

Effects of invasive plant patch size and distance on the pollination and reproduction of native boreal plants

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Abstract: In pollinator-limited ecosystems in the earliest stages of the invasion process, the effects of invasive plants on the pollination and reproduction of co-flowering native plants may be particularly sensitive to the distance between native and non-native plants. Our study tests how the distance from invasive plant patches affects the pollination and reproduction of two native boreal shrubs. We established circular sites with plots of flowering *Vaccinium vitis-idaea* L. and *Rhododendron groenlandicum* (Oeder) Kron and Judd spanning from 1 to 40 m from the site center. In 2011 and 2012, we added flowering non-native *Melilotus albus* Medik. to the center of sites in small patches (40 individuals) or large patches (120 individuals) and left other sites as controls. In some cases, the effects of *M. albus* were uniform across the 40 m distance, such as the change in *V. vitis-idaea* seed production when large patches of *M. albus* were added. In other cases, relationships with distance were found, and changes in percent pollination or seed production occurred most rapidly over the first 10 m from the patch. Our data supports the hypothesis that the detectable impact an invasive species has on the pollination of native species is affected by the spatial scale over which it is evaluated.

Key words: boreal forest, invasive species, pollination, seed set, spatial scale.

Résumé : Dans les écosystèmes limités en pollinisateurs aux premiers stades du processus d'envahissement, les effets de plantes envahissantes sur la pollinisation et la reproduction de plantes indigènes en co-floraison peuvent être particulièrement sensibles à la distance entre les plantes indigènes et non indigènes. L'étude des auteurs teste expérimentalement comment la distance de parcelles de plantes envahissantes affecte la pollinisation et la reproduction de deux arbustes boréaux indigènes. Ils ont établi des sites circulaires avec des parcelles de *Vaccinium vitis-idaea* L. et *Rhododendron groenlandicum* (Oeder) Kron and Judd, des espèces à fleurs, s'étendant de 1 à 40 m du centre du site. En 2011 et 2012, ils ont ajouté l'espèce à fleurs non indigène *Melilotus albus* Medik. au centre des sites en petites (40 individus) ou larges (120 individus) parcelles, et laissé les autres sites comme contrôles. Dans certains cas, les effets de *M. albus* étaient uniformes à travers les 40 m de distance, comme le changement dans la production de graines par *V. vitis-idaea* lorsque de grandes parcelles de *M. albus* étaient ajoutées. Dans d'autres cas, des relations en fonction de la distance étaient trouvées, et les changements dans le pourcentage de pollinisation ou la production de graines survenaient plus rapidement dans les premiers 10 m à partir de la parcelle. Leurs données appuient l'hypothèse que l'impact détectable qu'une espèce envahissante a sur la pollinisation d'espèces indigènes est affecté par l'échelle spatiale sur laquelle il est évalué. [Traduit par la Rédaction]

Mots-clés : forêt boréale, espèce envahissante, pollinisation, grenaison, échelle spatiale.

Introduction

Invasive plants can directly compete with native plants for light, water, and nutrients, which can have consequences for plant communities and ecosystem processes (reviewed in Levine et al. 2003; Skurski et al. 2014). Indirect competition for pollinator services can also occur in the presence of invasive plants that have highly rewarding inflorescences (Chittka and Schürkens 2001).

Because many pollinating insects fly substantial distances to obtain floral resources (Osborne et al. 1999; Beekman and Ratnieks 2000; Gathmann and Tscharrnke 2002; Knight et al. 2005), the spatial scale at which entomophilous invasive plants can affect the reproductive success of native plants is much greater than the effects of direct competition. Some studies have reported net negative effects of invasive plants on the pollination of

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native plants by decreasing visitation rates to native plants (Waser 1983; Campbell 1985; Brown et al. 2002; Kandori et al. 2009) or increasing heterospecific pollen transfer (Morales and Traveset 2008). Other studies report overall positive effects through a “pollinator magnet” effect or by increasing pollinator carrying capacity of a site (Moragues and Traveset 2005; Lopezaraiza-Mikel et al. 2007; Tepedino et al. 2008), or no effects (Bartomeus et al. 2008).

Most field studies investigating the impact of invasive plants on pollination of native plants occur in relatively small scale plots or transects (plot/transect size in these studies range from 18 m² to 200 m²) with the invasive plants dispersed throughout (Lopezaraiza-Mikel et al. 2007; Bartomeus et al. 2008, 2010; Muñoz and Cavieres 2008; Flanagan et al. 2010; Da Silva et al. 2013). Some authors acknowledge that the scale of their investigation may alter the direction of the interaction between invasive plants, pollinators, and native plant species that they are able to detect (Lopezaraiza-Mikel et al. 2007; Jakobsson et al. 2009). For example, Lopezaraiza-Mikel et al. (2007) found facilitative effects of invasive *Impatiens glandulifera* on pollinator visitation to native plants. They speculated, however, that competition could be occurring at larger scales if highly mobile insects like *Bombus* spp. or *Apis mellifera* are being drawn to the invasive plant patch, leaving plants further away, outside their experimental plots, in a deficit for pollinator services. In another example, Jakobsson et al. (2009) compared pollinator visitation rates to native plants in three treatments: (i) large scale areas infested with invasive plants; (ii) large scale areas infested with invasive plants with small scale plots where the invasive plant was removed; and (iii) large scale uninvaded areas. They found that pollinator visits to native plants in the small scale removal plots were greater than in large scale invaded sites or in uninvaded sites. **These studies suggest that the native plants may be experiencing diverse, and perhaps contrasting, reproductive outcomes depending on their proximity to the invasive plant patch.**

In boreal forest ecosystems, the distance between a native insect-pollinated plant and a patch of abundant invasive flowers may be particularly important in determining the reproductive consequences. Throughout the northern boreal region in North America, there are still very few instances where invasive plants have spread off of the human disturbance footprint relative to other places (Rose and Hermanutz 2004; Bella 2011; Sanderson et al. 2012; AKEPIC 2014). These sites tend to be characteristic of early invasion stages, with isolated patches of the non-native species occurring within native vegetation rather than diffused across large areas (Rose and Hermanutz 2004; Bella 2011; Sanderson et al. 2012; AKEPIC 2014). Given the very limited pollinator pools in the boreal forest (Kevan et al. 1993), an invasive plant patch with large numbers of flowers and high nectar

rewards could attract pollinators from substantial distances. Plants far from the patch could suffer decreases in pollinator services during a short boreal flowering season. Both the number of flowering invasive flowers in the patch and the density of conspecific flowers in the plant neighborhood would also be expected to alter the spatial distribution of the impacts on native plant pollination by changing the attractiveness of the plot for visiting pollinators (Bosch and Waser 2001; Muñoz and Cavieres 2008; Molina-Montenegro et al. 2008; Flanagan et al. 2010).

