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PLANT-MICROBE-ANIMAL INTERACTIONS – ORIGINAL RESEARCH

Effects of non-native *Melilotus albus* on pollination and reproduction in two boreal shrubs

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Abstract The establishment of abundantly flowered, highly rewarding non-native plant species is expected to have strong consequences for native plants through altered pollination services, particularly in boreal forest where the flowering season is short and the pollinator pool is small. In 18 boreal forest sites, we added flowering *Melilotus albus* to some sites and left some sites as controls in 2 different years to test if the invasive plant influences the pollination and reproductive success of two co-flowering ericaceous species: *Vaccinium vitis-idaea* and *Rhododendron groenlandicum.* We found that *M. albus* increased the pollinator diversity and tended to increase visitation rates to the focal native plant species compared to control sites. *Melilotus albus* facilitated greater seed production per berry in *V. vitis-idaea* when we added 120 plants compared to when we added 40 plants or in control sites. In *R. groenlandicum,* increasing numbers of *M. albus* inflorescences lowered conspecific pollen loads and percentage of flowers pollinated; however, no differences in fruit set were detected. The number of *M. albus* inflorescences had greater importance in explaining *R. groenlandicum* pollination compared to other environmental variables such as weather and number of native flowers, and had greater importance in lower quality black spruce sites than in mixed deciduous and white spruce sites for explaining the percentage of *V. vitis-idaea* flowers pollinated. Our data suggest that the identity of new pollinators attracted to the invaded sites, degree of shared pollinators between invasive and native species, and variation in resource limitation among sites are likely determining factors in the reproductive responses of boreal native plants in the presence of an invasive.

Keywords Fruit set · Invasive species · *Ledum palustre* ssp. *groenlandicum* · Seed set · *Rhododendron groenlandicum* · *Vaccinium vitis-idaea*

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Introduction

Non-native plants that invade flowering plant communities can have diverse effects on the reproductive success

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of native plants. Competitive effects of non-native plant introductions on pollination of native species occur through two often co-occurring mechanisms: (a) decreases in pollen quantity, and (b) decreases in pollen quality (Waser 1978). Non-native plant invasions can reduce pollen quantity delivered to native plants by decreasing visitation rates to the native species as a result of pollinator preference for the invasive flowers (Waser 1983; Campbell 1985; Brown et al. 2002; Kandori et al. 2009). Non-native species can decrease pollen quality if they increase the amount of self- or heterospecific pollen being delivered (Morales and Traveset 2008). Conversely, some studies have demonstrated that the presence of invasive plants increased overall pollinator abundances or visitation rates to the entire community, which increased pollen quantity, fruit yield and seed production (Moragues and Traveset 2005; Tepedino et al. 2008). Other studies have found no measurable impacts of invasive plants on the pollination and reproduction of native plants (Bartomeus et al. 2008a). The range of effects invasive plants can have on the pollination of native plants suggests that unique attributes within the plant and pollinator communities can have a large influence on the impact of the invasive plants.

The abundance of invasive plant flowers within the flowering plant community at a site changes pollen flow to the native plants and subsequent reproductive success (Muñoz and Cavieres 2008; Molina-Montenegro et al. 2008; Flanagan et al. 2010). The relative influence an invasive plant has on the reproduction of native plants may also vary with other factors that would be expected to affect plant reproduction, such as habitat type, weather, and inter- or intraspecific competition with other native flowers. Pollinator visitation rates can differ among different habitat types due to differences in conspecific and heterospecific flower abundances, amount of shade, or availability of pollinator nesting sites (Westrich 1996; Gathmann and Tscharntke 2002; Westphal et al. 2003; Bartomeus et al. 2010). Differences in weather between years or between sites can change pollination services by influencing the time available for pollinator flight activity (Kuchko 1988; Tuell and Isaacs 2010), by affecting which types of pollinators are active (Corbett et al. 1993), and by directly affecting resources for flower and fruit growth and maintenance (Jacquemart 1997; Krebs et al. 2009).

