

Non-native and native shrubs have differing impacts on species diversity and composition of associated plant communities

Vojtěch Lanta · Terho Hyvönen · Kai Norrdahl

Received: 12 April 2013 / Accepted: 12 October 2013 / Published online: 29 October 2013
© Springer Science+Business Media Dordrecht 2013

Abstract The spread of non-native plants has been depicted as a serious threat to biodiversity. However, it remains unclear whether the indigenoussness of the invading plant plays a marked role for the ecological consequences of an invasion as few studies have compared the ecological impacts of non-native shrubs with structurally or functionally comparable native shrubs. We studied patches of introduced and native shrubs to assess whether there are general differences in plant species composition or biomass between patches formed by non-native versus native shrubs. The indigenoussness of the shrub (non-native vs. native) did not explain the variation in soil nutrients, neither the production of shoot biomass or allocation of growth to different parts of the shoot. The amount of light reaching ground level did not differ between patches of a non-native and a native shrub. However,

species richness and biomass of herbaceous plants were lower in patches of non-native than native shrubs and the amount of litter was higher below non-native than native shrubs. Our results suggest that the indigenoussness of the patch-forming plant may be an important factor for the diversity and composition of associated herbaceous vegetation. Based on our results, resource availability (light and nutrients) is not a sufficient explanation for the negative effects of non-native shrubs on plant communities. Further research is needed to investigate whether alternative explanations, such as the novelty of the toxic compounds produced by non-native plants, can explain the differences we observed.

Keywords Non-native species · Plant community · Resource competition · Rosaceae · Shrubs · Species richness

Electronic supplementary material The online version of this article (doi:[10.1007/s11258-013-0272-0](https://doi.org/10.1007/s11258-013-0272-0)) contains supplementary material, which is available to authorized users.

V. Lanta (✉) · K. Norrdahl
Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland
e-mail: vojlan@utu.fi

K. Norrdahl
e-mail: kainor@utu.fi

T. Hyvönen
Plant Production Research, MTT Agrifood Research Finland, 31600 Jokioinen, Finland
e-mail: terho.hyvonen@mtt.fi

Introduction

The composition of most plant communities has changed or is currently changing because of human activity. One important source of environmental change is the spread of plants beyond their historical range. Humans have moved thousands of plant species out of their natural range for many purposes (Richardson and Rejmánek 2011). When these plants become naturalized or invasive in a new environment, evolutionary novel combinations of plant species may lead

to novel environmental conditions in the ecosystem. This may alter the entire community in a way that leads many species to local extinction (Eldridge et al. 2011).

Invasion of alien plants has often been interpreted as a novel, detrimental threat to native communities (Manchester and Bullock 2000; Bucharová and van Kleunen 2009; Wilson et al. 2009; Hejda et al. 2009; Richardson and Rejmánek 2011; Eldridge et al. 2011). However, the spread of competitively superior native species can also significantly alter plant communities. In fact, this commonly occurs during succession. This raises a question of whether the environmental changes caused by invading non-native plants are fundamentally different from those caused by native plants invading a community. Even if the invading plant would be novel, the ecological process could just be seen as a variant of natural succession rather than a major threat to native communities. Thus, instead of focusing on the indigenoussness of the invasive species, the focus should be aimed on the environmental impacts of the invasion (Davis et al. 2011).

The ecological consequences of the spread of non-native plants have been well studied (e.g., Vilá et al. 2011; van Kleunen et al. 2011; Stohlgren et al. 2011), but few studies (Fogarty and Facelli 1999; Brudvig and Evans 2006; Feng and Fu 2008; Cincotta et al. 2009) have compared the ecological changes caused by habitat-forming alien plants, such as robust shrubs or trees, to the changes caused by invading natural plants with a similar structure. Therefore, it remains unclear whether these two scenarios are comparable cases of plant invasions along a temporal succession, or if the evolutionary novelty of communities with non-native species brings something critically different to temporally dynamic ecosystems.

Cross-comparison between communities dominated by different non-native and native shrub species represents a potential approach for increasing our understanding of the ecological differences between habitat-forming non-native versus native plants (Daehler 2003). Various non-natives are known to decrease local plant diversity (Gaertner et al. 2009; Hejda et al. 2009) through negative effects on functioning of resident ecosystems (Byers et al. 2002; Simberloff et al. 2003) and alteration of the rate of nutrient cycling (Ehrenfeld 2010). However, it is not yet clear how the ecological differences depend on soil properties, biotic relationships, and invaders themselves (Levine et al. 2003).

We compared patches formed by three planted non-native and two native shrubs, all growing in comparable human-modified environments in Finland, Northern Europe. Our goal was to assess whether there are differences in plant species composition or biomass between patches formed by non-native versus native shrubs. We hypothesized that altered resource availability (light and nutrients) is one of the key mechanisms explaining why invasions of shrubs alter the composition of the plant community. We expected non-native species to deplete the soil nutrient pools and to reduce the light penetrating through the canopy (shading) more effectively than native species. This was assumed to take place with the aid of greater investment in the growth and the shading leaves of non-native species. Different parts of the shoots (leaves, branches, and reproductive organs) are likely to contribute differently to shading, so a greater investment in shading leaves might reduce the availability of light under the canopy. Therefore, we focused on resource availability, and studied whether shrub indigenoussness (non-native or native) played a significant role in soil nutrient content or biomass allocation to leaves, branches, and reproductive organs of canopy-forming shrubs.