Melilotus albus Medik. (sweetclover), is a highly rewarding invasive plant, which has established along much of the anthropogenic footprint in Alaska and has incipient populations within intact boreal forests. *Melilotus albus* is native to Eurasia and was introduced to Alaska in 1913 as a potential cold-hardy forage and nitrogen-fixing crop (Irwin 1945; Klebesadel 1992), and now occurs throughout Alaska from Metlakatla (55.122°N, 131.561°W) to north of Coldfoot (67.286°N, 150.171°W) at the base of the Brooks Mountain Range (AKEPIC 2014). Aside from several roadsides and a few glacial river floodplains where large continuous patches have established (Conn et al. 2008; Spellman and Wurtz 2011), it only occurs in small discreet patches within intact boreal forest sites (Villano and Mulder 2008; AKEPIC 2014; Spellman et al. 2014). Particularly in comparison with native boreal insect-pollinated plants, *M. albus* offers considerable nectar and pollen resources to floral visitors (Peterson 1989; Malacalza et al. 2005; Tepedino et al. 2008) with an extremely high number of flowers per plant (up to 350 000 flowers per plant; Royer and Dickinson 1999).

We conducted a 2 year experiment to investigate whether adding *M. albus* to boreal forest sites altered the pollination and reproductive success of native *Vaccinium vitis-idaea* L. (lingonberry or lowbush cranberry) and *Rhododendron groenlandicum* (Oeder) Kron and Judd (formerly *Ledum palustre* subsp. *groenlandicum*; Labrador tea). We previously reported on the mean effects of *M. albus* addition on the reproduction of these species at an approximately 0.5 ha site scale (Spellman et al. 2015). At this scale, pollinator activity and diversity increased when *M. albus* was added to sites. The presence of *M. albus* did not increase the pollination rates or the amount of conspecific pollen deposited in *V. vitis-idaea*. However, the number of seeds per fruit of *V. vitis-idaea* increased when we added high densities of the invasive plant flowers to the site. Pollination rates of *Rhododendron groenlandicum* modestly decreased with increasing numbers of *M. albus* flowers, but we did not detect a change in amount of seeds produced per fruit.

In the instances where we did not find an effect of *M. albus*, however, there remained two possibilities: (i) there was, indeed, no effect, or (ii) there was a compensatory effect resulting from both positive and negative relationships across the 1–40 m distance between the

Table 1. Number of sites for each species in 2011 and 2012 by treatment.

Species	Year and treatment				
	2011		2012		
	Control	Mel 40	Control	Mel 40	Mel 120
<i>Vaccinium vitis-idaea</i>	6	10	6	6	6
<i>Rhododendron groenlandicum</i>	4	11	4	6	4

Note: “Mel40” indicates that 40 *Melilotus albus* plants were added; “Mel120” indicates 120 *M. albus* plants were added.

native flowers and the invasive plant patch. For example, native plants close to *M. albus* may have benefitted from the pollinators’ attraction to the abundant floral resources, and experienced increased visitation rates. The few studies that have considered the relationship between proximity to an invasive plant and pollination of native plants found highest visitation rates or highest heterospecific pollen deposition immediately adjacent to the invasive plant patch (Moragues and Traveset 2005; Nielsen et al. 2008; Takakura et al. 2011; Cawoy et al. 2012). In sites with limited pollinator availability, greater pollinator activity near the invasive plant patch could reduce visitation rates to native plants at further distances.

In this study, we investigate the spatial pattern of the effects within our sites. We ask the following questions: (i) What pattern best describes the relationship between focal species pollination and distance from the site center in sites without *M. albus*, and sites with small or large patches of *M. albus* added? (ii) Can the results we found for the impacts of invasive plant additions on mean pollination and seed production be explained by an interaction between *Melilotus* addition and distance from the patch?

Materials and methods

Study area

Sites were located within the Bonanza Creek Boreal Long Term Ecological Research Program (BNZ LTER) research areas near Fairbanks, Alaska (Bonanza Creek Experimental Forest, 64.709°N, 148.326°W, and Caribou and Poker Creeks Research Watershed, 65.141°N, 147.457°W). Sites were selected to contain abundant flowering *V. vitis-idaea* and *R. groenlandicum* in the understory. Dominant tree species at the sites included *Betula neoalaskana* Sarg., *Populus tremuloides* Michx., *Picea glauca* (Moench) Voss, and *Picea mariana* Mill. Other insect-pollinated native species flowering at the sites at the time of the experiment included *Cornus canadensis* L., *Geocaulon lividum* (Richardson) Fernald, *Moehringia lateriflora* (L.) Fenzl, *Rosa acicularis* Lindl., *Rubus chamaemorus* L., *Salix* spp. L., *Vaccinium uliginosum* L., and *Viburnum edule* (Michx.) Raf. *Melilotus albus* did not occur at any of these sites. Compared with the 30 year average precipitation and temperature for June (3.6 cm, 15.4 °C), in 2011, precipitation was higher and temperatures were close to average (4.5 cm, 15.8 °C), and in 2012, precipitation was

close to average but temperatures were substantially higher (3.5 cm, 16.4 °C; Alaska Climate Research Center 2014). During the flowering period of *V. vitis-idaea* and *R. groenlandicum* at our sites, we measured 173 h of rain and a mean temperature of 13.6 °C in 2011, and 97 h of rain and a mean temperature of 15.0 °C in 2012.

Experimental design

We selected sites spaced >300 m apart to minimize pollinator movement between sites. Sites were circular and extended 40 m in all directions from the site center. Within each site, 25 circular plots were established for each of the occurring focal species (1 m² plots for *V. vitis-idaea*, and 1.77 m² plots for *R. groenlandicum*). We standardized the distribution of plots across the 40 m radius range by placing five plots in within five distance ranges from the site center: 1–2 m, 3–5 m, 8–10 m, 15–20 m, and 25–40 m. We chose this distribution of plots because of the expectation that the greatest effects would be closer to the invasive plant patch, based on literature accounts (Moragues and Traveset 2005; Nielsen et al. 2008; Takakura et al. 2011; Cawoy et al. 2012), while still allowing for the possibility of detecting larger scale impacts. Within these plots, five *V. vitis-idaea* or five *R. groenlandicum* stems were marked for tracking fruit and seed production.

In 2011, sites were randomly assigned to have 40 flowering *M. albus* plants that were grown in a greenhouse added to the site center (designated “Mel40”) or to remain control sites (no *M. albus* added). In 2012, we repeated the design and added a treatment with 120 *M. albus* (designated “Mel120”) to address the influence of invasive plant patch size on native plant reproductive success (presented in Spellman et al. 2015). The number of sites for each focal species in each year and treatment are shown in Table 1. Both focal species co-occurred in all but three sites in 2011 and four sites in 2012.