Relative to other forest types, boreal forest ecosystems tend to have fewer flowering species, smaller pollinator pools, and shorter flowering periods (Kevan et al. 1993). These factors could intensify the potential negative or positive impacts of non-native plant invasions on the reproductive success of neighboring native plant species (cf. Carlson et al. 2008). Despite the fact that the boreal forest is one of the largest terrestrial biomes on Earth [a third of the world's forested land (Shugart et al. 1992)], to date we could find only a single study on the impact of invasive plants on the pollination and reproductive success of native plants in the boreal forest that has been published in English in the peer-reviewed literature (see Totland et al. 2006). This single study found that the experimental outplanting of non-native *Phacelia tanacetifolia* strongly decreased pollinator visitation to a native boreal plant species (*Melampyrum pratense*) but did not change fruit set or seed production (Totland et al. 2006). High resource limitations on plant reproduction in boreal forest habitats may explain why the substantial change in pollinator visitation to the native plant did not lead to a change in reproductive success. Without stigmatic pollen load data, however, the Totland et al. (2006) study could not disentangle the relative influence of pollen limitation and resource limitation on plant reproduction in their field sites.

Compared to other places, low levels of anthropogenic disturbance and cold climate have limited the introduction and survival rates of non-native plants in the boreal forest (Sanderson et al. 2012). However, the number of non-native species occurring within Alaska increased by 46 % between 1941 and 2006 (Carlson and Shephard 2007). Increases in the number and extent of non-native species in Alaska may be attributed in large part to increases in human population and associated disturbances [e.g., more roads, resource extraction (Walker and Walker 1991; US Census Bureau 2010; Carlson and Shephard 2007)] and increased influx of propagules via imported agricultural and horticultural commodities (Conn et al. 2008a). Climatic shifts in Alaska such as warmer winters (Serreze et al. 2000) and longer growing seasons (Myneni et al. 1997) have also increased the likelihood of invasive plant success.

A few species, such as *Melilotus albus* Medik., have spread rapidly throughout the state, primarily along road corridors (AKEPIC 2014). *M. albus* is one of the few non-native species in Alaska that has also spread widely into naturally disturbed areas such as river floodplains (Conn et al. 2008b; Spellman and Wurtz 2011) and wildfire scars (Spellman et al. 2014). *M. albus* is native to Eurasia and was introduced to Alaska in 1913 as a potential cold-hardy forage and nitrogen-fixing crop (Irwin 1945), and now occurs throughout Alaska from as far south as Metlakatla (55.122ºN, −131.561ºW) to north of Coldfoot (67.286ºN, −150.171ºW) at the base of the Brooks Mountain Range (AKEPIC 2014). *M. albus* can reduce native seedling recruitment along glacial river floodplains by directly competing with native plants for light (Spellman and Wurtz 2011). Additionally, this species 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)], particularly in comparison to native boreal insect-pollinated plants that

offer less pollen and nectar rewards. As a result, *M. albus* invasions could also alter plant communities by changing the pollination and reproductive success of native boreal plants.

In many of the instances of *M. albus* invasion documented in or adjacent to burned boreal forest (Villano and Mulder 2008), the understory is dominated by *Vaccinium vitis-idaea* L. (lingonberry or lowbush cranberry) and *Rhododendron groenlandicum* (Oeder) Kron and Judd (formerly *Ledum palustre* ssp. *groelandicum*; Labrador tea), two abundant insect-pollinated Ericaceous plant species that have broad circumboreal distributions (Hultén 1968). These species are of cultural, subsistence, and economic importance (Garibaldi 1999; Quiner 2005; Holloway 2006; Nelson et al. 2008). Because both species overlap with *M. albus* in habitat (Villano and Mulder 2008), flowering times (personal observation), and pollinator communities (Turkington et al. 1978; Eckardt 1987; Davis et al. 2003; Dlusski et al. 2005; Tepedino et al. 2008), we chose to focus on *V. vitis-idaea* and *R. groenlandicum* in this study. Within interior Alaska, bumblebees (*Bombus* spp.), syrphid flies (Syrphidae), and solitary bees (*Adrena* spp.) are the pollinators that carry the greatest amount of *V. vitis-idaea* pollen (Davis et al. 2003), but other pollinator guilds carry its pollen as well [e.g., Lepidopterans, other flies, beetles (Davis 2002)]. *R. groenlandicum* is visited by pollinators in all the aforementioned guilds (personal observation). *M. albus* has generalist flowers visited by a wide range of species, including solitary bees, bumblebees, wasps, flies, butterflies, and moths (Coe and Martin 1920; Turkington et al. 1978; Tepedino et al. 2008). *V. vitis-idaea* and *R. groenlandicum* are self-compatible (Jacquemart and Thompson 1996; Jacquemart 1997; Wheelwright et al. 2006). Both species, however, have decreased fruit and seed set when insect pollinators are excluded and increase fruit set and seed production when they are supplemented with outcross pollen (Hall and Beil 1970; Fröborg 1996; Jacquemart and Thompson 1996; Davis 2002; Wheelwright et al. 2006). This was confirmed in interior Alaska, where flowers from which pollinators were excluded showed a 79 and 18 % reduction in fruit set for *V. vitis-idaea* and *R. groenlandicum,* respectively, compared to flowers open to insect pollination (C. P. H. Mulder and K. V. Spellman, unpublished data).

