

The distribution of a non-native (*Rosa multiflora*) and native (*Kalmia latifolia*) shrub in mature closed-canopy forests across soil fertility gradients

Cynthia D. Huebner · Jim Steinman ·
Todd F. Hutchinson · Todd E. Ristau ·
Alejandro A. Royo

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Abstract

Background and aims A soil fertility gradient, ranging from infertile to highly fertile soils, may define whether or not a plant will establish and spread at a site. We evaluated whether or not such a fertility gradient exists for *Rosa multiflora* Thunb., a nonnative invasive shrub, and *Kalmia latifolia* L., a native problem shrub, in closed-canopy forests of the eastern U.S.

Methods We sampled soil and vegetation at the regional scale, along four randomly located 1-km transects in 70+ year-old undisturbed forests in each of three national forests in Ohio, Pennsylvania and West Virginia. We

also sampled soil, vegetation and leaf tissue at the local scale, from ten individual shrubs of each species in each national forest.

Results Regional analyses showed a significant fertility gradient with Ohio being the most fertile and West Virginia the least. Soil fertility was associated with pH (most acidic in West Virginia and least acidic in Ohio) and elevation (highest in West Virginia and lowest in Ohio). At the local level, *R. multiflora* was associated with soil Ca:Al ratios greater than 0.5, and *K. latifolia* was associated with Ca:Al ratios less than 0.3. *Rosa multiflora* foliage contained higher concentrations of Ca, Mg, and K than *K. latifolia*, while *K. latifolia* foliage contained higher concentrations of Mn and Zn.

Conclusions Our research documents the importance of soil fertility as a predictor of the establishment of invasive and expansive shrubs. This study further shows that *R. multiflora* can establish and spread across a broader range of soil conditions than *K. latifolia*.

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C. D. Huebner (✉)
Northern Research Station, USDA Forest Service,
180 Canfield St., Morgantown, WV 26505, USA
e-mail: chuebner@fs.fed.us

C. D. Huebner
e-mail: cindy.huebner@gmail.com

J. Steinman
State and Private Forestry, USDA Forest Service,
11 Campus Blvd. Ste 200, Newtown Square, PA 19073, USA

T. F. Hutchinson
Northern Research Station, USDA Forest Service,
359 Main Rd, Delaware, OH 43015, USA

T. E. Ristau · A. A. Royo
Northern Research Station, USDA Forest Service,
P.O. Box 267, Irvine, PA 16329, USA

Keywords Invasive nonnative plant · Expansive native plant · *Kalmia latifolia* · *Rosa multiflora* · Soil fertility gradient

Abbreviations

FIA Forest inventory and analysis
ICP-AES Inductively coupled plasma atomic emission spectroscopy
NMS Nonmetric multidimensional scaling
UTM Universal transverse mercator coordinate system

Introduction

Soils provide individual plants with essential macro- and micronutrients, but at lower pH, higher availability of Al (Foy et al. 1978) can cause toxic effects in plants such as inhibiting cell division, membrane transport, energy transfer, and nutrient uptake, especially Ca and Mg (Cronan and Grigal 1995). Infertile soils often are characterized by low pH (high availability of H⁺ and Al) and Ca and Mg deficiencies (Wolt 1990). While not universally accepted as a measure of soil fertility, a Ca:Al molar ratio below 1 indicates a threshold point, or endpoint, at which forest ecosystems are at risk of being incapable of sustaining a productive forest (Cronan and Grigal 1995; Schoenholtz et al. 2000). Soil fertility may be best estimated by directly measuring total N, and extractable K, Ca, and Mg. (Schoenholtz et al. 2000). C:N ratios are also used as an estimate of soil fertility, with high levels representing less fertile soils, possibly because C suppresses nitrification (Miegroet et al. 1990). Heilman (1974) found that forest soils with C:N ratios > 27 produced low levels of nitrate.

Soil fertility helps define plant richness and plant community composition (Marage and Gégout 2009). Also, plant species richness has been shown to decrease with decreasing soil pH (Gilbert and Lechowicz 2005), at least between pH 2.5 and 4.7 (Peppler-Lisbach and Kleyer 2009). Conversely, plants have been successfully used as bio-indicators of soil quality (Horsley et al. 2008) and nutrient content, with plants predicting exchangeable Ca amounts and the Ca:Al molar ratios (Gégout et al. 2003). Ellenberg soil indicator values (based on vascular plant species of Central Europe) for soil quality show that many plant species tolerate a relatively wide range of pH values and, thus, are not good predictors of soil pH. However, this indicator can predict soil quality in terms of summer soil moisture content and exchangeable calcium (Schaffers and Sýkora 2000).

In addition to parent material (Hamilton et al. 1978; Bockheim 1980; Kronberg and Nesbitt 1981), soil age, and glaciation (Kronberg and Nesbitt 1981), soil fertility has been shown to be correlated with several topographic variables, including elevation. Soils with higher temperature, greater levels of moisture and organic matter and better litter quality tend also to have abundant and active microbial activity (Vitousek 1982; Drury et al. 1991; Bonito et al. 2003; Unger et al.

2010). Because of higher temperatures and higher soil moisture, soil N mineralization rates tend to increase with decreasing elevation. However, faster rates of soil N mineralization have been found at higher elevations in some sites (e.g., the southern Appalachian Mountains) most likely due to corresponding high levels of organic matter and vegetation with higher litter quality (Garten 2004; Knoepp and Swank 1998; Bonito et al. 2003).

Kalmia latifolia L. is a native evergreen shrub or small tree, reaching heights of 3 m, possibly up to 10 m (Gleason and Cronquist 1993). It is typically associated with warm, dry exposed upslope sites of eastern U.S. forests (Monk et al. 1985; Lipscomb and Nilsen 1990; Chastain and Townsend 2008) and, like many ericaceous species, it is more abundant on acidic soils (Damman 1971; Bloom and Mallik 2004). In sites that have been overtaken by *K. latifolia*, it may not be possible to determine if this association with acidic soils is evidence of preference for such soils or a result of *K. latifolia*'s expansion or both. The terms 'expansive' and 'interfering' are used in place of the term 'invasive' because *K. latifolia* is native and not a new entity to the areas it is dominating. *Kalmia latifolia* can become expansive (Richardson et al. 2000; Pyšek et al. 2004) and interfere with tree regeneration (Kaeser et al. 2008), especially after a disturbance such as a gypsy moth defoliation event (Chastain and Townsend 2008), a timber harvest (Moroni et al. 2009), fire suppression (Brose and Waldrop 2010), or increasing soil acidity via acid deposition (Bailey et al. 2005). *Kalmia latifolia*'s slowly decomposing evergreen leaves may also serve to sequester N and P in soils (McGinty 1972; Thomas and Grigal 1976). However, the release of phenolic acid associated with ericaceous species may inhibit N mineralization rates (Bloom and Mallik 2006). This inhibition of N mineralization may exert top-down control of local nutrient cycling (Ehrenfeld et al. 2005), enabling *K. latifolia* to become dominant over other plant species not adapted to conditions associated with acidic soils, one condition of which may be lower soil fertility. Other native plant species may be negatively affected because of their inability to compete for light once *K. latifolia* becomes dominant. In addition, *K. latifolia* may out-compete other species because of direct soil Al toxicity (Beier et al. 2005) resulting from this species' association with acidic soils (Dietzel and Rao 2009). Chelating phenols may serve to detoxify Al, enabling species high in polyphenols to colonize acidic sites (Northup et al.

1995). Thus, *K. latifolia* may facilitate its own establishment and expansion by perpetuating stressful soil conditions. The slow decomposition of plant tissue high in plant polyphenols creates a mor-type humus that sequesters some nutrients, such as Ca and Mg, providing a medium for root growth (Northup et al. 1998). *Kalmia latifolia* may also expand by utilizing heavy metals in existing acidic soils such that their leaf tissue becomes less susceptible to herbivory (Rascio and Navari-Izzo 2011). Essential micronutrients, such as Fe, Mn, and Zn, may act as heavy metals once they reach toxic levels (Marschner 1995).