Melilotus albus was added to the Mel40 or Mel120 sites at the time that *V. vitis-idaea* and *R. groenlandicum* flower buds emerged, but had not yet opened. *Melilotus albus* plants were grown in the greenhouse in cylindrical pots (7 cm diameter at the top, 22 cm in length); each pot contained one individual with 5–181 inflorescences (mean of 49 ± 18 flowers per inflorescence). Either 40 or 120 pots were placed in the center of the site in holes of similar dimensions so that the top of the pot was flush with the ground surface. The number of inflorescences

added to each site ranged from 334 to 942 (16 366 to 46 158 total flowers) for the Mel40 sites, and 1068 to 1608 (52 332 to 78 792 total flowers) for the Mel120 sites. Density of the *M. albus* was 15 plants per square metre, resulting in patch sizes of approximately 2.6 m² and 8 m². These dimensions are comparable to the patch sizes found within burned boreal forest in interior Alaska, which are typically in the earliest of invasion stages where they occur (Villano and Mulder 2008). Once flowers of focal native species had dropped their petals (18–28 days after *M. albus* addition), *M. albus* was removed from the sites. To prevent accidental introductions, we removed any immature seeds that appeared on the *M. albus* plants throughout the duration of the experiment. Sites were also visited a year following the experiments to confirm that no *M. albus* plants were present.

Pollination

We collected *V. vitis-idaea* and *R. groenlandicum* stigmas from randomly selected open flowers near each of our marked focal plants. We did not take stigmas from marked plants to avoid interfering with fruit set. Three (in 2011) or five (in 2012) *V. vitis-idaea* and five *R. groenlandicum* stigmas were collected from each of the 25 plots in each site approximately 14 days after the *M. albus* plants were added. The stigmas were mounted on microscope slides and stained with a basic fuchsin gel (Kearns and Inouye 1993). Each tetrad (in the case of *R. groenlandicum* and *V. vitis-idaea* pollen) or pollen grain (all other species) on the stigma was identified to genus (using anthers collected from all flowering species at the sites for reference) and counted under a compound light microscope. We calculated the percent of well-pollinated flowers in each plot using these pollen counts. Flowers were considered to be “well pollinated” when they had 10 or more conspecific pollen tetrads on the stigma. We selected this threshold because fruit production was greatest when the pollen loads exceeded this pollen level for both focal species in control sites (data presented in Spellman et al. 2015). Further, the maximum seed number per fruit in the *V. vitis-idaea* control plots across the 2 years of study was 47, indicating that >10 pollen tetrads were necessary for maximum seed production. Few stigmas had zero pollen grains on them, making the presence or absence of pollen inadequate for the detection of variation in the proportion of flowers that were pollinated.

Seed production

To determine seed production per fruit in *V. vitis-idaea*, we dissected up to five berries per marked plant and counted the number of seeds produced under a dissecting microscope. For *R. groenlandicum*, which has minute seeds that are released as the fruit ages and dries, we dried inflorescences at 65 °C until the fruits opened and released the seeds. The mass of the seeds was divided by the number of fruits on the inflorescences to derive seed mass per fruit.

Local conspecific flower density

Since flower density often affects pollination (Bosch and Waser 2001), high variation in density can mask the effects of pollinator activity. To provide an estimate of local conspecific flower density, we counted the number of conspecific flowers and flower buds present within each of the 25 plots per site at the time we added the *M. albus*.

Analysis

We performed the statistical analyses using SAS version 9.1 (SAS Institute, Cary, North Carolina). We used percent flowers receiving ≥10 pollen tetrads (“% pollinated flowers”) and number of seeds per fruit for *V. vitis-idaea*, or seed mass per fruit for *R. groenlandicum* (“seeds per fruit”) as our response variables. Mean seed mass per fruit of *R. groenlandicum* for each plot was square-root transformed to meet the assumptions of normality and constant variance. All analyses were conducted on plot-level means.

To determine the best relationship between the response variable and the distance from the site center for each year and treatment, we used a generalized linear mixed model (GLMM) Akaike Information Criterion (AIC) model comparison approach. Site was included as a random effect. We compared distance effects that were linear ($y = \text{site} + \text{distance}$), quadratic ($y = \text{site} + \text{distance} + \text{distance}^2$), logarithmic ($y = \text{site} + \log_{10}(\text{distance})$), and uniform across the site ($y = \text{site}$). Because conspecific flower densities tended to be lower near the center of the site (see the section on Results), we included the conspecific flower density in the plot in the design. If conspecific flower density is driving the relationship over distance then including it will result in a better model than just including distance. To determine whether accounting for conspecific flower density in the plot improved the model, we compared the aforementioned models both with and without local conspecific flower density included as a covariate. We also included the null model ($y = \text{mean}$) for a total of nine candidate models. We then ranked the models using the AIC score and calculated the model weight to evaluate the strength of evidence for each model to explain the native plant pollination and reproduction across the distance range in the sites (Burnham and Anderson 2002). Because the vast majority of relationships were best explained using a log-linear model (see section on Results) we tested for an interaction between the log of distance and treatment (GLMM Type 3 test of fixed effects).

Results

Regardless of the species or the response variable, the best models for relationship with distance to the center of the plot were either uniform (no change with distance) or linear-log (an increase or decrease with the log of the distance) (Tables 2 and 3). In no case did a linear or quadratic relationship emerge as the best model (Tables 2

Table 2. Mixed model comparison for percent flowers pollinated and number of seeds per fruit of *Vaccinium vitis-idaea* for each year and treatment type.

Response variable	Year	Treatment	Model	AICc	ΔAIC_c	Weight
%Flowers pollinated	2011	Control	Site	1339.6	0.0	1.00
			Site+log(distance)	1377.8	38.2	0.00
			Site+flwr dens+log(distance)	1380.4	40.8	0.00
		Mel40	Site+log(distance)	2259.4	0.0	0.76
			Site+distance+distance ²	2263.1	3.7	0.12
			Site+flwr dens+log(distance)	2263.4	4.0	0.10
	2012	Control	Site+log(distance)	1322.5	0.0	0.49
			Site+flwr dens+log(distance)	1322.9	0.4	0.40
			Site+distance	1327.1	4.6	0.05
		Mel40	Site+flwr dens+log(distance)	1259.6	0.0	0.60
			Site+log(distance)	1260.7	1.1	0.35
			Site+flwr dens	1266.8	7.2	0.02
		Mel120	Site	1272.0	0.0	1.00
			Site+log(distance)	1313.3	41.3	0.00
			Site+flwr dens+log(distance)	1315.8	43.8	0.00
No. of seeds per fruit	2011	Control	Site	706.7	0.0	1.00
			Site+log(distance)	741.3	34.6	0.00
			Site+distance	747.7	41.0	0.00
		Mel40	Site+log(distance)	1322.4	0.0	0.69
			Site+flwr dens+log(distance)	1324.7	2.3	0.22
			Site+distance	1327.3	4.9	0.06
	2012	Control	Site	673.2	0.0	1.00
			Site+log(distance)	697.8	24.6	0.00
			Site+distance	702.3	29.1	0.00
		Mel40	Site	890.2	0.0	1.00
			Site+log(distance)	910.7	20.5	0.00
			None (mean)	911.7	21.5	0.00
		Mel120	Site	801.7	0.0	1.00
			Site+log(distance)	823.8	22.1	0.00
			None (mean)	825.6	23.9	0.00