Methods

Study species

Our study system consisted of non-native shrubs that had been planted as decorative patches along roads (non-native species) and native shrub patches located in close vicinity to roads (native species). At least two of the native shrub patches originated from plantations, the rest had colonized the sites either as seeds or with earth moving (relocated soil may have included plant parts in addition to seeds). To avoid the issue of phylogenetic correlations, we selected for the study only members of the family Rosaceae. *Sorbaria sorbifolia* (L.) A. Braun (false spirea, $N = 12$), *Rosa rugosa* Thunb. (hedgerow rose, $N = 4$), and *Amelanchier spicata* (Lam.) K. Koch (dwarf serviceberry, $N = 4$) were non-native species. *Rubus idaeus* L. (raspberry, $N = 8$) and *Prunus padus* L. (bird cherry, $N = 4$) were selected as native reference species. *S. sorbifolia* and *R. rugosa* are native to temperate areas of East Asia including southern Siberia, and *A. spicata*

comes from North America. *R. rugosa* and *A. spicata* are considered to be problematic invasive species in Finland (Finland's National Strategy on Invasive Alien Species 2012) as they produce viable seeds and are able to disperse effectively and outcompete low-growing native vegetation (these characteristics fulfill the definition of invasiveness as stated in Pyšek et al. (2004). The seeds of *S. sorbifolia* do not disperse as efficiently but the plant is able to spread locally by forming belowground stolons and also by seeds, threatening indigenous flora (Finland's National Strategy on Invasive Alien Species 2012). In our study patches, *S. sorbifolia*, *R. rugosa*, and native *R. idaeus* were less than 2 m high and differ in their physiology from the taller (up to 3 m in our study patches) *A. spicata* and *P. padus*. Branches of *A. spicata* and a native equivalent *P. padus* formed a closed canopy higher above ground than the arching stems of the members of the first group.

Study sites

The study was conducted in South-western Finland, in close vicinity to three towns: Turku (60°27'05"N, 22°16'00"E), Paimio (12 km east of Turku; 60°27'25"N, 22°41'10"E), and Salo (50 km east of Turku; 60°23'10"N, 23°07'30"E). The study area is situated within the hemiboreal vegetation zone and consists of a mosaic of inhabited areas, forests, and agricultural fields along a main road that connects Scandinavia to Russia (European route E18). During 2 years 2010–2011, we monitored 22 (14 non-native and eight native), six (four non-native and two native), and four (two non-native and two native) patches in Turku (all shrub species), Paimio (all shrub species), and Salo (*S. sorbifolia* and *R. idaeus*) regions,

respectively. The sites of the *S. sorbifolia* patches were chosen along the road so that the distances between patches increased from west to east; in the study plan, distances from the first patch (situating northwest of Turku) to the other patches were ca. 500 m, 2, 5, 10, 25, and 50 km, measured along the road. This design was chosen to capture possible spatial variation within the region. We chose the *S. sorbifolia* stands that were closest to the preplanned spatial points and formed an obvious patch within lower-growing vegetation. The patches of the other shrub species were chosen as close to the *S. sorbifolia* patches as possible, using the same criteria (an obvious patch).

The average distance of the patches from the nearest road was 22.6 ± 9.2 m (mean \pm SE) and the average size of a patch was 25.4 ± 4.1 m (maximum length) and 5.5 ± 0.4 m (width at central part). For details consult Table 1. The distances between the patches varied from about 0.03 up to 12, 0.03–0.7 and 0.2–3.5 km within Turku, Paimio, and Salo regions, respectively. All patches represented a shrub 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 years old.

Soil properties and biomass allocation

Nutrients were extracted from two homogenized mixed samples per surface layer (0–5 cm) and per moderately deep soil layer (deeper soil, 5–25 cm), dug in each patch in September 2011. Both surface and deeper soils were examined because they may differ in chemical and structural composition and because plants may have differing responses or impacts on

Table 1 Basic characteristics of the patches selected for the study

	Indigenesness	Number of patches	Maximum length (m)	Width in central part (m)	Distance from the nearest road (m)
<i>Sorbaria sorbifolia</i>	Non-native	12	37.0 ± 9.3	4.9 ± 0.6	15.5 ± 5.3
<i>Rubus idaeus</i>	Native	8	14.4 ± 2.5	6.1 ± 1.0	52.6 ± 35.6
<i>Rosa rugosa</i>	Non-native	4	15.0 ± 2.9	4.5 ± 0.5	10.4 ± 4.2
<i>Prunus padus</i>	Native	4	10.4 ± 2.4	6.1 ± 1.1	14.8 ± 1.9
<i>Amelanchier spicata</i>	Non-native	4	37.8 ± 4.3	7.6 ± 1.8	4.1 ± 2.0

The figures present the mean value with standard errors. The patches resembled ellipses; the maximum length corresponds to the largest distance between antipodal points on the ellipse (transverse diameter) and the width in central part to the smallest distance across the ellipse (conjugate diameter)

the nutrient contents of top and deeper soils depending on plant species (Dassonville et al. 2008). Soil analysis was done in the laboratory of MTT Agrifood Research Finland, which is an accredited testing laboratory. As we were interested in the competition for resources, we determined soil nutrients primarily associated with plant growth (Fitter 1997); i.e., primary (nitrogen, phosphorus, and potassium) and secondary (calcium and magnesium) macronutrients, and pH which influences the availability of nutrients in the soil. For determination of phosphorus (P), calcium (Ca), magnesium (Mg), and potassium (K), air-dried soil samples were extracted with acidic ammonium acetate solution (pH 4.65, AAAC 1:10 for 1 h; Vuorinen and Mäkitie 1955). Concentrations of Ca, Mg, and K were measured using IRIS ICP-OES spectrometer (Thermo Jarrell Ash, USA) and P by auto-analyzer (Skalar, The Netherlands) using ammonium–molybdate complex. Organic carbon and total nitrogen contents were determined using a C–N-autoanalyzer (LECO CN-2000, Leco Corporation, USA). The pH was measured from soil–water suspension (1:2.5). Proportion of clay particles (<0.002 mm) was measured to estimate physical soil characteristics; particle size distribution of fine soil fragments was determined by the pipette method based on sedimentation (Elonen 1971).

To find out if the biomass allocation to different parts of the shoot differs between the non-native and native species, seven to ten (ten shoots in *R. rugosa* patches) plant shoots were arbitrarily selected from each patch. We measured biomass allocation into supportive vegetative parts (branches), leaves and reproductive organs (pooled flowers and fruits). The shoots were collected in July 2011 when reproductive organs matured in all species. Biomass was oven-dried at 80 °C and weighed. Data were further related to soil properties and indigenosity of the patch-forming shrub.