Rosa multiflora Thunb. is a nonnative invasive shrub originating from Asia with possible preferences for mesic soils (Huebner and Tobin 2006) high in nutrients or with low C:N ratios (Greenberg et al. 1997; Lungren et al. 2004; McDonald et al. 2008). This species has been present in the U.S. since approximately 1886 and was extensively planted in the 1930s on agricultural lands to function as a ‘living fence’ or hedgerow, soil stabilizer and a source of food for wildlife (Dugan 1960; Derr 1992). While *R. multiflora* appears to be most often associated with disturbed sites such as old fields or pastures and roadsides, it is commonly found in closed canopy forests too, perhaps in response to pre-existing canopy gaps (Huebner 2003). *Rosa multiflora*’s growth and reproduction does appear to be limited by low light levels associated with closed-canopy forests (Banasiak and Meiners 2009), but it can persist under closed canopy conditions (Huebner 2003; Huebner and Tobin 2006). *Rosa multiflora* grows more rapidly than associated native species in response to experimental increases in soil fertility (Gurevitch et al. 2008), possibly giving it a competitive advantage. Leaves of *R. multiflora* may decompose relatively rapidly (Ashton et al. 2005). Thus, *R. multiflora* may perpetuate its own establishment and spread by increasing soil nutrient concentrations.

According to data from FIA (a national systematic inventory of the woody species of the U.S. with plots located every 2,400 ha), *R. multiflora* and *K. latifolia* have a distinct distribution pattern across Ohio, West Virginia and Pennsylvania, with *R. multiflora* more abundant in Ohio and *K. latifolia* more abundant in West Virginia and Pennsylvania (Fig. 1a and b).

We address the following questions: (1) does *R. multiflora* occur more commonly in high fertility soil and *K. latifolia* in low fertility soil? How do these plant-soil relationships correlate with any regional and local

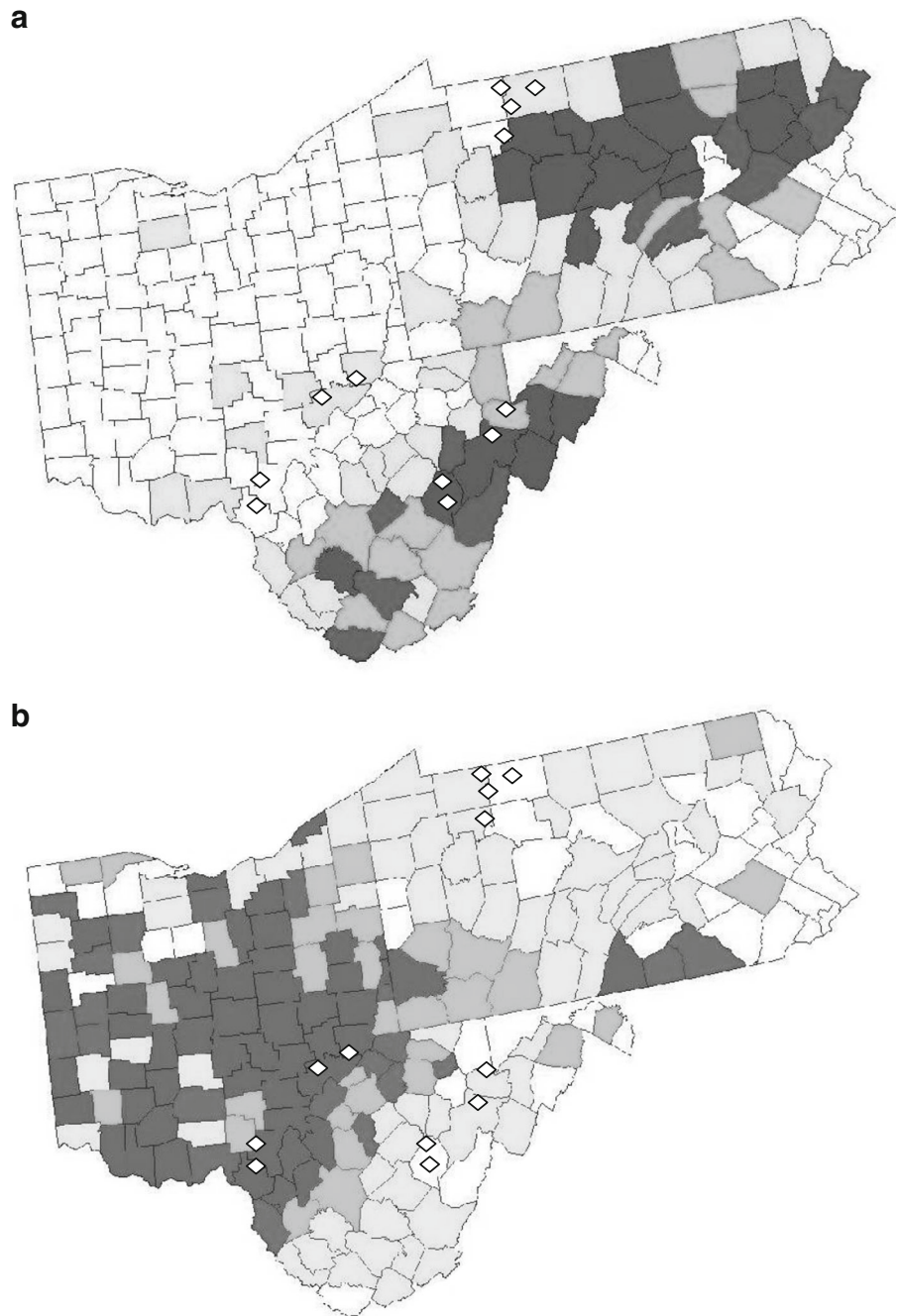
topographic differences and indicator plants? (2) How do leaf tissue nutrients of *R. multiflora* and *K. latifolia* compare with each other and correspond with soil nutrients associated with each respective species across a soil fertility gradient?

Materials and methods

Study area

Sites are located within undisturbed forests at least 70 years in age within the Wayne (OH), Allegheny (PA), and Monongahela (WV) National Forests. The entire study area falls within the Appalachian Plateau province, including the unglaciated Allegheny Plateau in OH, the unglaciated Allegheny High Plateau in PA and the Allegheny Mountain section in WV (also unglaciated). Elevations in OH range between 170 and 300 m (Sutherland et al. 2003; NOAA 2008), in PA 320–680 m (Kaeser et al. 2008; NOAA 2008), and in WV 460–1620 m (Clarkson 1966; NOAA 2008). Average annual precipitation for OH, PA, and WV is approximately 110 cm, 118 cm, and 125 cm, respectively (NOAA 2008). The soils of the OH Allegheny Plateau are underlain primarily by acidic sandstones, shales, and coals, but scattered bands of limestone are also found (King 1979). The OH soils are primarily silt loams of colluvial and residual origin, with relatively low pH and nutrient availability, but with increased pH and nutrient availability in the limestone bands (Boerner et al. 2003). The soils of the Allegheny High Plateau in PA are acidic and infertile, and developed from residuum derived from sandstone and shale. The soils have relatively low cation exchange capacity due to the presence of kaolinite, a dominant clay mineral in the soil (Bailey et al. 2005). Some soils within these PA sites are derived from limestone and chert (Abrams and Ruffner 1995). The soils of the Allegheny Mountain section in WV mountains and high-elevation valleys are capped with sandstone and shale; side slopes are composed of sandstone, shale, limestone, and siltstone (Pyle et al. 1982), with sandstone and siltstone prevailing (Core 1966). WV soils in our study are primarily acidic (Clarkson 1966; Adams and Angradi 1996; Boerner and Sutherland 1997). While all soils are unglaciated, there is a variety of possible parent materials, and, consequently, soil ages, within each national forest that may help define soil fertility values.

