in each patch was three in the interior and three at the edge of the patch (a total of 18 leaf litter bags in each patch). The total number of litter bags was 288 (2 shrub species by 8 patches by 18 bags in each patch); nine bags were not found at the end of the experiment, leaving 279 litter bags for the statistical analyses. Leaf litter bags were collected on July 14, 2012.

As a neutral control measuring the decomposition capacity of cellulose by soil microbes, we used similar-sized litter bags filled with 3 g (0.1 oz) of standard cellulose material (cotton wool, Pumpuli Oy, Forssa, Finland). Cotton wool is a mass of thin fibers, hence a smaller mesh size (0.3 mm) was chosen to ensure that the thin fibers stayed inside the bag. The cellulose bags (10 in each patch; $n = 160$) were buried (on October 7, 2011) 3 to 5 cm deep in the soil in the center of a patch. Cellulose bags were collected on May 1 ($n = 1$ replicate per patch) and July 27, 2012 ($n = 9$ replicates per patch). After retrieval, adhering soil and soil fauna were removed from the litter bags by brushing or swiftly rinsing with water. Thereafter, samples were dried for 3 d at 60 C and then weighed. The percentage of dry weight loss of the samples was assesed.

Surface Soil Properties. To characterize soil properties of the studied patches, we collected two homogenized mixed samples (volume 0.6 L [0.6 qt]) of soil surface layer (soil depth 0 to 5 cm) from each patch in September 2011. Soil was transferred to the laboratory of MTT Agrifood Research Finland, Jokioinen, Finland, where the samples were analyzed. The pH was measured from a soil–water suspension (1 : 2.5). Total organic carbon and total nitrogen contents (%) were determined using a C-N-autoanalyzer (LECO CN-2000, Leco Corporation, MI, USA). For determination of calcium, potassium, magnesium, and phosphate, air-dried soil samples were extracted with acidic ammonium acetate solution (pH 4.65, AAAc

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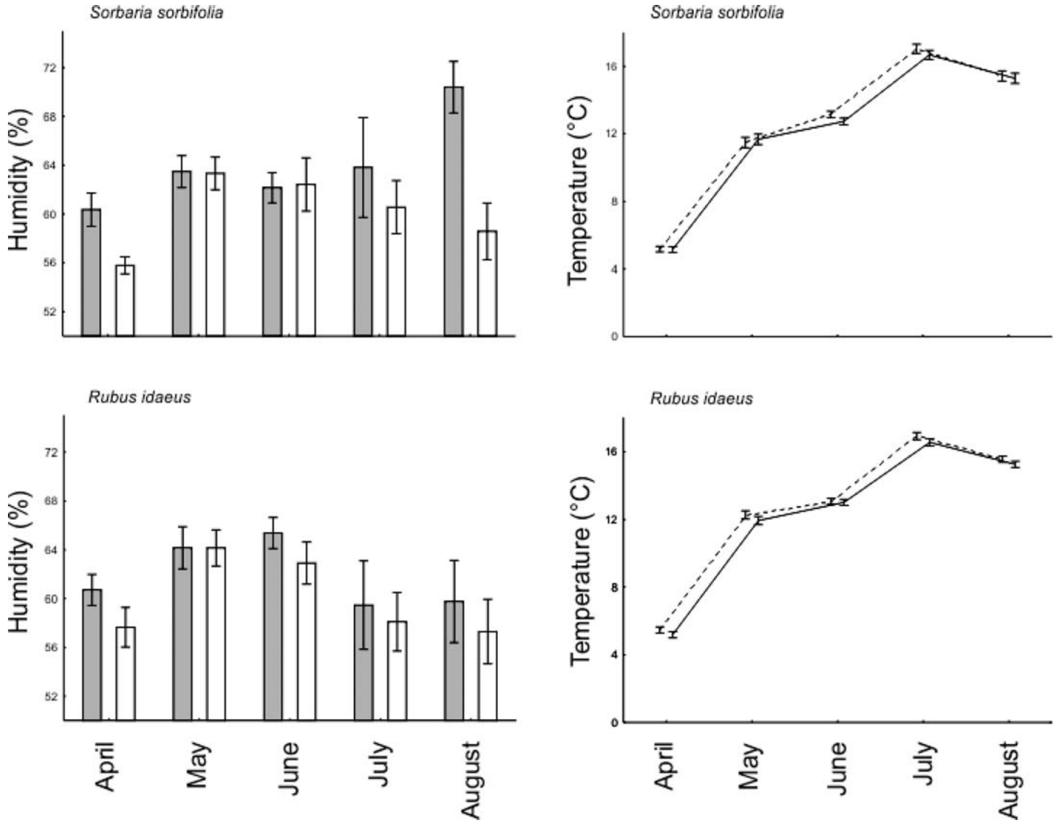