We conducted a preliminary observational study during the summer of 2010 to compare insect pollinator visitation to native plants and *V. vitis-idaea* fruit set at sites with and without *M. albus* along the roadside. These sites were located throughout interior Alaska, along the Steese, Elliot, and Dalton highways. The abundance of insect pollinators observed at sites with flowering *M. albus* was approximately two times higher than at sites without *M. albus* (L. C. Schneller, unpublished data). The sites with *M.*

albus also had a greater proportion of *V. vitis-idaea* flowers setting fruit compared to sites without *M. albus* present (49 ± 20 % in sites with *M. albus*, 16 ± 7 % in sites without *M. albus*; C. P. H. Mulder, unpublished data). However, we could not attribute these changes in pollinator activity and *V. vitis-idaea* fruit set to the presence of *M. albus*, as site conditions that favor *M. albus* establishment may also favor higher pollinator activity, and promote greater abundance of native flowers and greater fruit set. To disentangle potential confounding environmental effects, we conducted a controlled *M. albus* addition experiment, which we report here. Specifically, we ask these questions:

1. Does *M. albus* addition alter *V. vitis-idaea* and *R. groenlandicum* pollination and reproduction?
2. Does the abundance of *M. albus* vary the effect it has on pollination and reproduction of these native plants?
3. How important is the influence of *M. albus* relative to other factors expected to influence native plant reproduction such as weather and number of native flowers?

Materials and methods

Study area

During the growing seasons in 2011 and 2012, we located boreal forest sites within the Bonanza Creek Boreal Long-Term Ecological Research Program 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 flowering *V. vitis-idaea* and *R. groenlandicum,* and primarily occurred in two habitat types: (a) "mixed" sites that contain deciduous tree species (*Betula neoalaskana* Sarg. and/or *Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss); and (b) black spruce (*Picea mariana* Mill.) sites (Appendix 1). The mixed sites tended to occur on gentle hill slopes (3–10 % grade) or at the tops of hills with understory vegetation composed primarily of the two focal species, *Vaccinium uliginosum*, *Rosa acicularis*, *Viburnum edule, Salix* spp.*, Alnus viridis, Geocaulon lividum,* and *Cornus canadensis*. The black spruce sites occurred in low-lying areas with minimal slope (0–3 % grade) and understory vegetation composed primarily of the two focal species, *Vaccinium uliginosum*, *Rubus chamaemorus*, *Salix* spp., and moss species. The mixed deciduous and white spruce stands had greater average canopy cover than the black spruce sites (56 % in mixed deciduous-spruce sites and 17 % in black spruce sites) and greater abundances of native flowers (~1.8 times the number of flowers per square meter).

Table 1 Number of sites for each species and in different habitat types in 2011 and 2012 by treatment

Species	Habitat type	Year and treatment				
		2011		2012		
		Control	Mel 40	Control	Mel 40	Mel 120
Vaccinium vitis-idaea	Mixed	4	5	4	2	5
	Black spruce	2	5	2	4	1
	Total	6	10	6	6	6
Rhododendron groenlandicum	Mixed	2	5	2	2	3
	Black spruce	2	6	2	4	1
	Total	4	11	4	6	4

MEL 40 forty *M. albus* plants added, *MEL 120* one hundred and twenty *M. albus* plants added

Experimental design

In 2011, we selected 17 sites placed greater than 300 m apart to minimize pollinator movement between sites. Nine sites were in mixed deciduous and spruce sites and eight were in black spruce forest sites. Sites were circular and extended 40 m in all directions from the site center. *M. albus* did not occur at any of these sites. Eleven sites were randomly assigned to have 40 greenhouse-grown flowering second-year *M. albus* plants added to the site center (Mel 40), and six were control sites (no *M. albus* added). The sites contained one or both of the focal native species, with 16 sites containing *V. vitis-idaea* and 15 sites containing *R. groenlandicum* (Table 1).