To compare the composition and species richness of herbaceous vegetation (low-growing herbs, grasses, and tree seedlings) in patches, we collected above-ground biomass from four 0.5 m × 0.5 m plots per each patch in August 2011. Plants were separated into species, oven-dried and weighed. The plots were situated at main cardinal directions (north, south, east, west), all within a 1-m wide edge zone inside the patch (similarly as the four inside plots schematically displayed for reference data in Fig. S1). Central parts of non-native patches had little or no vegetation. Comparisons based on the central parts of the patches

of non-native (no or very sparse herbaceous vegetation) and native (some vegetation) shrubs would therefore have yielded very obvious differences. Collection of vegetation data in the edge zones rather than central parts of the patches can be regarded as a conservative approach, and also allowed us to observe which plants are likely to tolerate the spread of these non-native shrubs better than others.

Light environment

In five *R. idaeus* and five *S. sorbifolia* patches photosynthetically active radiation (PAR; radiation within the wavelength range 400–700 nm) was repeatedly measured using quantum sensors (Delta-T Devices Ltd., UK) to see if the light availability below the shrubs differed and whether this depends on the phase of the growing season. The sensors were placed at six fixed positions within each patch: five at ground level inside a patch and one (control) above the patch canopy. PAR values were recorded at 5 min intervals between 9 a.m. and 2 p.m. using DL2e Data Logger (Delta-T Devices Ltd.). Measurements lasted 1 day in each patch and were carried out three times: in late May (21 May–31 May 2011), late June (21 June–30 June 2011), and late July/early August (19 July–2 August 2011). Sensors were always located at the same position within a patch. Prior to analysis, means were calculated for the 9 a.m.–2 p.m. period; and afterward, light reduction (%), based on ratio between PAR values measured inside of a patch and data from the control sensor, was derived. This approach allowed an estimation of the amount of light transmittance inside the patches as compared to levels above the vegetation.

To study the direct effect of light level reduction on plant composition inside shrub patches, data on cover (%) of each species and data on number of plant species present in 0.5 m × 0.5 m squares were recorded in spots where the sensors were placed. This survey was conducted in late June 2011.

Reference data

To test whether the results obtained from our intensively studied model system can be generalized across various species of similar growth form and occurring in human-modified habitats, we inspected herbaceous vegetation for species composition and plant species richness: (1) in addition 32 patches formed by the

study species used in our model system; (2) in 27 patches formed by other non-native species; (3) in addition native 21 shrubs (Table S1); all occurring in the study region. The shrubs belong to 24 species of Caprifoliaceae, Cornaceae, Rosaceae, and Salicaceae families. The sampling design was identical to the one used in our model system, except that we included comparable vegetation plots outside the patches to compare the vegetation inside the patches to the surrounding herbaceous vegetation. Detailed descriptions of sampling procedure and data processing are given in electronic supplementary material (Fig. S1).

Data analysis

Biomass allocation, absolute biomass values (log transformed), and percent allocations (arc-sin \sqrt{x} transformed biomass data on branches, leaves, and reproductive organs of the shrubs) were analyzed using linear mixed-effects models (LME) with the restriction likelihood estimation method (REML) to estimate the model parameters. The LME explicitly estimates the covariance at the different levels of a hierarchical structure. Percent allocation data were used because it could be expected that the magnitude of allocation is proportional to the productivity of the plant. Biomass allocation into branches, leaves, and reproductive organs were responses, and shrub indigenusness (non-native vs. native) and soil properties of the deeper soil layer were fixed factors. Patch ID nested within shrub species were considered as random variables. This model structure insured that an appropriate number of degrees of freedom (df) was used in parameter estimation. To control for spatial autocorrelations in data, the effect of geographical position on biomass allocation was tested using simple correlation (latitude, longitude) and ANOVA (when tested for differences between three town regions). The effect of geographical position on vegetation composition was tested using CCA (described below). Also patch size parameters (length and width) were used as covariates in the first LME and CCA models but were excluded from the final models as the effect of patch size was always non-significant (results not shown). Between-site comparisons in deeper soil properties (5–25 cm) were evaluated using ANOVA (with patches nested within shrub species and invasion status to account the hierarchical structure of data) and

a Tukey's post hoc comparison. Effects of shrub indigenusness (non-native vs. native) and deeper soil properties (a covariate) on surface soil properties (0–5 cm) were evaluated using analysis of covariance (ANCOVA).

The differences in the composition of herbaceous vegetation based on biomass data were analyzed using canonical correspondence analysis (CCA; ter Braak and Šmilauer 2002). Each patch was characterized with soil properties (eight continuous variables; listed in Table 2) and shrub indigenusness (non-native vs. native). The properties of both shallow (0–5 cm) and deeper soil (5–25 cm) layers were combined because nutrients in both layers may be important for the herbaceous vegetation. All these parameters were considered as environmental variables and were subjected to forward selection, mainly to see the sequence of contributions of individual variables. The amount of variability explained by individual variables was calculated by dividing corresponding eigenvalues by total inertia. A variable was included to the model if F value >1 . The significance of each variable was evaluated using Monte Carlo (MC) permutation (499 permutations). The four observations within a patch were averaged. Square-root transformation of the biomass data was applied in order to dampen out the effect of abundant species. Species richness (log transformed) and total biomass in the non-native and native patches were compared using ANOVA.