Figure 1. Monthly mean temperature (C; lines) and relative humidity (%; columns) in the study patches during summer 2012. Dark columns and solid line refer to conditions at the center of the patches, light columns and dashed line to those at the edge of the study patches.

1 : 10 for 1h) as described by Vuorinen and Mäkitie (1955). Concentrations of calcium, potassium, and magnesium were measured by IRIS Advantage inductively coupled optical plasma emission spectrometer (Thermo Jarrell Ash, MA, USA) and phospate by autoanalyzer (San++ continuous flow analyzer, Skalar, the Netherlands) using ammonium–molybdate complexation.

Microclimatic Conditions. In 2012, air temperature and relative air humidity were measured using Gemini TGP-4500 (Gemini Data Loggers, UK) data loggers placed on the edge ($n = 1$) and in the interior ($n = 1$) of each patch, ca. 10 cm above the soil surface. Temperature and humidity were recorded at 30-min intervals from April to August. To estimate the effect of microclimatic conditions on leaf litter decomposition, mean values of temperature and relative humidity from May 1, 2012, to the end of the litter bag experiment (July 14, 2012) were used in statistical tests. All study sites were covered by a relatively thick (> 20 cm) snow layer during the winter (until early April) and we assumed that microclimates below snow were relatively similar. We assumed that little decomposition occurred in April due to low temperatures (Figure 1), therefore we used May 1 as the starting point in the calculation of the indices, reflecting microclimate during the main period of litter decomposition.

Data Analyses. Variation in percentage of dry weight loss of litter samples was evaluated using a linear mixed-effects model (LME). Shrub species identity (either *S. sorbifolia* or *Rubus idaeus*), position (interior vs. edge), bush by position interaction, identity of leaf material (three levels: *S. sorbifolia*, *Rosa rugosa*, *Rubus idaeus*), interaction between shrub species and leaf identity, and microclimatic conditions (mean air temperature and percent humidity for a period of 75 d) were fixed effects and patch identity (i.e., site) was a random effect in the analysis. We compared the full model and reduced models using the Akaike information criterion (AIC) scores, and selected the model with the lowest AIC scores as the most parsimonious one (Pinheiro and Bates 2000). LME analyses were also performed separately for *S. sorbifolia*, *Rubus idaeus*, and *Rosa rugosa* leaf litter samples, using two explanatory variables, shrub species identity (*S. sorbifolia* vs. *Rubus idaeus*) and position (interior vs. edge of a patch). All analyses were performed in R ver. 2.15 (R Development Core Team 2013); LMEs were fitted using the function lmer in R library *lme4*. P-values and 95% confidence

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Table 1. Final linear mixed-effects model (LME) of percentage of leaf litter loss, with shrub patch identity as a random effect. Position refers to the position of the litter bags within the shrub patch (interior vs. edge). Initial model also included as fixed effects shrub species identity, shrub species by position interaction, shrub species by leaf species interaction, and air temperature, which were removed during model selection. The fixed effect leaf species (three categories; *Rosa rugosa*, *Rubus idaeus*, and *Sorbaria sorbifolia*) was evaluated as two contrasts between two categories in the LME. The final model is the model with the lowest Akaike information criterion (AIC) value (−387.0) and the fewest necessary parameters to explain observed variation. Note that the AIC value of the initial model was −356.0.