Note: The table presents the top three models out of nine candidate models describing possible relationships between the response variable, site effects (included as the random effect), plot flower density ("flwr dens"), and distance from the site center ("distance") in null, linear, quadratic, or logarithmic forms. Candidate models included $y = \text{mean}$, $y = \text{site}$, $y = \text{site} + \text{distance}$, $y = \text{site} + \text{distance} + \text{distance}^2$, $y = \text{site} + \log(\text{distance})$, $y = \text{site} + \text{flwr dens} + \text{distance}$, $y = \text{site} + \text{flwr dens} + \text{distance} + \text{distance}^2$, $y = \text{site} + \text{flwr dens} + \log(\text{distance})$. Models with $\Delta AIC_c < 2$ are indicated in bold.

and 3). Where relationships with distance were found, changes in percent pollination or seed production occurred most rapidly over the first 10 m from the distance of the patch (Figs. 1 and 2).

Vaccinium vitis-idaea

In 2012, the local density of conspecific flowers surrounding *V. vitis-idaea* focal plants was included in the top models explaining the percent flowers pollinated in control and Mel40 sites (Table 2). In both cases a strongly competing model did not include the term (Table 2), and the overall effect on pollination rates was not significant (GLMM type 3 fixed effect: $F_{[1,386]} = 1.71$, $p = 0.19$). Flower density was not included in the 2011 percent flowers pollinated models or in the number of seeds per fruit models in either year (Table 2). The density of *V. vitis-idaea* was slightly lower in the plots closest to the site center (flowers per plot = $7.8 \times \log_{10}(\text{distance}) - 7.07$; $F_{[1,383]} = 2.72$, $p = 0.09$).

In 2011, the percentage of *V. vitis-idaea* flowers pollinated was uniform across the control sites, while a negative logarithmic relationship best described pollination

rates in sites with *M. albus* added (Table 2; Fig. 1A). Plants within 10 m of the invasive patch were better pollinated than average for the site, whereas those far away had lower pollination rates. In 2012, the pattern for the sites with 40 *M. albus* plants added was again a negative logarithmic relationship, but there was no relationship with distance for plots with 120 *M. albus* added, and control plots had a positive relationship with the log of distance (Fig. 1B). In both years the models suggest the least negative impact of *M. albus* for plants immediately adjacent to them, and the greatest negative effect farthest from the *M. albus* patch (Figs. 1A and 1B). However, there was no statistically significant interaction between treatment and log of distance (GLMM type 3 fixed effect $\log(\text{distance}) \times \text{treatment}$ interaction: 2011, $F_{[1,360]} = 0.95$, $p = 0.39$; 2012, $F_{[2,386]} = 1.82$, $p = 0.16$). For number of seeds per fruit, the best model for Mel40 plots in 2011 was a positive relationship with the log of distance, whereas all of the other best models showed no relationship with distance (Figs. 1C and 1D). Again, there was no evidence

Table 3. Mixed model comparison for the percent flowers pollinated and the square-root transformed mass of seeds per fruit of *Rhododendron groenlandicum* for each year and treatment type.

Response variable	Year	Treatment	Model	AICc	ΔAIC_c	Weight
%Flowers pollinated	2011	Control	Site+flwr dens+log(distance)	779.4	0.0	0.91
			Site+flwr dens	785.0	5.6	0.05
			Site+flwr dens+distance	785.8	6.4	0.04
		Mel40	Site+flwr dens+log(distance)	2004.1	0.0	0.92
			Site+flwr dens+distance	2010.1	6.0	0.05
			Site+flwr dens	2010.7	6.6	0.03
	2012	Control	Site	709.3	0.0	0.41
			Site+log(distance)	709.8	0.5	0.32
			Site+flwr dens+log(distance)	710.3	1.0	0.25
		Mel40	Site+log(distance)	1228.3	0.0	0.93
			Site+flwr dens+log(distance)	1234.2	5.9	0.05
			Site+distance	1236.3	8.0	0.02
		Mel120	Site+log(distance)	796.6	0.0	0.76
			Site+flwr dens+log(distance)	799.1	2.5	0.22
			Site+distance	804.4	7.8	0.12
Square-root transformed mass of seeds per fruit	2011	Control	Site+log(distance)	-624.5	0.0	1.00
			Site+distance	-611.3	13.2	0.00
			Site	-604.0	20.5	0.00
		Mel40	Site+log(distance)	-1582.9	0.0	0.96
			Site+distance	-1576.3	6.6	0.04
			Site+distance+distance ²	-1553.6	29.3	0.00
	2012	Control	Site+log(distance)	-554.1	0	0.88
			None (mean)	-548.9	5.2	0.07
			Site+distance	-547.5	6.6	0.03
		Mel40	Site+log(distance)	-835.8	0.0	0.96
			Site+distance	-829.3	6.5	0.04
			Site+flwr dens	-824.7	11.1	0.00
		Mel120	None (mean)	-560.0	0.0	0.99
			Site+log(distance)	-549.7	10.3	0.01
			Site+distance	-543.6	16.4	0.00

Note: The table presents the top three models out of nine candidate models describing possible relationships between the response variable, site effects ("site," included as the random effect), plot flower density ("flwr dens"), and distance from the site center ("distance") in null, linear, quadratic, or logarithmic forms. Candidate models included $y = \text{mean}$, $y = \text{site}$, $y = \text{site} + \text{distance}$, $y = \text{site} + \text{distance} + \text{distance}^2$, $y = \text{site} + \log(\text{distance})$, $y = \text{site} + \text{flwr dens} + \text{distance}$, $y = \text{site} + \text{flwr dens} + \text{distance} + \text{distance}^2$, $y = \text{site} + \text{flwr dens} + \log(\text{distance})$. Models with $\Delta AIC_c < 2$ are indicated in bold.

for a significant interaction (GLMM type 3 fixed effect: 2011, $F_{[1,294]} = 2.20$, $p = 0.14$; 2012, $F_{[2,360]} = 0.95$, $p = 0.39$).