Variation in the light reduction data (averaged over patch) was evaluated using LME. We used month (May, June, and July), species identity (*S. sorbifolia* vs. *R. idaeus*) and month \times species identity interaction as fixed effects, and patch as a random effect to follow repeated observation scheme. Because data normality did not improve after transformations, P values and 95 % confidence intervals were calculated using Markov chain MC simulations in a library *languageR*. To assess the species–environment relationship, the effect of available light on plant cover data (square-root transformed) was evaluated using CCA with MC permutation (499). Light reduction level inside the patches was used as the only predictor and affiliation either to *S. sorbifolia* or to *R. idaeus* patch as a covariate, and vice versa. Spearman's rank correlation was used to test (1) the association between light transmission and the number of species present in the plot, and (2) the association between Simpson's

Table 2 Soil properties (mean \pm SE) of deeper soils in the patches of the five studied species (upper part of the table), and *F* values of analyses of variance for the effects of indigenouness, species and patch identity (patch ID nested within species and invasion status to account the hierarchical structure of data) on these soil properties

	N	pH	Clay (%)	Total N (%)	Ca ²⁺ (mg/l)	K ⁺ (mg/l)	Mg ²⁺ (mg/l)	PO ₄ ³⁻ (mg/l)	Total C (%)
Sorbaria	24	6.2 \pm 0.1 ^{ab}	27.7 \pm 3.2 ^a	0.16 \pm 0.01 ^a	1884.3 \pm 109.1 ^{ab}	195.3 \pm 17.6 ^a	318.0 \pm 43.4 ^a	12.6 \pm 2.0 ^a	2.9 \pm 0.3 ^a
Rosa	8	6.6 \pm 0.2 ^a	43.9 \pm 4.9 ^a	0.14 \pm 0.02 ^a	2601.5 \pm 602.1 ^a	270.5 \pm 20.6 ^{ab}	603.3 \pm 139.5 ^b	10.1 \pm 3.1 ^a	1.9 \pm 0.2 ^a
Amelanchier	8	6.2 \pm 0.2 ^{abc}	38.4 \pm 6.7 ^a	0.30 \pm 0.06 ^b	2278.3 \pm 282.1 ^a	197.7 \pm 24.4 ^{ab}	321.6 \pm 72.7 ^{abc}	11.8 \pm 1.8 ^a	5.4 \pm 1.2 ^b
Prunus	8	5.8 \pm 0.1 ^{bc}	21.6 \pm 5.2 ^a	0.23 \pm 0.03 ^{ab}	1482.8 \pm 164.3 ^{ab}	234.1 \pm 43.5 ^{ab}	173.7 \pm 24.6 ^{ac}	23.4 \pm 5.4 ^a	3.2 \pm 0.4 ^{ab}
Rubus	16	5.7 \pm 0.1 ^c	29.3 \pm 4.6 ^a	0.16 \pm 0.03 ^a	1184.9 \pm 142.2 ^b	306.1 \pm 46.0 ^b	251.7 \pm 51.3 ^{ac}	12.7 \pm 2.1 ^a	1.9 \pm 0.3 ^a
ANOVA									
Indigenouness		61.1***	15.4***	0.23 ^{n.s.}	24.5***	33.0***	15.8***	9.3**	21.1***
Shrub species		5.4**	18.4***	23.9***	3.1*	9.1***	8.6***	7.2***	36.4***
Patch		4.3***	13.9***	7.7***	2.2*	12.3***	4.2***	5.7***	10.2***

Different superscript letters indicate significant differences between species at $P < 0.05$ (Tukey's post hoc comparison)* $P < 0.05$, *** $P < 0.001$

reciprocal index of diversity (Magurran 1988) and the distance from the closest road to control the influence of disturbance caused by transport (e.g., increased water run-off around roads). Reciprocal Simpson's index is based on cover proportions of individual species composing a community—the value one refers to a community containing only one species; the higher the values, the greater the diversity. All statistical analyses except CCAs were performed in R v 2.15 (R Development Core Team 2013).

Results

Soil properties and biomass allocation

Patches grew in different soil conditions. Differences in the soil parameters were generally larger between than within shrub species (Table 2) but the range of parameter values overlapped. On average, patches of *R. idaeus* and *P. padus* appeared to have somewhat lower pH and level of calcium than the patches of other species, but the patch-level values overlapped (Table 2). Patches of the tallest shrubs, *A. spicata* and *P. padus* pooled, were associated with significantly higher levels of C than the patches of lower-growing species (*S. sorbifolia*, *R. rugosa*, and *R. idaeus* pooled) (ANOVA, df = 1,234, $F = 54.1$, $P < 0.001$). Besides high values of magnesium and calcium content in *R. rugosa* patches, the among-species differences did not form a consistent pattern (Table 2). When grouped as non-native or native, there appeared to be differences in the soil properties between the groups, except for N content (Table 2).

We also analyzed the potentially differing impacts of non-native and native plants on the properties of surface soil layer (0–5 cm) using the deeper soil layer properties (5–25 cm) as covariates. Values of pH (mean \pm SE = 6.35 \pm 0.09), Ca (in mg/l; 2,533.8 \pm 95.2), and total C (in %, 6.63 \pm 0.66) were higher in non-native than in native patches (pH: 5.95 \pm 0.10, total C: 3.92 \pm 0.40, Ca: 1,583.4 \pm 155.9) (Table 3). In contrast, K concentration (in mg/l) was higher in native (382.3 \pm 57.4) than in non-native (281.4 \pm 30.9) patches. However, the properties of the deeper soil layer explained a larger share of variation than the indigenouness of a shrub. The indigenouness of the habitat-forming shrub did not seem to play a role for N or P contents of the top soil. These results suggest that

plant indigenouness did not have a marked impact on the nutrient contents of top soils, with the possible exceptions of Ca and K concentrations as revealed by significant interaction of indigenouness \times deeper soil.

Geographical position of a patch (latitude and longitude) did not affect any analysis of biomass production or allocation (correlations between latitude/longitude and allocation data related to a patch were non-significant; $r \leq 0.20$). No difference in allocation between Turku, Paimio, and Salo regions was found (ANOVA, $P > 0.05$). Geographical position of a patch also did not play any role in species composition (CCA, $F = 2.02$, $P = 0.25$, 3.1 % of variance explained). Therefore, geographical position was disregarded in further analyses.