	Estimate	Lower 95% HPD[a]	Upper 95% HPD	P
(Intercept)	(0.616)	(0.318)	(0.898)	(0.001)
Position	0.038	0.011	0.063	**0.006**[b]
Leaf species (*Rubus idaeus* vs. *Rosa rugosa*)	−0.070	−0.099	−0.039	**0.001**
Leaf species (*S. sorbifolia* vs. *Rosa rugosa*)	−0.263	−0.294	−0.235	**0.001**
Relative humidity	0.005	0.000	0.009	**0.048**

[a] Abbreviation: HPD, highest probability density.

[b] Bolded values indicate statistical significance.

intervals were estimated using Markov chain Monte Carlo simulations in library *languageR*. Variation in percentage of dry weight loss of cellulose samples was evaluated using LME with shrub species identity (*S. sorbifolia* vs. *Rubus idaeus*) as fixed effect and patch identity as random effect. Decomposition rates of cellulose during summer were derived as percentage of dry weight loss in July minus percentage of dry weight loss in May and were evaluated by ANOVA.

ANOVA was used to test for differences in soil nutrients in *S. sorbifolia* and *Rubus idaeus* patches. Percentage data on total N and total C were *arc-sin* ($\sqrt{x}$) transformed and the rest of parameters were ln-transformed prior to the analyses. The association of soil properties and decomposition (% dry leaf loss) in the shrub patches was tested using Spearman's rank correlation analysis. Changes in microclimatic conditions were analyzed using repeated measures ANOVA with two variables (shrub species and position) as the fixed factors, and month as the repeated measures factor. To test the effects of spatial distribution of study patches on leaf decomposition, a correlation between leaf loss and a dissimilarity matrix on the geographical positions of study patches was assessed using a Mantel test (function mantel in R library *vegan*). The test was run separately for *Rosa rugosa*, *Rubus idaeus*, and *S. sorbifolia* leaves. Euclidian distances between patches were derived from the global positioning system coordinates of the patches.

Results and Discussion

Background Information. The vegetation survey revealed an obvious pattern demonstrating that patches formed by *S. sorbifolia* hosted significantly fewer herb species (1.0 ± 0.3 species per 0.25 m^2) and accumulated more leaf litter (78.2 ± 4.8% cover per 0.25 m^2) than patches of *Rubus idaeus* (3.5 ± 0.5 species; litter coverage 21.4 ± 5.9%) (ANOVA: F = 14.1, P = 0.006, and F = 21.6, P = 0.002 for log-transformed species number and arcsine-transformed litter cover, respectively). Marked differences in the accumulation of leaf litter despite comparable biomass production hint that there may be relevant differences in the decomposition rate of leaf litter between the two types of patches. Major differences in the plant species richness suggest biologically important differences in the environment provided by the patches of the two shrub species.

Decomposition. Percentage of dry leaf litter loss depended on species origin of leaf material as shown in final LME (P = 0.001; Table 1). The percentage of dry leaf loss was smallest in *S. sorbifolia* (65.6 ± 1.4%) and largest in *Rosa rugosa* (91.9 ± 0.7%). The percentage of dry leaf loss of native *Rubus idaeus* was 84.9 ± 1.3%. The leaf litter loss was slightly higher in the interior (82.8 ± 1.3%) than at the edge (78.7 ± 1.4%) of the patches (P = 0.010; Table 1). There was no difference in litter loss between *S. sorbifolia* and *Rubus idaeus* patches (lower 95% HPD (highest probability density) interval = −0.079, upper 95% HPD interval = 0.013, P = 0.210) and also the interaction between environment (patch-forming shrub) and litter origin was nonsignificant; the nonsignificant interaction term was removed from the final model. Humidity had a positive relationship with leaf decomposition (Table 1); however, the effect of mean temperature was not significant (lower 95% HPD interval = −0.070, upper 95% HPD interval = 0.015, P = 0.246).