Rhododendron groenlandicum

Conspecific flower density at the plant neighborhood scale had a positive relationship with the percentage of *R. groenlandicum* flowers pollinated in 2011 (Table 3; GLMM type 3 fixed effect: $F_{[1,282]} = 4.63$, $p = 0.03$; parameter estimates: control = 0.06, Mel 40 = 0.03). The conspecific flower density tended to be lower near the site center (flowers per plot = $20.2 \times \log_{10}(\text{distance}) - 19.3$, GLMM type 3 fixed effect: $F_{[1,312]} = 3.55$, $p = 0.06$). Flower density was not included in the top models for percent *R. groenlandicum* flowers pollinated in 2012, or for seed mass per fruit in either year (Table 3).

The best model for the relationship between the percentage of flowers pollinated in 2011 and log of distance was positive for the control sites and negative for the Mel40 sites, although both effects were weak (Table 3; Fig. 2A). In 2012, the percentage of flowers pollinated did not change with distance from control

sites but had a strong positive log-relationship with distance for both *M. albus* addition treatments. *Rhododendron groenlandicum* within 10 m of the invasive patch had approximately 10% fewer flowers pollinated than average for the site (Fig. 2B). Again, however, there was no statistically significant interaction in the GLMM model (2011, $F_{[1,282]} = 0.17$, $p = 0.68$; 2012, $F_{[1,270]} = 0.11$, $p = 0.90$). In both years, seed mass per fruit had a positive relationship with log of distance in control sites but no change with distance in sites with *M. albus* added (Figs. 2C, 2D; Table 3). This resulted in a significant interaction between treatment and distance in 2011 ($F_{[1,312]} = 5.01$, $p = 0.02$) but not in 2012 ($F_{[2,286]} = 0.54$, $p = 0.58$).

Discussion

Our data supports the hypothesis that the detectable impact an invasive species has on the pollination of native species is affected by the spatial scale over which it is evaluated. The percentage of flowers pollinated was better explained by models that included the logarithm of

Fig. 1. Relationship between distance from the site center and percent flowers pollinated for *Vaccinium vitis-idaea* (A, B) and seeds per fruit (C, D) in the control sites, and sites with 40 or 120 *Melilotus albus* plants added in 2011 and 2012. Each line represents the best supported model after the site effects, and in some cases plot flower density effects, had been removed to isolate the distance effect; *, $p < 0.05$ and †, $p < 0.10$ for differences between treatment means.

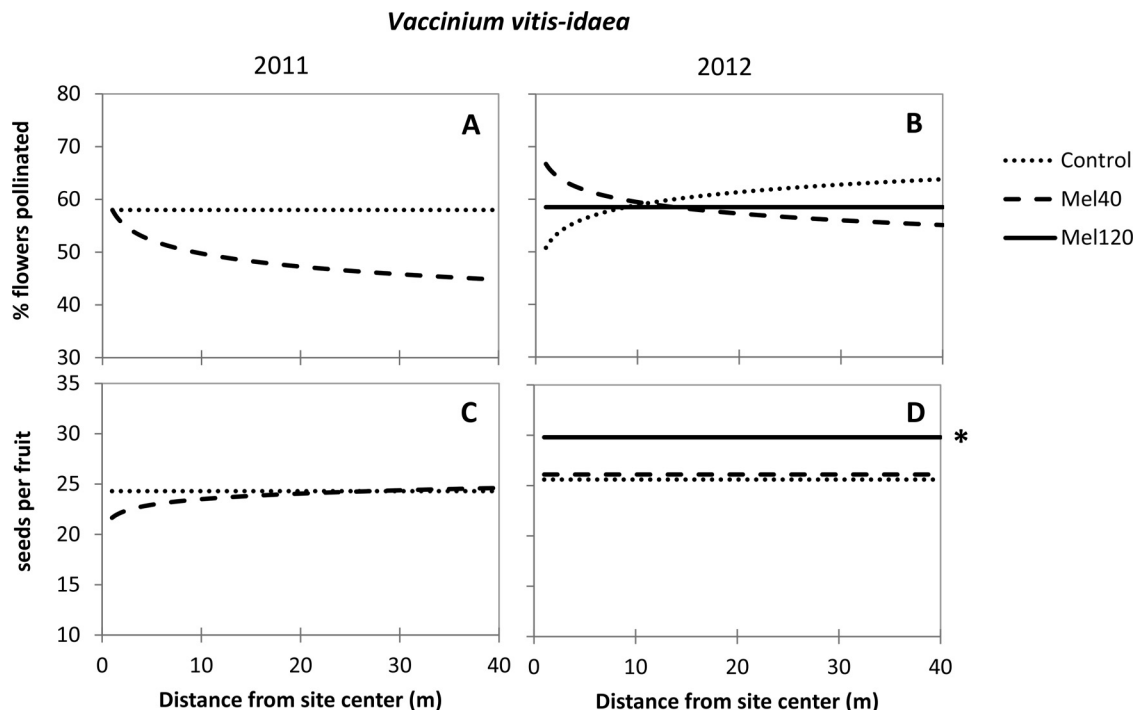
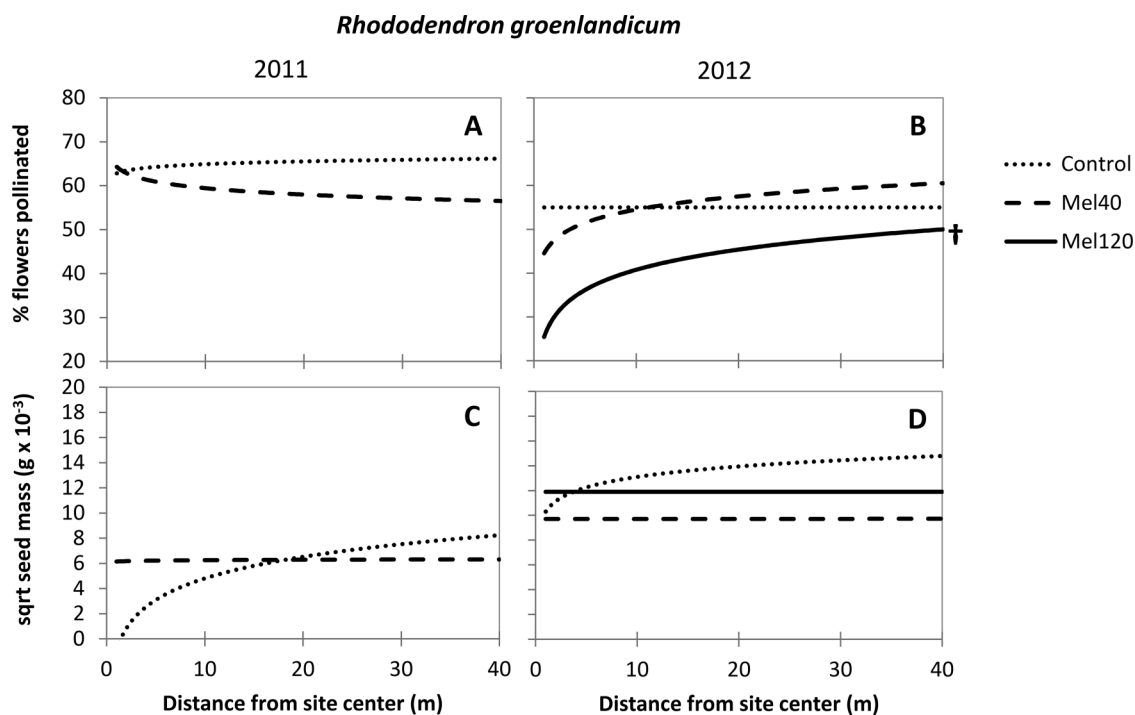