In 2012, we discontinued the site that did not have *V. vitis-idaea* and added two new sites to bring the total number of sites to 18. To address the influence of invasive plant patch size on the reproductive success of our focal species, we added a higher *M. albus* addition level to our design in 2012 (120 plants added; Mel 120). The 18 sites were allocated to each of the three treatment levels: control, Mel 40, and Mel 120 (six sites each). To compare years directly, we retained the same treatments in six of the sites (three control and three Mel 40 sites). The remaining three control sites, three Mel 40 sites and six Mel 120 sites were randomly assigned. We assigned sites without respect to habitat type, but had multiple sites of each treatment in each with the exception of a single black spruce site that received the Mel 120 treatment (Table 1).

M. albus was added to the Mel 40 or Mel 120 sites at the time that *V. vitis-idaea* and *R. groenlandicum* flower buds emerged, but had not yet opened. *M. albus* were grown in the greenhouse in conetainer pots (7 cm diameter at the top, 22 cm in length); each pot contained one individual with five to 181 inflorescences [mean ($\pm$SE) 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 each pot was flush with the ground surface. *M. albus* density was 15 plants m^{-2}, resulting in circular patches approximately 2.6 and 8 m^2 in size. The range in number of inflorescences added to each site was 334–942 (16,366–46,158 total flowers) for Mel 40 sites and 1068–1608 (52,332–78,792 total flowers) for Mel 120 sites. The addition levels we used (Mel 40 and Mel 120) were comparable to the patch sizes and stem densities 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.

Within each site, 25 circular plots were established for each of the occurring focal species (1-m^2 plot for *V. vitis-idaea*, and 1.77-m^2 plot for *R. groenlandicum*) ranging from 1 to 40 m from the site center. Five plots were placed within five distance ranges from the site center: 1–2, 3–5, 8–10, 15–20 and 25–40 m. Within these plots, five *V. vitis-idaea* or five *R. groenlandicum* ramets were marked for tracking fruit set and seed production. In the 1- to 2-m distance category, focal plants were always selected outside of the *M. albus* patch to avoid plants where the root systems may have been damaged during the *M. albus* transplanting. This study focuses on whole-site impacts of *M. albus* on focal native species reproduction, and spatial variation of the effects within sites will be discussed in a forthcoming paper.

Pollinator activity and community

In 2011, we observed insect pollinator activity in 15 of the 17 sites (four control sites and 11 Mel 40 sites). We did not observe pollinator activity in 2012. Pollinator observations occurred between 8 a.m. and 6 p.m. during calm, rain-free periods from 6 to 18 June 2011. One focal plot per distance

category was randomly chosen for a 2-m × 2-m pollinator observation of 15 min, for a total of five observations per site. For each observation, we counted the total number of open flowers and then recorded pollinator landings on open flowers of focal species within the plot. Observed pollinators were grouped into categories (butterflies, wasps, bumblebees, solitary bees, syrphid flies, and non-syrphid flies) for field identification. We calculated visitation rates using insect landings per number of flowers per hour of observation in each plot within each of the 15 sites used for observations (12 sites with *V. vitis-idaea* present and 14 sites with *R. groenlandicum* present). We used four pairs of sites (the four control sites each paired with a Mel 40 site that was observed on the same day) to assess differences in the pollinator community composition between the treatments. Due to the overall low number of pollinator sightings in these sites, we pooled observations in the four control sites and the four Mel 40 sites to calculate Simpson's diversity index and proportional similarity (Brower and Zar 1984).

Pollination

To measure pollen deposition, 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 ~14 days after the *M. albus* was added. The stigmas were mounted on microscope slides and stained with a basic fuchsin gel (Kearns and Inouye 1993). Each pollen tetrad (in the case of *R. groenlandicum* and *V. vitis-idaea* pollen) or pollen grain (in the case of other species) on the stigma was identified to genus (using anther vouchers we collected from all flowering species at the sites as a reference) and counted under a compound light microscope. The proportion of heterospecific pollen grains on the stigmas was low (3.2 ± 0.3 % for *V. vitis-idaea* and 0.8 ± 0.2 % for *R. groenlandicum*), so only conspecific pollen loads on the stigmas were used in the final analysis.