Species-level analyses on leaf litter loss gave somewhat differing results for the species (Table 2). *Sorbaria sorbifolia* leaves decayed significantly faster in the interior of shrub patches than at the edge (P = 0.046; Figure 2), but the leaf litter loss rate was similar in both nonnative and native shrub patches (Table 3). Leaves of *Rubus idaeus* decayed

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Table 2. Results of linear mixed-effects model analyses for *Sorbaria sorbifolia*, *Rubus idaeus*, and *Rosa rugosa* litter loss. Two effects were used as the explanatory variables, shrub species identity (*S. sorbifolia* vs. *Rubus idaeus*) and position (interior vs. edge).

Leaf litter	Effect	Estimate	Lower 95% HPD[a]	Upper 95% HPD	P
Sorbaria sorbifolia	(Intercept)	(0.627)	(0.568)	(0.681)	(0.001)
	Shrub species	−0.004	−0.080	0.086	0.940
	Position	0.075	0.005	0.155	**0.046**[b]
	Shrub species × position	−0.026	−0.130	0.078	0.606
Rubus idaeus	(Intercept)	(0.866)	(0.810)	(0.925)	(0.001)
	Shrub species	−0.095	−0.186	−0.012	**0.032**
	Position	0.027	−0.040	0.100	0.468
	Shrub species × position	0.068	−0.026	0.168	0.174
Rosa rugosa	(Intercept)	(0.920)	(0.894)	(0.954)	(0.001)
	Shrub species	−0.010	−0.050	0.038	0.604
	Position	0.008	−0.033	0.045	0.694
	Shrub species × position	−0.002	−0.060	0.053	0.994

[a] Abbreviation: HPD, highest probability density.

[b] Bolded values indicate statistical significance.

faster in native *Rubus idaeus* than in nonnative *S. sorbifolia* patches (Figure 2), but there were no clear differences between the interior and edge parts of the shrub patches. The percentage of loss of *Rosa rugosa* leaves did not deviate markedly between the sites (Table 3). Spatial distribution of the 16 shrub patches did not affect leaf decomposition (correlation between leaf loss and geographical position: $r = -0.14$ (P = 0.87), $r = -0.09$ (P = 0.78), and $r = 0.08$ (P = 0.20) for *Rosa rugosa*, *Rubus idaeus*, and *S. sorbifolia* leaves, respectively).

We did not observe significant differences in dry weight loss of buried cellulose material between nonnative *S. sorbifolia* (in July, mean 53.0%) and native *Rubus idaeus* (mean 55.4%) patches (lower 95% HPD interval = −0.10, upper 95% HPD interval = 0.13, P = 0.925). The decomposition of buried cellulose samples was low (about 15%) during the cold winter to spring period, but it was rather rapid in the warmer summer season (Fig. 3).