The indigenouness of the shrub (non-native vs. native) did not explain a significant amount of the variation in leaf biomass, biomass of branches and reproductive organs (Table 4) or allocation (relative values) to branches, leaves, and reproductive organs ($P > 0.05$). Biomass production was negatively related to the proportion of clay particles but positively related to K and Mg (Table 4). Allocation of biomass to branches was positively related to high levels of Mg in the soil; otherwise the inspected soil parameters were not related to the allocation of biomass to different above-ground parts (Table 4).

The environmental variables (soil properties and shrub indigenouness) explained 20.8 and 15.3 % of total variability in herbaceous species composition data considering soil properties from surface or deeper soil layers, respectively. Stepwise forward analysis revealed that pH and P contents in the surface soil layer were the most influential variables explaining plant composition. The next variable to enter the model was carbon contents followed by the indigenouness of the shrub (Table 5), however, their effects were not significant. Each of the variables included in the model explained less than 3 % of total variation (Table 5). Species richness was significantly lower in the non-native ($N = 20$, mean \pm SE = 7.0 ± 0.8) than in the native ($N = 12$, 8.9 ± 0.7) patches (ANOVA; $df = 1,30$, $F = 4.15$, $P = 0.050$). Identity of the shrub species was not significantly related with species richness (ANOVA; $df = 4,27$, $F = 1.63$, $P = 0.195$). Total biomass of ground layer vegetation was significantly lower in the non-native ($N = 20$, 4.5 ± 1.2) than in the native ($N = 12$, 19.7 ± 3.9) patches (ANOVA;

$df = 1,30$, $F = 20.39$, $P < 0.001$). The species diversity of plants in the understory (Simpson's reciprocal diversity index) did not correlate with the distance from the closest road (Spearman, $N = 32$, $\rho = 0.13$, $P = 0.49$).

Light environment

We did not observe any significant difference in light reduction between *S. sorbifolia* and *R. idaeus* patches (Fig. 1; LME, estimate [lower HPD (highest probability density); upper HPD] = -0.033 [-0.157 ; 0.075], $P = 0.57$). Light intensity was lower in June than in May because the growing leaves formed a closed canopy by the end of June (LME, -0.132 [-0.239 ; -0.010], $P = 0.031$). Unexpectedly, the corresponding difference between July and May was not significant (LME, -0.031 [-0.141 ; 0.074], $P = 0.60$). The month \times species identity interaction was not significant revealing that the light conditions within the patches of both shrub species varied similarly.

Patterns in plant composition were related to light reduction data as based on analysis of plant cover data (CCA, $F = 2.22$, $P = 0.0080$, 5.3 % of variance explained). A positive association with light appeared to be most evident in the forbs *Aegopodium podagraria*, *Anthriscus sylvestris*, *Taraxacum officinale*, *Fagopyrum convolvulus*, and *Galeopsis speciosa*. Plant communities also differed between *S. sorbifolia* and *R. idaeus* patches (CCA, $F = 1.61$, $P = 0.0240$, 3.9 % of variance explained) when keeping light reduction as a covariate. The amount of PAR recorded in a sensor correlated positively with the number of plant species around the sensor (Spearman, $N = 50$, $\rho = 0.36$, $P = 0.011$).

Reference data

The number of plant species, species diversity of plants, and the cover of mosses were significantly higher in the patches formed by native than non-native shrubs (Table S1, Fig. 2). In contrast, the amount of litter was higher in the patches of non-native shrubs. The amount of litter correlated negatively with the number of plant species ($r = -0.16$, $P < 0.0001$) and the cover of herbaceous plants ($r = -0.12$, $P = 0.002$). There was also a higher proportion of bare ground inside than outside the patches. The proportion of bare ground correlated negatively with

Table 3 Results of analysis of covariance (F values) for the effect of shrub indigenusness (non-native vs. native) on soil properties in surface layer (0–5 cm)

	DF	pH	Clay (%)	Total N (%)	Ca ²⁺ (mg/l)	K ⁺ (mg/l)	Mg ²⁺ (mg/l)	PO ₄ ³⁻ (mg/l)	Total C (%)
		F	F	F	F	F	F	F	F
Intercept	25	25,000.0***	381.5***	606.9***	1,087.4***	1,022.4***	280.8***	104.1***	279.6***
Indigenusness	3	24.1*	1.5	1.5	49.6**	23.9*	8.8	0.37	15.3*
Deeper soil	25	63.6***	177.7***	39.5***	24.6***	216.0***	185.3***	76.6***	23.3***
Indigenusness \times deeper soil	25	0.4	0.9	2.1	7.8**	5.8*	0.59	0.5	0.05

Corresponding value in the deeper soil layer served as a covariate. Species identity was used as a random effect in the analyses

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4 Results of linear mixed-effects models of log-transformed biomass and percent allocations into branches, leaves, and reproductive organs

	Branches (Log)		Leaves (Log)	Reproductive organs (Log)	Total (Log)	Branches (%)	Leaves (%)	Reproductive organs (%)
	DF	t value	t value	t value	t value	t value	t value	t value
(Intercept)	204	0.46	1.90	-0.12	1.42	0.58	3.53***	-0.65
Non-native versus native	1	-0.46	-0.13	0.88	-0.18	-0.98	0.24	0.49
Total N	19	-0.69	-1.03	-0.45	-0.95	0.00	0.14	0.05
pH	19	0.53	0.01	0.59	0.48	0.59	-1.33	1.12
Ca	19	-0.61	-0.34	-0.39	-0.63	-0.56	0.80	-0.47
K	19	1.23	2.13*	1.46	1.99	-0.55	-0.54	0.91
Mg	19	2.29*	1.77	0.68	1.88	2.65*	-0.89	-0.60
P	19	-0.45	-1.23	-1.35	-0.92	0.48	-0.01	-0.61
Clay	19	-1.01	-2.23*	-0.74	-1.54	-0.02	-0.79	0.51
Total C	19	0.99	1.18	1.12	1.36	0.02	-0.76	0.59

* $P < 0.05$, *** $P < 0.001$

the number of plant species ($r = -0.59$, $P < 0.001$) and the cover of herbaceous vegetation ($r = -0.59$, $P < 0.001$).