Flowers were considered to be "well pollinated" when they had ten or more pollen tetrads on the stigma. We selected this threshold because and fruit production was greatest when the pollen loads exceeded this pollen level for both focal species in control sites (Appendix 2). Further, the maximum seed number per fruit in *V. vitis-idaea* control plots across the 2 years of study was 47, indicating that greater than ten pollen tetrads was 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.

Fruit set and seed production

We calculated percent fruit set as the percentage of flower buds on marked plants at the beginning of our experiment that produced fruit by the end of the growing season. 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 weight of the seeds was divided by the number of fruits on the inflorescences to derive seed mass per fruit.

Environmental covariates

We measured weather and vegetation variables that we expected to influence our response variables. Temperature and relative humidity (RH) during the experimental period (time of *M. albus* addition to time of *M. albus* removal in the site or nearest *M. albus* addition site for control sites) were obtained every 30 min using a HOBO-Pro data logger (Onset Computer, Cape Cod, MA) fixed 0.5 m above the ground surface at the center of each site. Number of hours of rain was estimated as number of hours with RH ≥ 100 %. Tree canopy cover was estimated for each of the 25 plots using a convex spherical crown densiometer (model A; Forest Densiometers, Bartlesville, OK) on the north and south edges of the plot. We visually estimated the percent shrub cover present above the *V. vitis-idaea* (up to 1 m in height) in each plot. *R. groenlandicum* was the tallest understory plant in the plots where it occurred, so shrub cover over this species was not a factor. To provide an estimate of flower abundance and richness, we counted the number of open flowers and flower buds present for each insect-pollinated species within the 25 plots at the time of *M. albus* addition.

Analysis

To test for differences in pollinator visitation rates between control and Mel 40 treatments, we used a non-parametric Wilcoxon rank sum test on site-level averages across five plots per site. All our other response variables were calculated as averages of 25 focal plant plots per site and met the assumptions of normality and constant variance. We performed the statistical analyses on the plant and environmental data using SAS version 9.1 (SAS Institute, Cary, NC) and the pollinator data using R version 2.14.2 (R Development Core Team 2012).

To determine the influence of the *M. albus* addition treatment and year on *V. vitis-idaea* and *R. groenlandicum* pollination, fruit set and seed production, we conducted multivariate ANOVA (MANOVA) using site-level means

of response variables for *V. vitis-idaea* and *R. groenlandicum*. The response variables in the multivariate models included number of conspecific pollen grains delivered to stigmas (hereafter "conspecific pollen"), percent flowers receiving ten or more pollen grains or tetrads (hereafter "percent pollinated flowers"), percent flowers setting fruit (hereafter "percent fruit set"), and number of seeds per fruit for *V. vitis-idaea* or seed mass per fruit for *R. groenlandicum* (hereafter "seeds or seed mass per fruit"). We conducted several tests to disentangle treatment, year and site effects. We first tested for a treatment effect in each year individually. We then tested for year, treatment, and year by treatment interactions using both years but excluding the sites that received the Mel 120 treatment in 2012 (since this treatment was not imposed in 2011). Finally, we evaluated site and year effects using only sites where the treatment remained the same across both years of the experiment. Separate ANOVAs were then run to assess which individual response variable responded most strongly to treatment and year effects, and to allow us to disentangle the relative roles of pollen limitation and resource limitation on our focal species' reproductive responses. This resulted in 32 ANOVA tests (4 response variables × 4 ANOVA tests × 2 species). We found six significant tests (Table 2) compared

Table 2 ANOVA results for models testing for *Melilotus albus* addition treatment (*Trt*) effects for four individual response variables (total pollen on stigmas, percent flowers pollinated, percent flowers setting fruit, and number of seeds per fruit for *V. vitis-idaea* or seed mass per fruit for *R. groenlandicum*)