Fig. 2. Relationship between distance from the site center and percent flowers pollinated for *Rhododendron groenlandicum* (A, B) and square-root transformed seed mass per fruit (C, D) in the control sites, and sites with 40 or 120 *Melilotus albus* plants added in 2011 and 2012. Each line represents the best supported model after the site effects, and in some cases plot flower density effects, had been removed to isolate the distance effect; *, $p < 0.05$ and †, $p < 0.10$ for difference between treatment means.



distance than by those that did not in all but one case (Figs. 1 and 2). While there were also two instances of nonlinear relationships with distance in control plots, in both cases the direction of the relationship was the opposite of that for plots where *M. albus* was added, and they were likely driven by limitations of the experimental design (see further explanations below). Furthermore, evaluating changes over space helped unmask some effects of the presence of *M. albus* that were hidden in our whole-site comparisons. In contrast, there was little support for a change in *V. vitis-idaea* seed production over space with the addition of *M. albus*.

While we found evidence for shifts in pollination (and, to a lesser extent, seed production) with distance from the invasive patch, these shifts differed between years and species. Differences between years are likely due to different levels of competition for pollinators. In 2012, conditions were more favorable for pollination than in the cooler and rainier than average 2011 (Alaska Climate Research Center 2014), making competition for pollinators potentially greater in 2011. The most likely explanation for differences between species is that they have different primary pollinators; the presence of *M. albus* affects not only changes the abundance of pollinators but also their diversity and community composition (Spellman et al. 2015). The terminal umbrella-like clusters of flowers in *R. groenlandicum* are much more generalist than the small buzz-pollinated, bell-shaped *V. vitis-idaea* flowers (Davis 2002; Holloway 2006). In interior Alaska, bumblebees (*Bombus* spp.) and solitary bees are the primary pollinators for *V. vitis-idaea*, and wasps, flies, butterflies, and moths occasionally visit and carry pollen (Davis 2002; Davis et al. 2003, Holloway 2006). *Rhododendron groenlandicum* is visited by a wider range of primary pollinators, including all the aforementioned guilds, with the greatest number of visits from Lepidopterans when they were present (approx. 65% of the visits; L. Schneller, unpublished data, 2014). Butterflies, syrphid flies, other types of flies, and wasps were only present in site where we added *M. albus*, whereas bumblebees and solitary bees were present in all sites (Spellman et al. 2015). Other studies have found that the identity and degree of overlap of the primary pollinators are important for determining the direction and scale of an invasive plant's impact on the pollination of native species (Moragues and Traveset 2005; Jakobsson et al. 2009; Jakobsson and Padron 2014). The foraging strategy of the primary pollinators of our focal species and their presence or absence in the sites with and without *M. albus* helps provide mechanistic explanations of why we observed effects at different scales, which we explain for specific cases below.

For *V. vitis-idaea*, we had earlier reported no overall effect of adding *M. albus* on the percent of flowers pollinated (Spellman et al. 2015). However, this may be due to differing effects at different distances from the invasive

patch. The best model suggested that in the Mel40 treatment pollination was greatest close to the small patch of *M. albus* in both years and declined rapidly, suggesting that this species benefits from the attraction that *M. albus* has for pollinators only over very short distances (<10 m). This is consistent with previous studies that documented impacts of invasives primarily on pollination of natives directly adjacent to invasive plant patches (Moragues and Traveset 2005; Nielsen et al. 2008; Takakura et al. 2011; Cawoy et al. 2012). In contrast, pollination levels of *V. vitis-idaea* at sites with large patches of *M. albus* (Mel120 treatment) were uniform with distance, suggesting patch size may affect the range of the effect on non-native plants. This could be the result of new pollinator guilds being attracted to the site, such as Lepidopterans, which have increased flight distances between flowers relative to the pollinators in control sites (*Bombus* spp. and solitary bees) (Proctor et al. 1996).

The pattern for seeds per fruit was markedly different: seed production in 2011 was lowest near the invasive patch (Fig. 1C), despite the higher levels of pollination. While at first glance this is counterintuitive, this may indicate a change in the level of outcrossing experienced by these plants. *Vaccinium vitis-idaea* is a clonal species (Jacquemart and Thompson 1996). If pollinators attracted by *M. albus* remain in close proximity to that patch, then pollen transfer between individuals of *V. vitis-idaea* is likely to occur between ramets of the same genet. Since *V. vitis-idaea* is partially self-incompatible (Jacquemart and Thompson 1996), this is likely to lead to reduced fertilization rates. This effect would be expected particularly with the foraging strategy of *Bombus* spp., which optimizes trips by minimizing the flight distances between flowers in dense patches (Proctor et al. 1996).

Even though for the percentage of flowers pollinated (both years) and seeds per fruit (2011 only) the best models supported different relationships with distance in the control vs. treatment sites (e.g., logarithmic vs. linear, or positive vs. negative logarithmic relationships), and there was strong support for these best models, we did not detect a statistically significant interaction between treatment and distance in our GLMMs. We therefore cannot conclude that *V. vitis-idaea* had lower pollination at distances >10 m from the invasive species patch than it does at locations without the invasive plants. However, replication was much higher at the within-site level (25 plots per site) than the between-site level (4–11 replicates per treatment), so this may simply reflect low power to detect such an interaction.

Pollination rates for *R. groenlandicum* increased with greater densities of neighboring conspecific flowers in 2011, as has been demonstrated in other studies of flower density and pollination (Bosch and Waser 2001). However, patterns over space existed even after flower density was taken into account. We reported earlier on a reduction in percent flowers pollinated at when large

M. albus patches were added (Mel120) (Spellman et al. 2015); our results demonstrate that this difference is due primarily to a large reduction (>30%) in the percent of plants that were pollinated immediately adjacent to the *M. albus* patch. The same pattern (a positive log-linear relationship with distance) was visible for the Mel40 treatment, although the overall mean was greater.