Fig. 1 Distribution of **a** *Kalmia latifolia* and **b** *Rosa multiflora* using FIA data (includes forests of all ages). *White* represents 0 % cover of the species, *light grey* <5 %, *medium grey* 5–10 % cover, and *dark grey* >10 % cover averaged across all sampled FIA plots. *Diamonds* represent the approximate location of each regional 1-km transect



Study design

Regional scale environmental factors and shrub composition

This study was conducted from June - August 2007 and 2008. In 2007, we randomly located four 1-km transects within forests 70 years or older in each of the three

national forests resulting in 12 transects. Along each transect ten circular 100-m² plots were located every 100 m; any evident canopy gaps were not included in the 100 m (requiring that this area of the transect be excluded from the transect, thus extending the overall transect length) in order to control for any confounding effects of disturbance (Fig. 1a and b). All transects ran from west to east. Four circular 10-m² subplots were

nested within each of the 100-m² plots at each cardinal direction with the center of the 10-m² subplot located at a distance of 3.86 m from the center of the 100-m² plot. We estimated cover of all shrub species in each 10-m² subplot and calculated relative importance values. Plant nomenclature follows the International Integrated Taxonomic Information System (ITIS 2012). Four samples of the upper B horizon (to maintain consistency since depth of A horizon varied across the region) were taken from each cardinal direction just outside the 10-m² subplots and were combined for each 100-m² plot. Data obtained from soils included pH (in distilled water), total C and total N (both %, using combustion at 1,350 °C with a LECO CN 2000), Ca, K, Mg, P, Fe, Mn, and Zn (mg/kg or ppm, all measured using ICP-AES; Analytical Lab, University of Maine). Elevation (from the topographic maps), slope inclination (using a Suunto clinometer), aspect (linearized using $\text{SINE}(\circ - 135) + 1$ (Huebner and Vankat 2003), where ° is the slope aspect in degrees, with larger numbers representing drier slopes), and canopy cover (average of four spherical densiometer readings, taken in each cardinal direction, subtracted from 100 %) were collected at the center of each 100-m² plot.

Local scale environmental factors associated with K. latifolia and R. multiflora

In 2008, ten plots per national forest and species were established using *K. latifolia* and *R. multiflora* (shrubs being at least 2 m in diameter) as the focal center of each plot. Focal species were at least 25 m apart to ensure independent samples. Shrubs were randomly selected from existing historic and recent shrub location data of botanists within each state and fuzzed location information from FIA data for some sites in PA. These plots were located within 70+ year old forests and openings and other disturbances were avoided. UTM coordinates of each shrub can be provided upon request. No selected shrubs were part of a large, spreading population with individuals of the same focal species at least 10 m from another individual of either species.

Eight B-horizon soil samples (four from under the shrub canopy and four 2 m away from the shrub canopy edge) were collected and mixed from each of the 60 shrub plots. Soils were analyzed for the same components as soils from the regional-scale transects. Topographic and canopy cover data were collected at

each shrub. Ten leaves from each shrub were collected, with two from each general cardinal direction and two located centrally within the crown, for nutrient analysis. Nutrients measured in plant tissue included: total N and C (both %, using combustion at 1,350 °C with a LECO CN2000), Ca, K, Mg, P, Fe, Mn, and Zn (mg/kg or ppm, all measured using ICP-AES; Analytical Lab, University of Maine). Tissue analyses data were collected to relate measured soil nutrient availability with plant nutrient uptake and storage. We sampled eight 1-m² plots, four under and four within 2 m of each shrub canopy edge, in which we estimated cover for each herbaceous, shrub, and vine species and cover and density for each tree seedling, for possible indicator species associated with *K. latifolia* and *R. multiflora*, respectively.

Analyses

The soil and plant nutrient data and topographic data were continuous response variables (fixed effects), each of which was analyzed separately using plots (a random effect for regional data) nested in both transect and national forest, and species and national forest (both random effects for the local data), including the species and national forest interaction using a generalized linear mixed model (Proc Glimmix, SAS v. 9.3). For the regional data, all the topographic variables, canopy opening, pH, K, P, Mg, Al, and Zn were best fit (best AIC values and lowest dispersion) with a normal distribution and identity link function, while total N, total C, C:N ratio, Ca, and Mn were best fit with a lognormal distribution and log link function. Ca:Al ratio was best fit with a lognormal distribution and an identity link function, while soil Fe was best fit with a gamma distribution and log link function. For the local data, all topographic variables, canopy opening, and soil variables were best fit with a lognormal distribution and identity link function, except for soil Ca, soil Mg, soil Al, and soil Mn, which were best fit using a lognormal distribution and log identity function. Also at the local level, all plant nutrient variables were best fit using a lognormal distribution and identity link function. All means were compared using the Tukey's multiple-comparison test. Although mixed model analysis (Proc Mixed) on transformed data gave similar results, use of traditional linear methods is considered inappropriate when data do not meet the normality and constant variance assumptions (SAS/STAT 9.3 2010). Hence,

we elected to use the more conservative generalized linear mixed models. The understory species composition data collected in 1-m² quadrats associated with individual *K. latifolia* and *R. multiflora* shrubs, were analyzed using NMS with a relative Sørensen distance measure and 500 iterations. Indicator species were determined for *K. latifolia* and *R. multiflora*, after Dufrêne and Legendre (1997), using the species tallied in each of the plots associated with *K. latifolia* and *R. multiflora*, respectively as a priori groups. This method calculates the proportional abundance and frequency of each species (of which there were 214 total) for each a priori group. These two proportions are then combined by multiplying them, resulting in the indicator value, which is expressed as a percentage with 0 showing no indication and 100 showing perfect indication. Statistical significance of each indicator value was determined using the Monte Carlo method (NMS, PCord v. 5).

Results

Regional differences in environmental factors and shrub species composition

Topography

As expected, national forests differed topographically in terms of elevation and slope inclination. WV was highest in elevation, followed by PA and OH, with each national forest being significantly different from the other (Tables 1 and 2). Slope inclination also differed between OH and PA and PA and WV, but was similar between OH and WV. Slope aspect did not differ among the national forests (Tables 1 and 2).

Canopy openness

There were differences in canopy opening among the national forests, despite having similar ages. In OH, spherical densiometer readings showed more open canopies than the readings for PA and WV. Canopy opening was similar between PA and WV (Tables 1 and 2).

Soil

Soil pH, Ca:Al ratio, and C:N ratio all differed among the national forests. Each national forest's pH was below 5.0 on average and soils in WV were more acidic than

soils in PA and OH; soils in PA were more acidic than soils in OH (Tables 1 and 2). OH soils had a higher Ca:Al ratio than PA and WV (Tables 1 and 2). WV had a higher C:N ratio than PA and OH (Tables 1 and 2).

Soils also differed among the national forests in terms of Ca, Mg, K, and P. OH soils had a greater concentration of Ca compared to both PA and WV (Tables 1 and 2). Concentrations of Mg and K followed a similar pattern with OH having the greatest concentrations of the three national forests (Table 1). OH had the smallest concentration of P with no significant difference between PA and WV soils (Tables 1 and 2).

Soil Al, Zn, and Fe differed among the national forests, with OH having lower Al, Zn, and Fe concentrations than both WV and PA (Tables 1 and 2). Soil Mn concentrations were similar among the national forests (Tables 1 and 2).

Shrub species composition

There were 20, 12, and 8 shrub species in OH, WV, and PA, respectively. *Smilax rotundifolia* L. was the most abundant shrub in both OH and WV and *Rubus* L. spp. was the most abundant shrub in PA. *Kalmia latifolia* was the fifth most abundant shrub in both WV and PA but it did not occur on the OH transects. *Berberis thunbergii* DC. (Japanese barberry, another non-native invasive shrub) occurred only in the WV and PA transects, *Lonicera x bella* Zabel (Bell's bush honeysuckle, also a non-native invasive shrub) only on the PA transects, and *R. multiflora* (ranking ninth in abundance) only on the OH transects. OH was the only national forest that had an exotic shrub that ranked in the top 10 shrub species based on relative importance values.