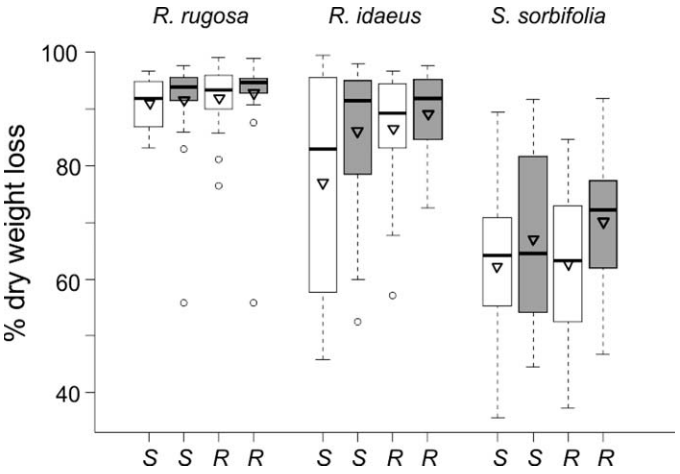

Figure 2. Decomposition of bagged *Rosa rugosa*, *Rubus idaeus*, and *Sorbaria sorbifolia* leaf litter in *S. sorbifolia* (*S*) and *Rubus idaeus* (*R*) patches. White and gray boxes refer to edge and interior environments, respectively. The minimum to maximum range (whiskers), quartile (boxes), median (lines), and mean values (triangles) are displayed.

Our results demonstrate that decomposition of the leaf material was predominantly associated with the species origin of leaf material and partly with microclimatic conditions at the site. Species identity of the patch-forming shrub as an environment for leaf decomposition played little or no role. Decomposition rate of cellulose material buried in the surface soil did not differ between the shrub environments either and thus gave a similar signal of decomposition rates to the leaf litter bags on soil.

Leaf source (reflecting different leaf chemistry and structure) was the main factor determining the rate of decomposition process. Of the three tested plant species, the decomposition rates of *S. sorbifolia* leaves were the slowest in both types of patches. The leaves of *S. sorbifolia* contain high levels of toxic hydrogen cyanide (Kim and Zee 2000) that probably contributed to the lower decomposition rate of the leaves of this species. In contrast to *S. sorbifolia*, the leaves of the other nonnative model species, *Rosa rugosa*, decomposed faster than the leaves of the native species, *Rubus idaeus*. This result was somewhat unexpected as the leaves of *Rosa rugosa* are relatively unpalatable to herbivores. The unpalatability of *Rosa rugosa* leaves is based on the combination of leaf structure and a set of different plant secondary chemicals (Bruun 2005), not solely on toxic substances as in the case of *S. sorbifolia*. The structural defenses of the leaves partly break during senescence and also some of the toxic compounds may break or evaporate before decomposition (Davies and Gan 2012; Thomas

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Table 3. Soil properties (mean ± SE) in the study patches, and F values of ANOVAs for the relationship of shrub species and the soil properties; $n = 8$ samples per shrub species.

	pH	Total N (%)	Total C (%)	Ca^{2+} (mg L^{-1})	K^{+} (mg L^{-1})	Mg^{2+} (mg L^{-1})	PO_4^{3-} (mg L^{-1})
Sorbaria sorbifolia	6.2 ± 0.1	0.40 ± 0.02	7.3 ± 0.8	2377.9 ± 127.4	249.9 ± 39.2	329.3 ± 46.7	20.7 ± 3.2
Rubus idaeus	5.9 ± 0.1	0.27 ± 0.03	3.4 ± 0.3	1431.9 ± 113.6	414.3 ± 54.6	273.7 ± 38.8	19.6 ± 2.7
F values	**4.2***[a]	**5.4***	**23.9*****	**28.9*****	**7.7****	0.6 (n.s.)[a]	0.0 (n.s.)[a]

[a] Bolded values indicate statistical significance.

[b] Abbreviation: n.s., not significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

2013). Possibly due to these changes, the mechanisms that protected the leaves of *Rosa rugosa* against herbivores did not slow down the decomposition of the leaves. On the contrary, the results showed that the leaves of *Rosa rugosa* decomposed faster than the leaves of the native *Rubus idaeus*. *Rubus idaeus* leaves contain relatively little lignin and a high proportion of water-soluble substances and nutrients compared to the leaves of many other woody species (e.g., Belovsky 1981; Staaf 1980), which indicates that the leaves should be easily decomposed. On the other hand, the leaves of *Rubus idaeus* also contain tannins that may deter some herbivores, such as the moose (*Alces alces*; Belovsky 1981). The slower decomposition of *Rubus idaeus* leaves as compared to *Rosa rugosa* may be due to tannins or comparable harmful chemicals in the leaves, or simply different structure. The enlarged epidermal cells of *Rosa rugosa* leaves may act as a water storage tissue (Tabuchi et al. 2010). As humidity appears to be positively related with decomposition rate, additional water in the cells may contribute to the faster rate of decomposition.