Seed production in *R. groenlandicum* was uniform over space for the *Melilotus* addition plots, but increased with distance from the center for control sites, and this effect was strong enough to result in a significant interaction between treatment type and distance in 2011. This pattern of reduced *R. groenlandicum* seed production near the center of the control sites may have been the result of our site design. We could not randomly select the location of the center of each site because of the requirement for 25 flowering individuals 1–2 m from the center. This spatial constraint for the distribution of plots near the site center increased the potential for within-genet pollen transfer and may have reduced seed set in this partially self-incompatible species (Wheelwright et al. 2006) compared with plots farther away. In sites where *M. albus* was added, the attraction of Lepidopterans may have increased out-crossing and seed production near the site center.

Overall, our results suggest caution in interpreting results from experimental studies, especially those limited to a single spatial scale. Effects of non-native species on pollination may have very different effects at other spatial scales, spatial effects for pollination may differ from those for seed set (especially for self-incompatible species), and the same non-native species may have different effects on different native plants with which it shares pollinators. Combined, these results suggest that to make accurate predictions about effects of non-native species on pollination and fruit set of native species, information will need to be obtained on multiple spatial scales for multiple species.

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References

(AKEPIC) Alaska Exotic Plant Information Clearing House. 2014. AKEPIC Mapping Project Inventory Field Data. University of Alaska Anchorage Alaska Natural Heritage Program and USDA Forest Service, Anchorage, Alaska [online]. Available

- from <http://akweeds.uaa.alaska.edu/> [accessed 13 November 2015].
- Alaska Climate Research Center. 2014. Monthly city summary archive. University of Alaska Fairbanks Geophysical Institute, Fairbanks, Alaska [online]. Available from <http://climate.gi.alaska.edu/city-archive/> [accessed 13 November 2015].
- Bartomeus, I., Bosch, J., and Vilà, M. 2008. High invasive pollen transfer, yet low deposition on native stigmas in a *Carpobrotus*-invaded community. *Ann. Bot.* **102**(3): 417–424. doi:10.1093/aob/mcn109. PMID:18593688.
- Bartomeus, I., Vilà, M., and Steffan-Dewenter, I. 2010. Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *J. Ecol.* **98**(2): 440–450. doi:10.1111/j.1365-2745.2009.01629.x.
- Beekman, M., and Ratnieks, F.L.W. 2000. Long-range foraging by the honey-bee, *Apis mellifera* L. *Funct. Ecol.* **14**(4): 490–496. doi:10.1046/j.1365-2435.2000.00443.
- Bella, E.M. 2011. Invasion prediction on Alaska trails: distribution, habitat, and trail use. *Invasive Plant Sci. Manage.* **4**(3): 296–305. doi:10.1614/IPSM-D-10-00083.1.
- Bosch, M., and Waser, N.M. 2001. Experimental manipulation of plant density and its effect on pollination and reproduction of two confamilial montane herbs. *Oecologia*, **126**(1): 76–83. doi:10.1007/s004420000488.
- Brown, B.J., Mitchell, R.J., and Graham, S.A. 2002. Competition for pollination between an invasive species (purple looses-trife) and a native congener. *Ecology*, **83**(8): 2328–2336. doi:10.1890/0012-9658(2002)083[2328:CFPBAI]2.0.CO;2.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Springer, New York.
- Campbell, D.R. 1985. Pollinator sharing and seed set of *Stellaria pubera*: competition for pollination. *Ecology*, **66**(2): 544–553. doi:10.2307/1940403.
- Cawoy, V., Jonard, M., Mayer, C., and Jacquemart, A.L. 2012. Do abundance and proximity of the alien *Impatiens glandulifera* affect pollination and reproductive success of two sympatric co-flowering native species? *J. Pollinat. Ecol.* **10**(17): 130–139.
- Chittka, L., and Schürkens, S. 2001. Successful invasion of a floral market. *Nature*, **411**: 653. doi:10.1038/35079676. PMID:11395755.
- Conn, J.S., Beattie, K.L., Shephard, M.A., Carlson, M.L., Lapina, I., Hebert, M., Gronquist, R., Densmore, R., and Rasy, M. 2008. Alaska *Melilotus* invasions: distribution, origin, and susceptibility of plant communities. *Arct. Antarct. Alp. Res.* **40**(2): 298–308. doi:10.1657/1523-0430(06-007)[CONN]2.0.CO;2.
- Da Silva, E.M., King, V.M., Russell-Mercier, J.L., and Sargent, R.D. 2013. Evidence for pollen limitation of a native plant in invaded communities. *Oecologia*, **172**(2): 469–476. doi:10.1007/s00442-012-2513-7. PMID:23129400.
- Davis, A.N. 2002. Pollination biology of the lingonberry, *Vaccinium vitis-idaea* subsp. *minus* L. MSc. thesis, University of Alaska Fairbanks, Fairbanks, Alaska.
- Davis, A.N., Holloway, P.S., and Kruse, J.J. 2003. Insect visitors and potential pollinators of lingonberries, *Vaccinium vitis-idaea* subsp. *minus*, in sub-arctic Alaska. *Acta Hort.* **626**: 441–446. doi:10.17660/actahortic.2003.626.60.
- Flanagan, R.J., Mitchell, R.J., and Karron, J.D. 2010. Increased relative abundance of an invasive competitor for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. *Oecologia*, **164**: 445–454. doi:10.1007/s00442-010-1693-2. PMID:20585807.
- Gathmann, A., and Tschardt, T. 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* **71**(5): 757–764. doi:10.1046/j.1365-2656.2002.00641.x.
- Holloway, P.S. 2006. Managing wild bog blueberry, lingonberry, cloudberry, and crowberry stands in Alaska. Report for Uni-