Local environmental factors associated with *K. latifolia* and *R. multiflora*

Topography

Although elevation of the sample points for each national forest differed as with the regional data, the two species were located at similar elevations. There was a significant interaction between species and national forest (Table 2). *Kalmia latifolia* occurred at higher elevations than *R. multiflora* in PA. The two species occurred at similar elevations in WV and OH (Table 1). Slope inclination differed among the national forests and between species, and there was a significant national forest

Table 1 Regional and local means and standard errors (in parentheses) for topographic, canopy openness, and soil nutrient variables as they differ by national forest for the regional means and by national forest and species for the local means

	Regional			Local					
	OH	PA	WV	OH		PA		WV	
				KL	RM	KL	RM	KL	RM
Topography									
Elevation (m)	293.25 (5.83)a	563.70 (9.39)b	968.63 (19.59)c	228.50 (5.04)A	253.50 (14.45)A	565.50 (10.26)B	481.00 (19.38)E	663.00 (20.33)C	668.00 (24.59)C
Slope inclination (degrees)	17.05 (1.18)a	9.05 (0.73)b	14.65 (1.27)a	42.20 (3.46)A	27.80 (3.50)AC	12.70 (1.95)BC	9.00 (1.45)B	28.90 (5.00)AC	9.30 (2.48)B
Aspect (linearized)	0.99 (0.13)a	0.90 (0.12)a	0.91 (0.11)a	0.77 (0.23)A	0.86 (0.23)A	0.61 (0.21)A	0.78 (0.26)A	1.29 (0.22)A	1.21 (0.24)A
Canopy									
Openness (%)	13.27 (1.22)a	7.95 (0.68)b	8.74 (0.82)b	7.64 (0.78)A	10.04 (0.77)AB	13.13 (1.91)B	11.28 (1.22)B	7.93 (0.77)A	11.28 (1.63)A
Soil									
pH	4.79 (0.05)a	4.60 (0.03)b	4.37 (0.03)c	4.27 (0.03)A	4.77 (0.16)B	4.54 (0.02)BC	4.59 (0.04)BC	4.48 (0.03)AC	4.52 (0.02)AC
Ca:Al	26.89 (18.60)a	0.73 (0.32)b	0.18 (0.10)b	0.10 (0.05)AD	22.01 (16.26)B	0.04 (0.01)A	0.49 (0.14)CD	0.04 (0.01)A	0.61 (0.23)C
C:N	12.51 (0.41)a	14.54 (0.57)a	16.25 (0.39)b	21.79 (1.23)A	11.51 (0.64)B	19.36 (0.69)A	10.06 (1.03)B	19.67 (0.47)A	11.86 (0.48)B
Ca	520.51 (90.84)a	102.97 (29.10)b	48.82 (15.19)c	30.03 (13.13)A	584.94 (150.80)B	10.33 (1.62)A	120.39 (31.08)D	13.79 (1.69)A	122.70 (31.70)D
Mg	83.54 (9.65)a	26.08 (7.04)b	14.01 (3.75)b	12.28 (4.61)AC	113.26 (29.24)B	5.51 (0.56)C	43.81 (13.23)D	7.69 (0.74)AC	28.55 (7.94)
K	61.37 (3.06)a	42.93 (1.92)b	45.52 (1.95)b	36.67 (4.31)AC	66.95 (11.20)B	24.89 (3.20)C	44.06 (5.05)AB	52.95 (4.29)AB	46.96 (3.30)AB
P	1.19 (0.09)a	1.90 (0.14)b	1.70 (0.12)b	1.36 (0.20)AB	1.79 (0.28)A	0.84 (0.22)B	1.08 (0.20)AB	1.51 (0.21)A	1.74 (0.20)A
Al	279.48 (21.57)a	459.92 (21.90)b	508.42 (27.48)b	305.78 (29.82)A	267.38 (65.55)A	257.82 (38.33)A	268.46 (19.86)A	363.23 (30.37)A	274.21 (25.68)A
Mn	14.32 (1.38)a	22.56 (3.64)a	17.28 (2.43)a	9.03 (6.26)AC	17.93 (6.29)AD	9.29 (1.79)AC	16.81 (3.02)AD	5.45 (2.05)C	32.93 (8.34)D
Zn	0.86 (0.10)a	1.31 (0.12)b	1.65 (0.15)b	1.10 (0.34)A	1.31 (0.23)A	1.01 (0.12)A	1.18 (0.24)A	1.52 (0.19)A	1.47 (0.40)A
Fe	2.19 (0.23)a	10.78 (1.90)b	17.01 (2.37)b	8.92 (1.90)AC	1.14 (0.43)B	4.48 (1.29)AC	3.75 (1.68)C	10.40 (2.49)A	2.06 (1.23)B

Significantly different variables were determined using a generalized linear mixed model. Comparisons of significance were made only within the regional and local categories. Regional values with different lower-case letters and local values with different upper case letters are significantly different at P -value ≤ 0.05 . *KL* *Kalmia latifolia* and *RM* *Rosa multiflora*

and species interaction (Table 2). *Kalmia latifolia* and *R. multiflora* differed by slope only in WV and not in

OH or PA (Table 1). Slope aspect did not differ among the national forests or between species (Tables 1 and 2).

Table 2 Generalized linear mixed model results comparing the variables of the regional transects and the local plots associated with individual plants of *K. latifolia* and *R. multiflora*

	Regional National Forest (NF)	Local National Forest (NF)	Species	NF × Species
Topography				
Elevation	685.07****	417.14****	0.61	6.42**
Slope inclination	14.24****	21.17****	20.19****	3.46**
Aspect	0.17	2.34	0.10	0.02
Canopy openness	9.38***	4.11*	3.45	2.43
Soil				
pH	22.19****	0.63	13.64***	8.13***
Ca:Al	42.49****	9.07***	80.00****	3.38*
C:N	12.15****	3.18*	166.39****	1.30
Ca	43.77****	8.86***	102.36****	0.46
Mg	18.14****	4.88*	54.79****	1.41
K	13.65****	9.35***	14.23***	6.39**
P	8.37****	8.64***	3.39	0.12
Al	17.39****	1.59	2.98	1.69
Mn	1.35	2.59	23.93****	3.60*
Zn	9.13***	0.29	0.09	1.35
Fe	23.73****	0.93	35.95****	4.27*
Plant tissue				
Ca	NA	18.84****	207.13****	3.09
Mg	NA	18.93****	78.93****	14.79***
K	NA	1.72	108.98****	1.68
P	NA	22.23****	50.75****	2.48
C:N	NA	16.48****	453.28****	1.09
Total N	NA	17.20****	248.38****	0.94
Total C	NA	13.46****	2708.53****	3.71*
Al	NA	1.35	11.18***	3.15
Mn	NA	10.48**	31.87****	1.31
Zn	NA	8.05*	57.72****	15.33***
Fe	NA	3.55	101.24****	3.55

Comparisons are made across the national forests for both the regional transects and local plots. Comparisons are also made between species and the interaction between national forest and species for the local plots. For the local plots, plant tissue results are given in addition to topographic, canopy opening, and soil results. Values shown are the *F* statistic with the *P*-values ≤ 0.05 but > 0.01 marked as *, ≤ 0.01 but > 0.001 as **, ≤ 0.001 but > 0.0001 as ***, and ≤ 0.0001 as ****. NA not applicable

Canopy openness

Canopy opening values differed among the national forests locally but not between the two species. Unlike the regional measurements, OH had the lowest canopy opening values, followed by WV and PA (Tables 1 and 2).

Soil

For both species, all soil variables were statistically similar directly under and 2 m away from each shrub, indicating that the shrubs were not having a measureable impact on the soil at the time of our study. Thus, soil

nutrient differences between the two species are unlikely to be due to the presence of the shrub (i.e., changes in soil nutrient composition brought about by the shrub species' litter decomposition or use of the soil resources), but instead should be indicative of a species' soil nutrient preference. Consequently, for subsequent analyses, we use only the data from soil collected under each shrub.

Soil pH at the local level did not differ among the national forests, but was different between species, and there was a significant national forest and species interaction (Table 2). The two species differed for soil pH only in OH, with *K. latifolia* occurring in soils having a lower pH than *R. multiflora*. The pH values of the soils associated with *R. multiflora* shrubs in OH were more similar to the pH values found regionally in OH along the broad-scale transects (Table 1).