Focal species	Data set	Source of variation	df	Error df	Conspecific pollen F	% Flowers pollinated F	% Fruit set F	Seeds or seed mass per fruit F
V. vitis-idaea	2011	Trt	1	14	0.01	1.04	0.03	0.13
	2012	Trt	2	15	0.27	0.02	1.09	6.30**
	2011 and 2012 excluding Mel 120	Year	1	24	0.01	1.20	12.06**	1.77
		Trt	1		0.19	0.45	1.59	0.04
		Year × Trt	1		0.28	0.71	1.39	0.19
	Sites where Trt remains same in 2011 and 2012	Site	5	5	2.09	0.82	1.39	0.66
		Year	1		0.36	0.06	7.67*	1.09
R. groenlandicum	2011	Trt	1	13	1.15	0.53	0.10	2.02
	2012	Trt	2	11	1.30	2.00	0.41	1.53
	2011 and 2012 excluding Mel 120	Year	1	21	1.17	1.31	0.12	24.58***
		Trt	1		0.35	0.25	0.04	0.13
		Year × Trt	1		0.54	0.26	0.04	4.57*
	Sites where Trt remains same in 2011 and 2012	Site	4	4	2.50	1.74	7.01	6.88
		Year	1		0.00	1.13	0.07	20.55*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Fig. 1 Pollinator visitation rates to *Vaccinium vitis-idaea* (**a**) and *Rhododendron groenlandicum* (**b**) flowers in sites without *Melilotus albus* added (*Control*) and in sites with 40 *M. albus* plants added (*Mel 40*). *Each box plot* shows the 1st quartile, median (*dark line*), and 3rd quartile, and *whiskers* show the minimum and maximum value range for pollinator visitation rates. Minimum, 1st quartile, and median values were equal to 0 in all cases
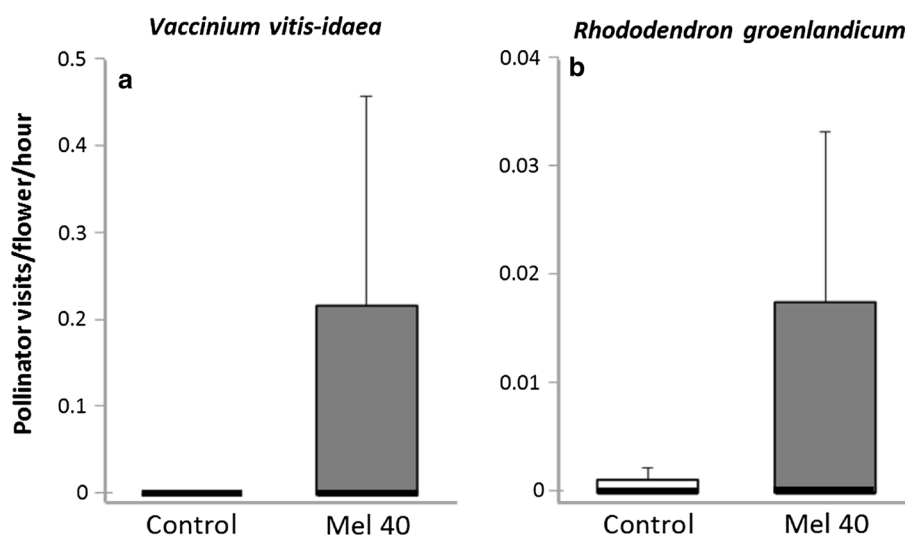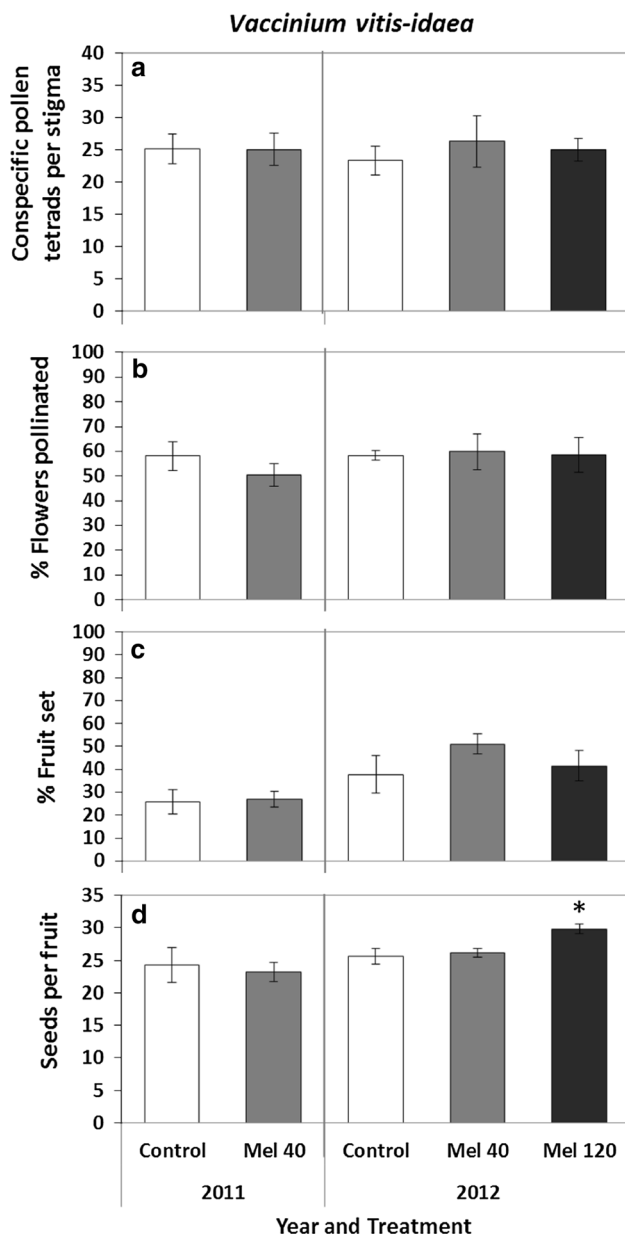
Fig. 2 *V. vitis-idaea* conspecific pollen loads on stigmas (**a**), percent flowers pollinated (**b**), percent flowers setting fruit (**c**), and number of seeds per fruit (**d**) in sites without *M. albus* (*Control*), Mel 40 sites, and sites with 120 *M. albus* plants added (*Mel 120*) during the summers of 2011 and 2012. *Bars* are mean ± SE of site-level averages for each treatment in each year. The Mel 120 treatment was only conducted in 2012. **p < 0.05, +p < 0.1* (for differences between treatment means)