The patches of native and non-native shrubs differed in vegetation compositions (CCA analysis: $F = 2.53$, $P = 0.002$). Species richness was similar in the plots sampled outside the patches, but the composition of vegetation in the plots located inside the patches was related to the indigenusness of the patch-forming shrub (Fig. S2) since the non-native patches had, on average, 2.5 species per $0.5 \text{ m} \times 0.5 \text{ m}$, while the corresponding figure for native patches was 3.5 species (Fig. 2).

Compositional dissimilarities expressed as Euclidean distance were apparently similar in patches of non-native and native shrubs (LME, $P > 0.05$), possibly because of high variation in the values among shrub

species (ANOVA, $df = 23,296$, $F = 3.33$, $P < 0.001$; Table S2). Compositional dissimilarities between family Rosaceae ($N = 55$ patches) and other plant families ($N = 25$) did not differ (LME; $df = 22, 240$, $t = 0.99$, $P = 0.34$) uncovering no family-identity effect. Reduction in species richness (expressed as the percentage reduction of the total number of species recorded inside vs. outside of a patch) correlated positively with dissimilarity between inside and outside (control) plots in both non-native and native shrubs (Fig. S3).

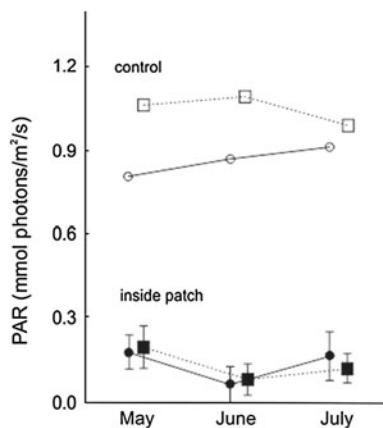
Discussion

Plant species richness and the biomass of herbaceous vegetation were lower in patches formed by non-

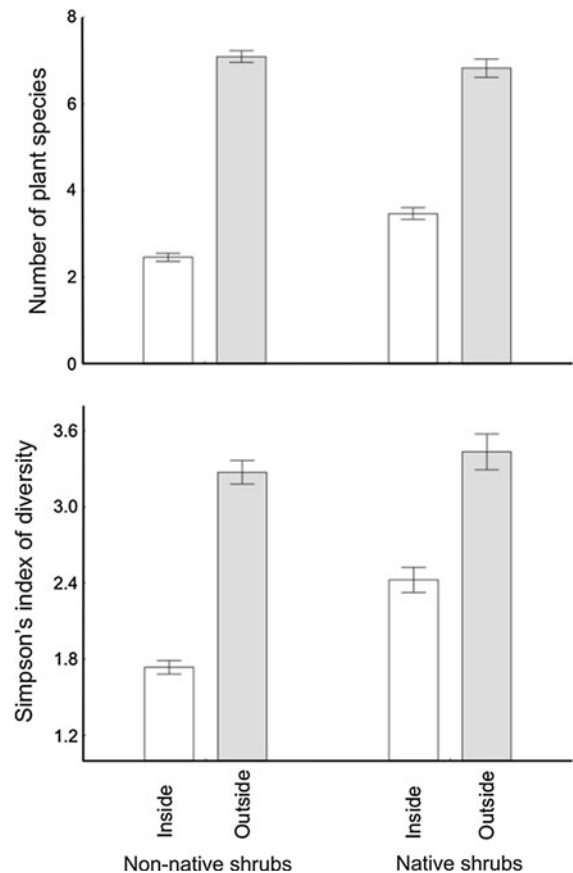
Table 5 Comparisons of the effects of indigenusness (non-native vs. native) and soil properties of two soil layers on plant community composition, based on CCA with forward selection

	F	P	Explained variability (%)
Surface soil layer (0–5 cm)			
All included explained 20.8 %			
pH	1.55	0.022	3.0
P	1.49	0.044	2.9
C (%)	1.21	0.152	2.4
Non-native versus native	1.08	0.290	2.1
Mg	1.46	0.088	2.7
Clay (%)	1.11	0.310	2.1
Deeper soil layer (5–25 cm)			
All included explained 15.3 %			
pH	1.38	0.056	2.2
C (%)	1.19	0.236	1.8
Non-native versus native	1.14	0.228	1.8
Mg	1.11	0.314	1.7

The order of variables corresponds to the order in which stepwise selection included the environmental variables into the model. Note that all the variables listed were included in a model based on a F value >1

**Fig. 1** Light conditions at ground level inside the patch compared with above the patch (control) from May to July 2011. No difference in light reduction between *S. sorbifolia* (squares, dotted line) and *R. idaeus* patches (circles, full line) was observed. Mean values (circles) and 0.95 confidence intervals (whiskers) are displayed

native than native species. This pattern was evident both in the intensively studied model system and in our reference data. Also several previous studies have reported the species richness of plants to be low below