The Ca:Al ratio did differ among the national forests and between species with significant national forest and species interactions (Table 2). Soil beneath *K. latifolia* had a lower Ca:Al ratio than soil beneath *R. multiflora* in all three national forests (Table 1). On average, *K. latifolia* shrubs were not likely to be found on sites with a Ca:Al ratio above 0.3, while *R. multiflora* shrubs were not likely to be found on sites with a Ca:Al ratio below 0.5. Only the OH soils associated with *R. multiflora* had a Ca:Al ratio above 1 (Table 1). Total C:N ratio was different between species but not among national forests (Table 2). The total C:N ratio was greater in soil under *K. latifolia* than in soil under *R. multiflora* in all three national forests (Table 1). C:N ratios for both species were below 27 (a C:N ratio of 27 or lower is a suggested threshold indicating greater soil nitrate availability; Heilman 1974).

Soil Ca differed among the national forests as well as between species (Table 2). In each national forest, *R. multiflora* was associated with much greater concentrations of Ca than was *K. latifolia*. Soil Mg shared the same pattern as Ca (Table 1). Soil K was also similar except that there was a significant national forest and species interaction (Table 2); K and Mg were not found at greater concentrations under *R. multiflora* than *K. latifolia* in WV, unlike OH and PA (Table 1). Although soil P differed among the national forests, it did not differ between species (Table 2).

Local soil Al did not differ among the national forests or between species (Tables 1 and 2). Soil Mn differed between species, but not among the national forests, and with a significant national forest and species interaction (Tables 1 and 2). Only WV had greater Mn under the *R. multiflora* shrubs than under the *K. latifolia* shrubs (Table 1). Soil Zn was similar among the national forests and between species (Table 2), though there was a trend for soil Zn to be lower under *K. latifolia* than *R. multiflora* in OH and PA (Table 1). Soil Fe differed between species but not among the national forests; there was a significant national forest and species interaction (Table 2). Soil Fe concentrations were greater under *K. latifolia* shrubs than *R. multiflora* shrubs in OH and WV, and there was a trend of a similar pattern in PA (Table 1).

Plant tissue

Plant tissue Ca, Mg and P concentrations differed among the national forests and species with a significant national forest and species interaction for Mg. Plant tissue K concentrations differed between species only (Table 2). In each state, *R. multiflora* tissue contained more Ca, Mg, K and P than did *K. latifolia* (Fig. 2a, b, c and d). Plant tissue total C:N ratio differed among the national forests and between species (Table 2). Total C:N ratio was greater for *K. latifolia* than *R. multiflora* in all three national forests (Fig. 3a). Total C amounts were greater for *K. latifolia* leaf tissue in each national forest, and *R. multiflora* leaf tissue had greater amounts of total N in all three national forests (Table 2; Fig. 3b and c).

Rosa multiflora contains more Al and Fe in its tissue than *K. latifolia* in all three national forests (Fig. 4a and d), with no significant national forest effects (Table 2). In contrast, *K. latifolia* tissue contained higher levels of both Mn and Zn than did *R. multiflora* (Fig. 4b and c). Tissue Mn concentrations differed among national forest and between species (Table 2). Tissue Zn concentrations were different among national forests and between species, with a significant national forest and species interaction (Table 2).

Species composition

The composition of understory vegetation (herb, shrub, and vine species) associated with *K. latifolia*

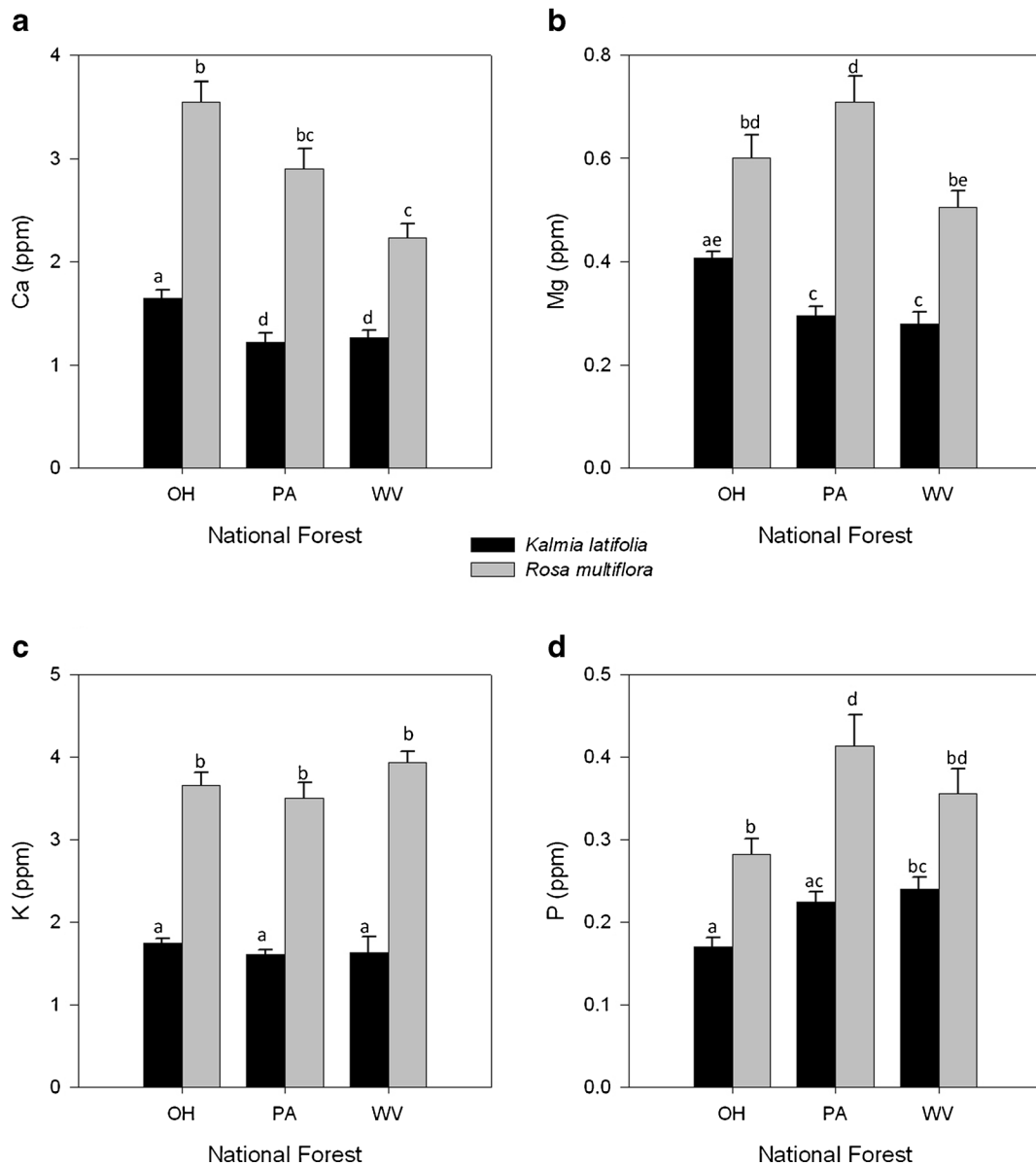


Fig. 2 Leaf tissue nutrient composition comparison of macronutrients **a** Ca, **b** Mg, **c** K, and **d** P using a generalized linear mixed model. Bars with different letters are significantly different at P -value ≤ 0.05

was distinct from that associated with *R. multiflora* in a 3-dimensional solution using NMS. Final stress and instability were 18.28 and 0.000001, respectively (Fig. 5). The top indicator species associated with *R. multiflora* included *Rubus* L. spp., *Viola pubescens* Aiton., and *Circaea lutetiana* L.. The top indicator species associated with *K. latifolia* included *Gaultheria procumbens* L., *Smilax rotundifolia* L., and *Mitchella repens* L. (Table 3).