- versity of Alaska Fairbanks and Natural Resource Conservation Service, Fairbanks, AK.
- Irwin, D.L. 1945. Forty-seven years of experimental work with grasses and legumes in Alaska. University of Alaska Agricultural Experiment Station Bulletin 12, College, Alaska.
- Jacquemart, A.L., and Thompson, J.D. 1996. Floral and pollination biology of three sympatric *Vaccinium* (Ericaceae) species in the upper Ardennes, Belgium. *Can. J. Bot.* **74**(2): 210–221. doi:10.1139/b96-025.
- Jakobsson, A., and Padrón, B. 2014. Does the invasive *Lupinus polyphyllus* increase pollinator visitation to a native herb through effects on pollinator population sizes? *Oecologia*, **174**: 217–226. doi:10.1007/s00442-013-2756-y. PMID:24061551.
- Jakobsson, A., Padrón, B., and Traveset, A. 2009. Competition for pollinators between invasive and native plants: effects of spatial scale of investigation (note). *Ecoscience*, **16**(1): 138–141. doi:10.2980/16-1-3193.
- Kandori, I., Hirao, T., Matsunaga, S., and Kurosaki, T. 2009. An invasive dandelion unilaterally reduces the reproduction of a native congener through competition for pollination. *Oecologia*, **159**(3): 559–569. doi:10.1007/s00442-008-1250-4. PMID:19153768.
- Kearns, C.A., and Inouye, D.W. 1993. Techniques for pollination biologists. University of Colorado Press, Niwot, Colo.
- Kevan, P.G., Tikhmenev, E.A., and Usui, M. 1993. Insects and plants in the pollination ecology of the boreal zone. *Ecol. Res.* **8**(3): 247–267. doi:10.1007/BF02347185.
- Klebesadel, L.J. 1992. Morphological, physiological, and winter-hardiness comparisons among latitudinal ecotypes of biennial sweetclover (*Melilotus* species) in subarctic Alaska. In *Agricultural and Forestry Experiment Station Bulletin 91*, School of Agriculture and Land Resources Management, University of Alaska Fairbanks, Palmer, Alaska.
- Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, R.A., and Goulson, D. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Mol. Ecol.* **14**(6): 1811–1820. doi:10.1111/j.1365-294X.2005.02540.x. PMID:15836652.
- Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., and Lavelle, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Biol. Sci. Ser. B*, **270**(1517): 775–781. doi:10.1098/rspb.2003.2327.
- Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R., and Memmott, J. 2007. The impact of an alien plant on a native plant-pollinator network: an experimental approach. *Ecol. Lett.* **10**(7): 539–550. doi:10.1111/j.1461-0248.2007.01055.x. PMID:17542933.
- Malacalza, N.H., Caccavari, M.A., Fagúndez, G., and Lupano, C.E. 2005. Unifloral honeys of the province of Buenos Aires, Argentina. *J. Sci. Food Agric.* **85**(8): 1389–1396. doi:10.1002/jsfa.2105.
- Molina-Montenegro, M.A., Badano, E.I., and Cavieres, L.A. 2008. Positive interactions among plant species for pollinator service: assessing the 'magnet species' concept with invasive species. *Oikos*, **117**(12): 1833–1839. doi:10.1111/j.0030-1299.2008.16896.x.
- Moragues, E., and Traveset, A. 2005. Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. *Biol. Conserv.* **122**(4): 611–619. doi:10.1016/j.biocon.2004.09.015.
- Morales, C.L., and Traveset, A. 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Crit. Rev. Plant Sci.* **27**(4): 221–238. doi:10.1080/07352680802205631.
- Muñoz, A.A., and Cavieres, L.A. 2008. The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *J. Ecol.* **96**(3): 459–467. doi:10.1111/j.1365-2745.2008.01361.x.
- Nielsen, C., Heimes, C., and Kollmann, J. 2008. Little evidence for negative effects of an invasive alien plant on pollinator services. *Biol. Invasions*, **10**(8): 1353–1363. doi:10.1007/s10530-007-9210-1.
- Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., and Edwards, A.S. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *J. Appl. Ecol.* **36**(4): 519–533. doi:10.1046/j.1365-2664.1999.00428.x.
- Peterson, S.F. 1989. Beekeeping under the northern lights. *Am. Bee J.* **129**: 33–35.
- Proctor, M., Yeo, P., and Lack, A. 1996. The natural history of pollination. Timber Press, Portland.
- Rose, M., and Hermanutz, L. 2004. Are boreal ecosystems susceptible to alien plant invasion? Evidence from protected areas. *Oecologia*, **139**(3): 467–477. doi:10.1007/s00442-004-1527-1.
- Royer, F., and Dickinson, R. 1999. Weeds of the Northern U.S. and Canada. The University of Alberta Press, Edmonton, Alta.
- Sanderson, L.A., McLaughlin, J.A., and Antunes, P.M. 2012. The last great forest: a review of the status of invasive species in the North American boreal forest. *Forestry*, **85**: 329–340. doi:10.1093/forestry/cps033.
- Skurski, T.C., Rew, L.J., and Maxwell, B.D. 2014. Mechanisms underlying nonindigenous plant impacts: a review of recent experimental research. *Invasive Plant Sci. Manage.* **7**(3): 432–444. doi:10.1614/IPSM-D-13-00099.1.
- Spellman, B.T., and Wurtz, T. 2011. Invasive white sweetclover (*Melilotus officinalis*) impacts native recruitment along rivers in interior Alaska. *Biol. Invasions*, **13**(8): 1779–1790. doi:10.1007/s10530-010-9931-4.
- Spellman, K.V., Mulder, C.P.H., and Hollingsworth, T.N. 2014. Susceptibility of burned black spruce (*Picea mariana*) forests to non-native plant invasions in Interior Alaska. *Biol. Invasions*, **16**(9): 1879–1895. doi:10.1007/s10530-013-0633-6.
- Spellman, K.V., Schneller, L.C., Mulder, C.P.H., and Carlson, M.L. 2015. Effects of non-native *Melilotus albus* on pollination and reproduction in two boreal shrubs. *Oecologia*, **179**(2): 495–507. doi:10.1007/s00442-015-3364-9. PMID:26071209.
- Takakura, K., Matsumoto, T., Nishida, T., and Nishida, S. 2011. Effective range of reproductive interference exerted by an alien dandelion, *Taraxacum officinale*, on a native congener. *J. Plant Res.* **124**(2): 269–276. doi:10.1007/s10265-010-0368-8. PMID:20676914.
- Tepedino, V.J., Bradley, B.A., and Griswold, T.L. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. *Nat. Areas J.* **28**(1): 44–50. doi:10.3375/0885-8608(2008)28[44:MFOIPJ]2.0.CO;2.
- Villano, K.L., and Mulder, C.P.H. 2008. Invasive plant spread in burned lands of interior Alaska. National Park Service-Alaska Region and National Aeronautics and Space Administration Technical Report, Fairbanks, Alaska. Available from <http://aknhp.uaa.alaska.edu/botany/akepic/publications/> [accessed 13 November 2015].
- Waser, N.M. 1983. Competition for pollination and floral character differences among sympatric plant species: a review of evidence. In *Handbook of experimental pollination biology*. Edited by C.E. Jones and R.J. Little. Van Nostrand Reinhold Inc., New York, pp. 277–293.
- Wheelwright, N.T., Dukeshire, E.E., Fontaine, J.B., Gutow, S.H., Moeller, D.A., Schuetz, J.G., Smith, T.M., Rodgers, S.L., and Zink, A.G. 2006. Pollinator limitation, autogamy and minimal inbreeding depression in insect-pollinated plants on a boreal island. *Am. Midland Nat.* **155**(1): 19–38. Available from doi:10.1674/0003-0031(2006)155[0019:PLAAMI]2.0.CO;2.