to the 1.6 expected by chance under $\alpha = 0.05$, and believe we can interpret our results with only a small risk of committing a type I error. We also treated the abundance of *M. albus* inflorescences added to each site as a continuous variable and used linear regression to determine if the number of *M. albus* inflorescences present influenced our four pollination and reproduction response variables.

To identify the relative importance of *M. albus* and the other environmental variables in explaining differences in pollination, fruit set, and seed production between sites, we calculated Akaike's information criterion (AIC) variable importance values for seven or eight site-level abiotic and biotic covariates using multiple linear regression on the four response variables for each of the focal species. The covariates included the number of *M. albus* inflorescences added to site, percent tree canopy cover per plot, percent shrub cover per plot (for *V. vitis-idaea* only), number of conspecific flowers per plot, number of all flowers per plot, flower richness per plot, and mean temperature and number of hours of rain during the addition experiment at the site. We included all possible models and ranked them using AIC adjusted for small sample size (AIC$_c$) (Burnham and Anderson 2002), then calculated cumulative AIC$_c$ weights ($0 \leq \sum \omega_i \leq 1$), or importance values, for each biotic or abiotic variable (Burnham and Anderson 2002; Arnold 2010). We considered importance values >0.55 as indicative of well-supported variables. Average parameter estimates for each well-supported variable were calculated using the set of best-supported models (those within two AIC$_c$ units of the model with the lowest AIC$_c$ score) to assess the direction of the response of each focal species to the parameter. Since canopy cover was lower in black spruce sites than in mixed deciduous-spruce sites, and it had an important positive relationship with pollination and seed production variables in *V. vitis-idaea* (Table 4), we re-ran the multiple linear regression analysis described above separately for the two habitat types to determine the relative importance of *M. albus* in the two habitat types.

Results

Effects of *M. albus* on pollinator activity and community

V. vitis-idaea

Three out of four control sites without *M. albus* had no pollinator visitation to *V. vitis-idaea* (mean = 0.0001 visits/flower per hour), while Mel 40 treatment sites had a range of visitation rates between 0 visits/flower per hour and 0.46 visits/flower per hour (mean = 0.113 visits/flower per hour) (Fig. 1a). This effect was not statistically significant ($W = 12.5, p = 0.544$).