Discussion

Question 1

Regional species and environmental variable comparisons

Though significantly different, revealing a pH gradient across the region, the pH values of the three national

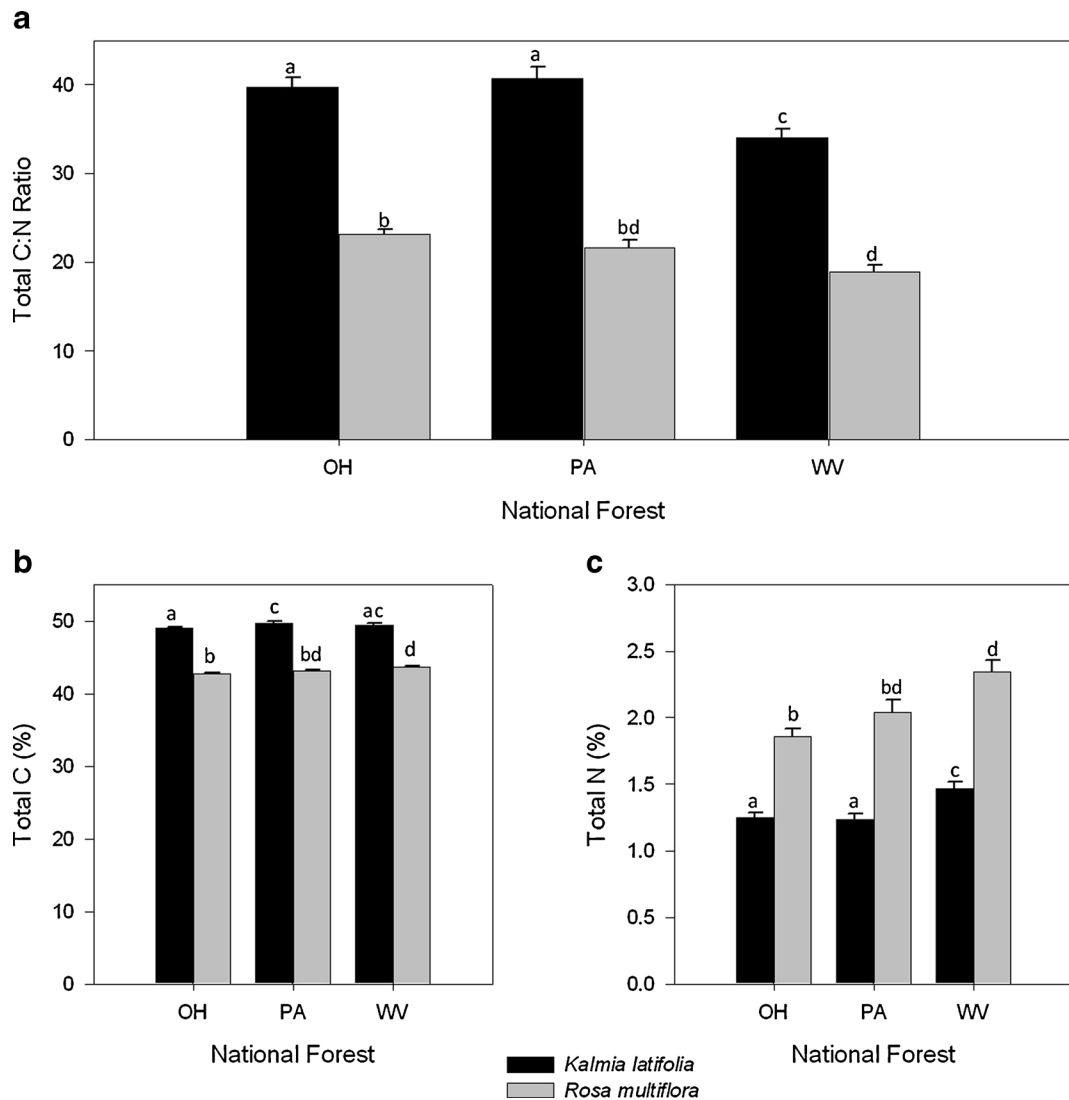


Fig. 3 Leaf tissue nutrient composition comparison of the C:N ratio including **a** total C:N, **b** total C, and **c** total N using a generalized linear mixed model. Bars with different lower-case letters are significantly different at P -value ≤ 0.05

forests are relatively close in value. In other studies in the unglaciated Allegheny Plateau in OH, soil pH has been measured as low as 3.52 (xeric soils on shale substrates) and as high as 6.5 (limestone soils) (Boerner et al. 2003). Our OH regional soil pH value (~ 4.8) may be indicative of a mixture of soils likely containing some limestone patches, which is comparable to values of 4.43, measured by Boerner and Sutherland (2003) in soils with some known interbedded limestone layers. Northern PA soils (sampled at similar depths, focusing on the B horizon) range between 3.8 (Drohan et al. 2002) and 4.3 (Bailey et al. 2005), making our value of 4.5 slightly less acidic. Our

WV pH values fell within the range of 4.20–4.68 reported by others for the Monongahela National Forest (Gilliam et al. 1996; Adams and Angradi 1996; Adams et al. 1997).

Like soil pH, there is a soil fertility gradient across the region, which is supported by the Ca:Al and C:N ratios. Indeed, PA and WV soil Ca:Al ratios are below 1, indicating poor soils that by definition may have difficulty sustaining or regenerating a forest (Cronan and Grigal 1995). Cronan and Grigal (1995) estimated that there is a 50 % chance of stressful plant growth response if the soil Ca:Al ratio is 1.0 or lower, a 75 % chance of a stressful response if the ratio is 0.5 or lower, and a nearly 100 %