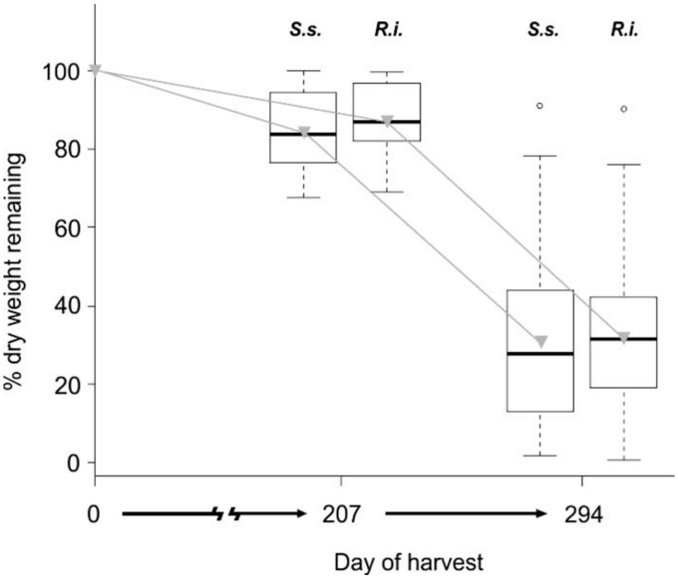

Figure 3. Decomposition of cellulose material in *Sorbaria sorbifolia* (*S.s.*) and *Rubus idaeus* (*R.i.*) patches after 207 and 294 d. The minimum to maximum range (whiskers), quartile (boxes), median (line), and mean values (gray triangles) are displayed.

Soil Properties and Microclimatic Conditions within Patches. Surface soil layers of the nonnative *S. sorbifolia* patches had on average significantly higher contents of total N, total C, and calcium, and a slightly higher pH level than the soils of native *Rubus idaeus* patches (Table 3). Concentration of potassium ions was higher in *Rubus idaeus* patches. In data pooled over two shrub species, the only correlation approaching statistical significance was found between pH values and the percentage of leaf decay of *S. sorbifolia* (Spearman's rank correlation; $n = 16$ patches, rho = 0.48, $P = 0.057$). No other associations between soil properties and percentage of leaf litter decay were significant. In *S. sorbifolia* patches, the only apparently significant correlation between soil properties and leaf litter decay was between pH values and the percentage of leaf decay of *S. sorbifolia* (Spearman's rank correlation; $n = 8$ patches, rho = 0.76, $P = 0.037$). In *Rubus idaeus* patches, none of the soil parameters were related with the percentage of leaf litter loss.

Air temperatures changed during the course of the year, but mean temperatures were similar between the central and edge parts of shrub patches as well as between the *S. sorbifolia* and *Rubus idaeus* patches (Figure 1). All patches were covered by snow during the winter; snow disappeared by early April, starting from the sunny edges of the study patches. A later melting of snow inside patches led to a higher relative humidity at the central vs. the edge parts of the patches in April (Figure 1). In May, humidity was quite similar in all sites. Differences in mean humidity between central and edge parts of the patches started to increase as leaves developed, so that in summer, mean humidity was higher inside than at edges of the patches (Figure 1; repeated measures ANOVA, df = 1, 28; F = 4.99, $P = 0.0337$). The seasonal pattern in relative humidity differed

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between the insides of *S. sorbifolia* and *Rubus idaeus* patches (Figure 1). Inside *Rubus idaeus* patches, mean humidity peaked in June whereas inside *S. sorbifolia* patches, humidity increased until August (interaction time by species: df = 4, 112; F = 3.00, P = 0.0215). Mean humidity at the edges of patches dropped from May to August (Figure 1).