**Fig. 2** The number of species and Simpson's reciprocal index of diversity inside and outside patches of non-native and native shrubs. The differences between non-native and native shrubs were statistically significant in both parameters ($P < 0.001$; Table S1). Bars refer to means and whiskers to standard error of mean

non-native shrubs or trees (Woods 1993; Holmes and Cowling 1997; Collier et al. 2002; Reinhart et al. 2005). Although our results indicate that the indigenusness of patch-forming vegetation may be an ecologically influential factor, we did not find evidence for the hypothesis that non-native species would be better resource competitors than structurally similar native species (Fogarty and Facelli 1999, Seabloom et al. 2006). Two findings, the positive correlation between the amount of radiation and the species richness of herbaceous plants and the fact that non-native patches hosted less species than native ones, suggest that light availability may have played a role during the colonization process and contributed to the obtained difference between patches formed by non-native versus native shrubs. However, non-native and

native shrubs allocated their biomass to shading leaves, branches, and reproductive organs in a comparable way. Also the quantity of PAR at the ground level appeared to be comparable within the patches formed by an alien (*S. sorbifolia*) and a native (*R. idaeus*) shrub species. These results suggest that light competition is not a sufficient explanation for the negative effects of non-native shrubs on plant communities. Soil nutrient contents differed among patches, but the differences in soil properties between patches formed by non-native versus native shrubs were small and did not explain why non-native species had a stronger negative effect on species richness of herbaceous plants than native species. Analyses of nutrients in the top soil suggest that indigenoussness of the habitat-forming shrub played a minor role in soil nutrient availability, but had no obvious impact on the levels of main nutrients nitrogen and phosphorus. In conclusion, our results suggest that reduced availability of resources (light and nutrients) is not a sufficient explanation for the impoverished plant community in patches formed by non-native plants.

The cover of litter was higher below non-native than native shrubs, although we did not find marked differences in the biomass production or allocation to different parts of the shoot. This suggests differences in decomposition rates below non-native and native shrubs. The factors that control decomposition rates of plant litter and thus soil mineralization processes are temperature, precipitation, soil fauna, and chemical composition (Prescott 2005). It is possible that reduced herbaceous cover under non-native shrubs may have reduced humidity at the surface of the soil and thereby retarded the decomposition of leaves. Yet, given the fact that patches of native and non-native shrubs experienced the same climate and the shrubs formed a closed canopy above the patch, soil fauna and the chemical composition of litter are more likely responsible for apparent differences in decomposition rates in our study system. Decomposition by fauna has been reported to be higher in native than in alien systems (Alonso et al. 2010; Castro-Díez et al. 2009, 2012) because the introduction of non-natives may alter the quality/quantity of litter entering the soils or alter the physical-chemical site properties below their canopy (Castro-Díez et al. 2012). Another factor contributing to high accumulation of litter might be toxic chemical compounds in the non-native plants; for instance, the leaves and flowers of *S. sorbifolia*

contain high levels of toxic hydrogen cyanide (Kim and Zee 2000).

Although the amount of litter correlated negatively with the number of plant species and the biomass of herbaceous vegetation, it is unlikely that high amount of litter would explain differences in the number of plant species between patches formed by non-native and native shrubs. Also the proportion of bare ground was relatively high below the shrubs, which indicates that a lack of bare ground was not an important constraint for plant colonization below the shrubs. In contrast, also the proportion of bare ground correlated negatively with the species number of plants and the biomass of herbs and grasses.

Reduction of species richness increased compositional difference (Fig. S3) between inside (shrub patch) and outside (control) environments and signifies that the impact on species richness is correlated with species composition. Only a limited number of species prosper in a given environment. Shrub invasion can lead to a major change in the environment that may cause a simultaneous reduction in the species richness and a rise in the compositional difference (Hejda et al. 2009; Santoro et al. 2012). This pattern was not associated with the indigenoussness of the invading shrub as a positive relationship was detected in patches formed by both non-native and native shrubs, suggesting that the mechanism is the same independent of the indigenoussness of the species.

The invasion of shading shrubs and trees may facilitate the colonization of shade-tolerant plants for example by reducing competition with herbaceous vegetation, providing a moist microclimate or protecting seedlings from disturbances (Callaway 1995; Holmgren et al. 2012). Although we noted that some shade-tolerant plants had slightly higher coverage inside than outside patches (e.g., the grass *Milium effusum* and the herbs *Geum urbanum*, *Galeopsis tetrahit*, *Anthriscus sylvestris*, and *Urtica dioica*), facilitation effects (Bruno et al. 2003) were not strong enough to compensate for the general decline in the species richness, cover and biomass of herbaceous vegetation within the shrub patches. A lower species richness and vegetation cover below non-native than native shrubs indicates that possible facilitation effects played a smaller role below non-native than native shrubs.

A comparison of plant communities in old shrub patches gives a good insight of the consequences of the

invasion of non-native versus native shrubs but leaves some uncertainty due to possible differences in the community prior to invasion. In the present study, native patches were selected to be in close vicinity of the non-native patches and with environmental conditions matching as closely as possible. We compared the vegetation inside the patches to the vegetation outside the patch, which should minimize possible bias due to differing local conditions. The colonization of the patches formed by planted shrubs may be slower, if the planting is associated with transfer of soils or a short-term use of mulch to reduce the growth of competing weeds. However, all patches appeared to be at least 15 years old and were surrounded by a comparable plant community. Differences in soil parameters between the non-native and native patches were small. Calcium content and pH differed slightly (more calcium and higher pH below shrubs of non-native than native species) but the levels of main nutrients, nitrogen and phosphorus, were comparable. In addition, at least two of the native *R. idaeus* patches appeared to originate from planted individuals. This suggests that the differences observed in this study cannot be explained solely by colonization limitation or the planting history. Therefore, we assume that our data give a credible picture of the main differences between non-native versus native shrub environments.

To conclude, we observed a lower number of plant species and a lower biomass of herbaceous vegetation in the patches formed by non-native species than those formed by comparable native species. This suggests that the indigenosity of the patch-forming plant may be an ecologically important factor. An invasion of a habitat-forming plant is likely to alter the availability of resources (Liao et al. 2008; Dassonville et al. 2008; Meisner et al. 2012). But, our results suggest that availability of resources (nutrient and light) is not a sufficient explanation for the negative effects of non-native shrubs on plant communities. This draws attention to the alternative explanations, such as allelopathy and changes in the associated community. The toxins produced by non-native plants may differ from those present in the native community. Assuming that native organisms have not been adapted to many of the toxic substances produced by non-native plants, the “novelty” of the chemical substances produced by non-native plants might explain the differing impacts of non-native and native plants on plant diversity and composition. Further

research is needed to investigate whether the alternative hypotheses can explain the differing impact of non-native and native shrubs on the diversity and composition of associated plant assemblages.