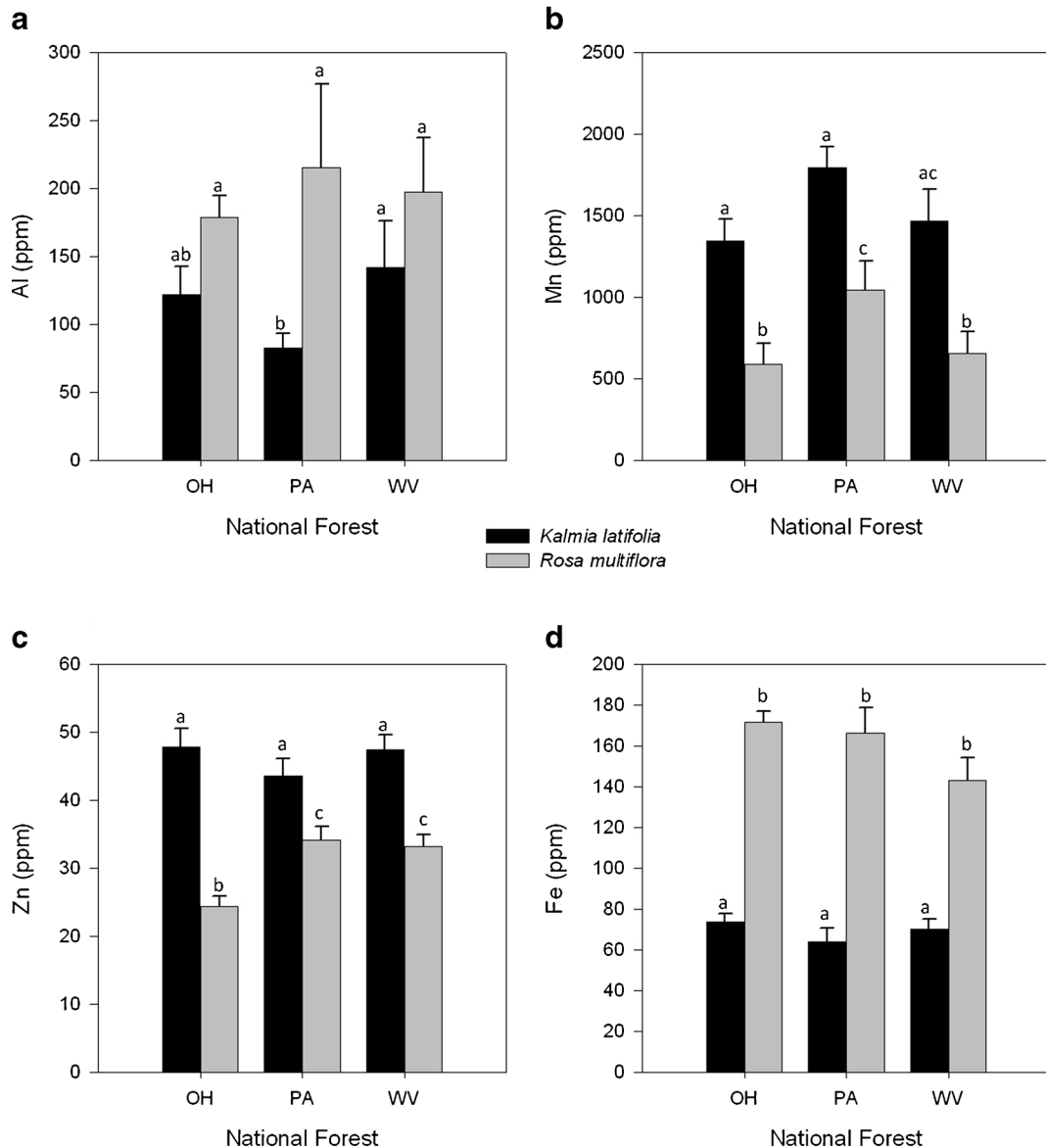


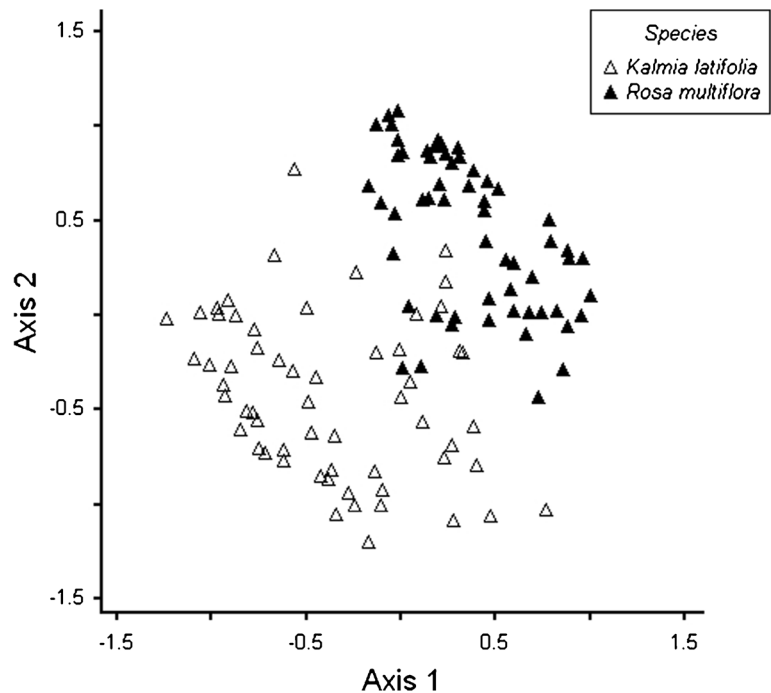
Fig. 4 Leaf tissue nutrient composition comparison of micronutrients and potential toxic nutrients (Al) or heavy metals (Mn and Zn) including **a** Al, **b** Mn, **c** Zn, and **d** Fe using a generalized linear mixed model. Bars with different letters are significantly different at P -value ≤ 0.05

chance of a stressful response if the ratio is 0.2 or lower. However, Ca:Al ratios are not universally accepted as an indicator of soil quality, but instead only a risk of stress (Schoenholtz et al. 2000). This may be because many forested sites (including the ones in this study) fall below this threshold and show no indication of plant stress. Other soil measures, including total N and extractable K, Ca, and Mg, may be better direct indicators of soil fertility (Schoenholtz et al. 2000). Low Ca:Al ratios (i.e., below 1) in PA and WV and even OH are not unusual

(Boerner and Sutherland 1997; Drohan et al. 2002). However, some plants are susceptible to mass die-back when growing on infertile sites combined with other stressors such as drought or insect defoliation. Examples of such die-backs have been documented for *Acer saccharum* Marsh. (Drohan et al. 2002; Horsley et al. 2002), *Quercus rubra* L. (Demchik and Sharpe 2000), and *Fraxinus americana* L. (Royo and Knight 2012).

While trees and other plant species, including *R. multiflora*, can clearly grow on sites with low soil

Fig. 5 NMS ordination showing a separation of local plots by species based on herb/shrub/vine species composition. Distance measure used was relative Sørensen with 500 iterations for a final 3-dimensional solution. Final stress and instability values were 18.28 and 0.000001, respectively



fertility, *K. latifolia* appears to be more likely to survive on those sites. Although we know that *R. multiflora* occurs in closed canopy forests of both PA and WV, it does appear from our sampling design that there is a greater probability of encountering *R. multiflora* in closed-canopy forests of OH than in closed canopy forests of PA and WV. Likewise, *K. latifolia* is less likely to be found in closed canopy forests of OH than in PA

and WV. The broad-scale FIA data (Fig. 1), which includes forests of all ages, also supports these likelihoods.

Our soil fertility gradient corresponds with an elevation gradient. The soil pH and fertility gradient may also correspond with a potential N deposition gradient, given that total N values (as well as total C values) were greatest for WV and lowest for OH. Boerner and Sutherland (1997) also found a similar pattern when

Table 3 Indicator species associated with *K. latifolia* and *R. multiflora* local plots

<i>K. latifolia</i>	IV%	<i>R. multiflora</i>	IV%
<i>Gaultheria procumbens</i> L.	43.5***	<i>Rubus</i> L. spp.	52.2***
<i>Smilax rotundifolia</i> L.	38.2**	<i>Viola pubescens</i> Aiton	48.3***
<i>Mitchella repens</i> L.	34.3***	<i>Circaea lutetiana</i> L.	45.0***
<i>Vaccinium pallidum</i> Aiton	31.5***	<i>Potentilla canadensis</i> L.	45.0***
<i>Vaccinium angustifolium</i> Aiton	23.2***	<i>Viola sororia</i> Willd.	43.3***
<i>Viburnum acerifolium</i> L.	21.7***	<i>Persicaria virginiana</i> (L.) Gaertn.	38.3***
<i>Vaccinium stamineum</i> L.	17.9**	<i>Parthenocissus quinquefolia</i> L. Planch	37.1***
<i>Medeola virginiana</i> L.	16.7**	<i>Viola blanda</i> Willd.	36.5***
		<i>Lindera benzoin</i> (L.) Blume	35.0***
		<i>Ageratina altissima</i> (L.) King & H. Rob	30.0***

Indicator values (IV) were determined using the Dufrière and Legendre method and statistical significance was determined using a Monte Carlo method. Only the top (closer to 100 %) 8 and 10 species for *K. latifolia* and *R. multiflora*, respectively with a P -value < 0.05 are listed for each species. P -values ≤ 0.05 but > 0.01 are marked as *, ≤ 0.01 but > 0.001 as **, ≤ 0.001 but > 0.0001 as ***, and ≤ 0.0001 as ****. While no more than 8 species met this criterion for *K. latifolia*, many more than 10 species met this criterion for *R. multiflora*

they compared pH, soil fertility and N saturation along a west to east gradient on sites in Illinois, Kentucky, Ohio, and West Virginia. Similarly, the soil gradient could reflect regional acid deposition (Krug and Frink 1983; Bailey et al. 2005), with greater impact noted in the less buffered PA and WV acidic soils, which may be experiencing greater natural processes of acidification (Krug and Frink 1983; McNulty et al. 2007). Unfortunately, because of the confounding effects of elevation, it is not possible to attribute the pH and soil fertility regional gradient in our study to a single cause as was also the case with Boerner and Sutherland's (1997) study.