Humidity and temperature, or their interaction, have been shown to affect decomposition rates in many environments but the relative importance of these abiotic factors appears to vary (e.g., Butenschoen et al. 2011; Prescott 2010; Robinson 2002). In our model system, temperature was probably the main factor causing seasonal differences in decomposition rates but humidity played a more influential role in the summer. During the summer season, the leaf litter of *S. sorbifolia* decomposed faster in the central than in the edge parts of the shrub patches. In the other species, this pattern was not statistically significant. Exposed edges of the patches experienced periodic drying during sunny days, which led to a lower mean humidity at edges compared to the central parts of the patches. This difference in the microclimate was enough to cause a small delay in the decomposition process.

On average, surface soils in the *S. sorbifolia* patches contained a higher level of carbon, nitrogen, and calcium than those of native *Rubus idaeus* patches, whereas the potassium levels were higher in *Rubus idaeus* patches. The cause of these differences remains unclear as we have no data on soil parameters at the time when the patches were established but it is likely that the differences in soil nutrient content were at least partly due to the direct or indirect impacts of the shrubs. None of the patches had been fertilized at least during their known growth history, so that possible surplus of nutrients at the time of planting should have been depleted during the > 15-yr growth history of the patches (Liao et al. 2008). *Rubus idaeus* leaves contain high levels of potassium (Staaf 1980), which may explain the higher potassium concentrations in the surface soils of *Rubus idaeus* patches. A previous study has reported increased nutrient pools in patches of seven highly invasive plant species (Dassonville et al. 2008), suggesting that enhanced nutrient uptake may be a common trait in invasive plants. Slower decomposition of litter and possibly also lower species number and abundance of other plant species in the patches of *S. sorbifolia* were likely to contribute to the differences in soil carbon and nitrogen contents. Previous studies have reported a higher decomposition rate at high than at low nutrient levels (Kaspari et al. 2008; Parsons et al. 2012). Yet, leaves of nonnative plants decomposed at fairly similar rates under both *S. sorbifolia* and *Rubus idaeus* shrubs. Decomposition rate of cellulose that had been buried in the surface soil was also similar in both kinds of patches. This suggests that the higher contents of carbon and nitrogen in the *S. sorbifolia* patches than in the *Rubus idaeus* patches were a consequence rather than a cause of lower decomposition rates of *S. sorbifolia* leaves.

Based on the temporal patterns in the decomposition of cellulose, most decomposition activity occurred during the warm summer season. As the winter season included snow-free periods in late autumn (October to November) and spring (April), the data do not reveal how much decomposition occurred during the coldest months when the sites were covered by snow. However, our results suggest low decomposition activity during the cold season as ca. 15% of cellulose disappeared between late autumn and spring (207 d) but most of the cellulose in the bags had been decomposed by the end of July (additional 87 d).

Conclusion. Our results demonstrate how the decomposition rate of leaves depends on species-specific differences in the quality of leaves rather than on the minor differences in the environments created by the patch-forming shrubs, at least within the group studied (shrubs belonging to the family Rosaceae). The predominant importance of litter origin has also been stressed in some previous studies (Cornelissen et al. 1999; Cornwell et al. 2008; Pérez-Harguindeguy et al. 2000), which suggests that our conclusion can be generalized to other plant families as well. The results suggest that evaluations based solely on changes in leaf litter quality (and quantity) may capture the essential changes in leaf decomposition rates after an invasion of a nonindigenous plant. However, our results also indicate that species-specific differences prevent generalizations across all species, so the consequences of plant invasions on decomposition rates should be evaluated at the level of plant species. Yet, the small number of studied species limits our suggestion as preliminary rather than conclusive, and it therefore needs to be confirmed with a larger number of plant species.

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