Acknowledgments We thank S. Härkönen and M. Willberg for assistance in the field work. The study was supported by the Academy of Finland.

References

- Alonso A, González-Muñoz N, Castro-Díez P (2010) Comparison of leaf decomposition and macroinvertebrate colonization between exotic and native trees in a freshwater ecosystem. *Ecol Res* 25:647–653
- Brudvig LA, Evans CV (2006) Competitive effects of native and exotic shrubs on *Quercus alba* seedlings. *Northeast Nat* 13:259–268
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion facilitation into ecological theory. *Trends Ecol Evol* 18:119–125
- Bucharová A, van Kleunen M (2009) Introduction history and species characteristics partly explain naturalization success of North American woody species. *J Ecol* 97:230–238
- Byers JE, Reichard S, Smith CS et al (2002) Directing research to reduce the impacts of nonindigenous species. *Conserv Biol* 16:630–640
- Callaway RM (1995) Positive interactions among plants. *Bot Rev* 61:306–349
- Castro-Díez P, González-Muñoz N, Alonso A et al (2009) Effects of exotic invasive trees on nitrogen cycling: a case study in central Spain. *Biol Invasions* 11:1973–1986
- Castro-Díez P, Fierro-Brynnenmeister N, González-Muñoz N, Gallardo A (2012) Effects of exotic and native tree leaf litter on soil properties of two contrasting sites in the Iberian Peninsula. *Plant Soil* 350:179–191
- Cincotta CL, Adams JM, Holzapfel C (2009) Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). *Biol Invasions* 11:379–388
- Collier MH, Vankat JL, Hughes MR (2002) Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *Am Midl Nat* 147:60–71
- Daehler CC (2003) Performance’s comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annu Rev Ecol Evol Syst* 34:183–211
- Dassonville N, Vanderhoeven S, Vanparys V et al (2008) Impacts of alien plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* 157:131–140
- Davis MA, Chew MK, Hobbs RJ et al (2011) Don’t judge species on their origins. *Nature* 474:153–154
- Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annu Rev Ecol Evol Syst* 41:59–80
- Eldridge DJ, Bowker MA, Maestre FT et al (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol Lett* 14:709–722

- Elonen P (1971) Particle size analysis of soil. *Acta Agric Fennica* 122:1–222
- Feng YL, Fu GL (2008) Nitrogen allocation, partitioning and use efficiency in three invasive plant species in comparison with their native congeners. *Biol Invasions* 10:891–902
- Finland's National Strategy on Invasive Alien Species (2012) Ministry of Agriculture and Forestry in Finland, Helsinki. http://www.mmm.fi/en/index/frontpage/natural_resources/invasive_alien_species.html. Accessed 6 March 2013
- Fitter A (1997) Nutrient acquisition. In: Crawley MJ (ed) *Plant ecology*. Blackwell, Oxford, pp 51–72
- Fogarty G, Facelli JM (1999) Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. *Plant Ecol* 144:27–35
- Gaertner M, Breeyen AD, Hui C, Richardson DM (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progr Phys Geogr* 33:319–338
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J Ecol* 97:393–403
- Holmes PM, Cowling RM (1997) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African Fynbos shrublands. *J Appl Ecol* 34:317–332
- Holmgren M, Gomez-Aparicio L, Quero JL, Valladares F (2012) Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. *Oecologia* 169:293–305
- Kim DK, Zee OP (2000) A new cyanogenic glycoside from *Sorbaria sorbifolia* var. *stepilla*. *Chem Pharm Bull* 48:1766–1767
- Levine JM, Vila M, D'Antonio CM et al (2003) Mechanisms underlying the impacts of exotic plant invasions. *Philos Trans R Soc B* 270:775–781
- Liao C, Peng R, Luo Y et al (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol* 177:706–714
- Magurran AE (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton
- Manchester SJ, Bullock JM (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. *J Appl Ecol* 37:845–864
- Meisner A, de Boer W, Cornelissen JHC, van der Putten WH (2012) Reciprocal effects of litter from exotic and congeneric native plant species via soil nutrients. *PLoS ONE* 7:e31596
- Prescott CE (2005) Do rates of litter decomposition tell us anything we really need to know? *For Ecol Manag* 220:66–74
- Pyšek P, Richardson DM, Rejmánek M et al (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53:131–143
- Reinhart KO, Greene E, Callaway RM (2005) Effects of *Acer platanoides* invasion on understory plant communities and tree regeneration in the northern Rocky Mountains. *Eco-geography* 28:573–582
- Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive species: a global review. *Divers Distrib* 17:788–809
- Santoro R, Carboni M, Carranza ML, Acosta ATR (2012) Focal species diversity patterns can provide diagnostic information on plant invasions. *J Nat Conserv* 20:85–91
- Seabloom EW, Williams JW, Slayback D et al (2006) Human impacts, plant invasion, and imperiled plant species in California. *Ecol Appl* 16:1338–1350
- Simberloff D, Relva MA, Nuñez M (2003) Introduced species and management of a *Nothofagus/Austrocedrus* forest. *Environ Manag* 31:263–275
- Stohlgren TJ, Pyšek P, Kartesz J et al (2011) Widespread plant species: natives versus aliens in our changing world. *Biol Invasions* 13:1931–1944
- R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 6 March 2013
- ter Braak CJF, Šmilauer P (2002) *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. Micro-computer Power, Ithaca
- van Kleunen M, Dawson W, Dostál P (2011) Research on invasive plant traits tells us a lot. *Trends Ecol Evol* 24:317
- Vilá M, Espinar JL, Hejda M et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708
- Vuorinen J, Mäkitie O (1955) The method of soil testing in use in Finland. *Agrogeol Publ* 63:1–44
- Wilson JR, Dormontt EE, Prentis PJ et al (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol Evol* 24:136–144
- Woods KD (1993) Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in 4 New-England forests. *Am Midl Nat* 130:62–74