Local – species and environmental variable comparisons

While *R. multiflora* shows a preference for more fertile soils (relatively high values of Ca:Al, Ca, and Mg, and higher pH values in OH) at the local level compared to *K. latifolia*, the values of Ca:Al are below 1 in PA and WV for soils associated with both species. Slightly shallower slopes and more open canopies may still explain the presence of *R. multiflora* in WV at the local level in addition to any apparent preference for more fertile soils. Nonetheless, other invasive exotic species prefer high fertility soils (Von Holle and Motzkin 2007) and the manipulative increase of soil fertility results in greater relative growth rates of invasive exotic species, but only if the treated site is initially a low fertility soil (e.g., pinelands; Gurevitch et al. 2008). The relative abundance of *R. multiflora* in more fertile soils suggests limited establishment of *R. multiflora* and a potential increase in mortality in less fertile soils. Also, because *K. latifolia* and *R. multiflora* share their environments with indicator plants, it may be possible to predict soil fertility and, consequently, future invasions or expansions by these two species using information about existing vegetation.

Rosa multiflora decline in relatively infertile soils has not been documented. However, Ca:Al ratios below 0.5, the lowest mean Ca:Al ratio associated with *R. multiflora* in our study, suggests a potential fertility threshold for *R. multiflora*. There is evidence of increased susceptibility to a known pathogen of *R. multiflora*, i.e., rose rosette disease, in plants growing in the shade vs. full sun (Epstein and Hill 1998), suggesting that stressed *R. multiflora* plants may be impacted negatively by other stressors. Associating declines in *R. multiflora* with

a known pathogen such as rose rosette disease would document the need for an additional stressor for declines to occur, like those documented for other species (Demchik and Sharpe 2000; Drohan et al. 2002; Horsley et al. 2002; Royo and Knight 2012).

Strategic management of *R. multiflora* may include (1) removing nearby propagule sources and not disturbing areas with high soil fertility, (2) increasing soil acidity possibly by adding an ammonium sulfate fertilizer (Bolan et al. 1991) or planting nitrogen-fixing legumes (well-nodulated legumes fix most N from the air and obtain most of their bases from the soil; Nyatsanga and Pierre 1973; Bolan et al. 1991), or (3) decreasing soil fertility by planting ericaceous shrubs (Moroni et al. 2009). Of course, in addition to reducing *R. multiflora*'s probability of establishment, adding ericaceous shrubs to the system may risk starting a native species expansion. Perhaps keeping the Ca:Al ratio above 0.3 but below 0.5 may be key to preventing invasion by *R. multiflora* and expansion of *K. latifolia*. More research is necessary concerning these potential soil fertility thresholds in addition to the likely costs associated with such soil manipulations.

In contrast, *K. latifolia* is abundant and competitive in more infertile soils with a possible mean Ca:Al ratio threshold of 0.3 or lower, but it is clearly limited and considered rare in more fertile soils, such as in OH (Marilyn Ort, personal communication). Indeed, if invasion by unwanted exotic plants were not a potential consequence, it might be feasible to prevent the spread of or even increase the mortality of *K. latifolia* shrubs from a site by increasing the soil pH with lime. There is some evidence of a negative response by *K. latifolia* to lime addition (Matysiak 2005), but information is lacking and most successful control of *Kalmia* spp. has been accomplished by using herbicide treatments (Krishnapillai 2009).

Question 2

Our study confirms that the apparent accumulation of Mn and Zn in *K. latifolia* leaves is not due to greater concentrations of these potentially toxic heavy metals in the soil near *K. latifolia*, providing evidence of hyperaccumulation by *K. latifolia* (Rascio and Navari-Izzo 2011). To our knowledge, hyperaccumulation of heavy metals has never been documented for *K. latifolia*. High levels of Mn and Zn could be toxic to herbivores, but additional research is needed to

document whether these tissue concentrations of Mn and Zn limit herbivory. There is some evidence of preference for low-Zn plants over high-Zn plants that may be due to the herbivores' ability to detect particular metal-induced metabolites (Rascio and Navari-Izzo 2011). If *K. latifolia*'s tissue composition acts as a defense against herbivores, this and the higher total C concentration in leaf tissue serve as evidence that *K. latifolia* is a K-selected species. Even if benefits against herbivory are lacking, *K. latifolia* appears to be successfully utilizing a stress-tolerant strategy (Grime 1977), but without any reduction in competitive ability (Taylor et al. 1990), which enables it to expand. The decomposition of *K. latifolia* leaves that are high in heavy metals could perpetuate *K. latifolia*'s dominance by making the soils toxic to other plant species not capable of utilizing the heavy metals (Mallik 2001). Although our study did not show higher concentrations of Mn or Zn in the soil associated with *K. latifolia*, such soil accumulation of these metals could occur over time with more shrub expansion.

The high C:N ratio found in this study along with high concentrations of phenolic compounds (Bloom and Mallik 2004; Ehrenfeld et al. 2005) leading to high soil acidity, may be the most likely mechanism behind *K. latifolia*'s ability to expand within its native range. Kraus et al. (2004) found that infertile soils were correlated with ericaceous leaf tissue that was higher in total phenols and condensed tannins than were plant tissue from plants grown in fertile soil. A positive feedback mechanism may be at work in which infertile soils increase plant tissue phenol concentrations and phenols lead to increases in soil acidity and infertility. Based on our results, the establishment of *K. latifolia* is likely only if the soil is already relatively infertile, which also decreases the competitive ability of other species, such as *R. multiflora*. Hence, our study further documents the importance of soil fertility conditions to the probable establishment and spread of invasive exotic and expansive native plants. *Kalmia latifolia*'s recent expansion also may be associated with canopy-opening disturbances (without fire), fire suppression (Krug and Frink 1983; Brose and Waldrop 2010), and increasing soil acidity due to acid deposition (Bailey et al. 2005) and natural soil formation (Krug and Frink 1983). Our study sites in WV and PA are located in areas noted to exceed critical soil acid loading values by over 500 eq ha⁻¹ year⁻¹ (McNulty et al. 2007), making

additional acidification by acid deposition especially critical for these areas.

Rosa multiflora's high concentration of most of the critical nutrients in its tissues and its similar uptake ability even in sites with lower soil nutrient concentrations indicates that this plant is an r-selected species or a ruderal species focusing on growth rather than protection. The ability to absorb essential nutrients in the soil rapidly could put *R. multiflora* at a competitive advantage over less capable plant species, such as *K. latifolia* in disturbed systems with abundant resources but not necessarily in closed-canopy forests (Banasiak and Meiners 2009; Meiners et al. 2008), especially forests with more acidic soils. Although we selected sites where neither species was dominant for our study, *R. multiflora*, like *K. latifolia*, may also be able to perpetuate site conditions (high soil fertility) that promote its establishment and spread. There is evidence for rapid leaf tissue decomposition by several invasive exotic plant species, including *R. multiflora* (Ehrenfeld 2003; Ashton et al. 2005). This may be another example of a positive feedback mechanism, in which rapid decomposition of leaf litter high in essential nutrients releases them to the soil, making them available once again for uptake. Nonetheless, while our results show that establishment and spread of *R. multiflora* may be less likely in closed-canopy forests with low soil fertility, colonization does occur in part because *R. multiflora* is relatively plastic in its apparent nutrient requirements. *Kalmia latifolia* is rarely found in highly fertile soils, but *R. multiflora* is not rare in relatively infertile soils.

Conclusions

Our research documents the importance of soil fertility conditions to the likelihood of establishment of a non-native invasive shrub and native expansive shrub. Our findings also provide support for soil fertility (Ca:Al ratio) thresholds of 0.3 or less for *K. latifolia* and 0.5 or greater for *R. multiflora*. *Rosa multiflora* has a broader soil fertility range for invasion than *K. latifolia*. Land managers can use our results to prioritize sites for management by (1) choosing not to disturb (i.e., harvest and/or burn) a forest stand, (2) predicting which forested sites are most likely to be impacted the most by unplanned stressors, such as insect defoliations, or (3) selecting where to focus *R. multiflora* and *K. latifolia* control efforts based on soil fertility

conditions. Our findings also provide possible soil fertility thresholds on which more aggressive soil manipulations for managing either *K. latifolia* or *R. multiflora* may be based.

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