R. groenlandicum

Three out of four control sites without *M. albus* had no pollinator visitation to *R. groenlandicum* (mean = 0.0006

Table 3 Linear regression analysis for *V. vitis-idaea* and *R. groenlandicum* pollination and reproduction responses to the number of *M. albus* inflorescences present at a site

Species	Response variable	Model *df*	Error *df*	*M. albus* inflorescences parameter estimate (SE)	*F*	*p*	R^2
V. vitis-idaea	Conspecific pollen	1	34	−0.0002 (0.002)	0.01	0.94	0.0002
	% Flowers pollinated	1	34	−0.00003 (0.00005)	0.41	0.52	0.01
	% Fruit set	1	34	0.001 (0.006)	0.05	0.82	0.002
	Seeds per fruit	1	34	0.002 (0.002)	2.07	0.16	0.06
R. groenlandicum	*Conspecific pollen*	*1*	*27*	*−0.007 (0.003)*	*3.82*	*0.06*	*0.12*
	% Flowers pollinated	*1*	*27*	*−0.01 (0.006)*	*4.05*	*0.05*	*0.13*
	% Fruit set	1	27	−0.005 (0.005)	0.99	0.33	0.04
	Seeds per fruit	1	27	0.0004 (0.002)	0.07	0.79	0.003

The number of *M. albus* inflorescences present in sites where it was added ranged from 334 to 1608 inflorescences (mean 795 ± 85). Individual *M. albus* plants had up to 181 inflorescences with approximately 50 flowers per inflorescence

Models with *p* < 0.1 are indicated in *italic*

visits/flower per hour), while Mel 40 treatment sites had a range of visitation rates between 0 visits/flower per hour and 0.034 visits/flower per hour (mean = 0.0076 visits/flower per hour) (Fig. 1b). This effect was not statistically significant ($W = 15$, $p = 0.458$).

Pollinator community

The pollinator guilds had 40 % proportional similarity between the pooled control and Mel 40 site pairs. More pollinator guilds visited the focal species in the Mel 40 sites than control sites. Butterflies, syrphid flies, other types of flies, and wasps were only present in the Mel 40 treatment sites, while bumblebees and solitary bees were present in control and Mel 40 sites. Only bees visited *V. vitis-idaea,* while a variety of pollinator guilds visited *R. groenlandicum.* The pollinator guild-level Simpson's *D* was 0.49 in the control sites and 0.77 in the Mel 40 sites.

Effects of *M. albus* on native plant pollination and reproduction

V. vitis-idaea

In our MANOVA, we found a marginal treatment effect on *V. vitis-idaea* pollination and reproduction in 2012, and a marginal year effect (Appendix 3). In 2012, Mel 120 sites produced four more seeds per berry on average compared to the control and Mel 40 sites, a significant increase of approximately 15 % (Table 2; Fig. 2d). Fruit set in 2012 was greater than in 2011 for *V. vitis-idaea* (Table 2; Fig. 2c) and the difference in fruit set in Mel 40 compared to the control sites mean was greater in 2012 than in 2011 [1.1 % increase in 2011, 13.4 % increase in 2012, $F_{(1,14)} = 5.26$, $p = 0.03$; Fig. 2c]. We did not detect any differences in the number of conspecific pollen grains on *V. vitis-idaea* stigmas or the percent well-pollinated flowers between treatments or between years in our ANOVA tests (Table 2; Fig. 2a, b). The number of conspecific pollen grains on stigmas, percent flowers pollinated, fruit set, and seeds per berry in *V. vitis-idaea* could not be explained by the number of *M. albus* inflorescences in the site (Table 3).

R. groenlandicum

We found a highly significant year effect for our *R. groenlandicum* MANOVA model testing for year, treatment, and interaction effects (Appendix 3). Seed mass per fruit was the individual variable driving this response (Table 2). There was more than double the mean seed mass per fruit in 2012 compared to 2011 (Fig. 3d). In 2011, Mel 40 sites had 42 % greater seed mass per fruit relative to the control sites, while in 2012 the Mel 40 sites had 24 % less seed mass per fruit relative to the control sites (Fig. 3d). The year by treatment interaction was also significant (Table 2). The number of *M. albus* inflorescences at a site decreased the number of *R. groenlandicum* pollen tetrads and percent flowers pollinated (a decrease of one tetrad or 1 % flowers pollinated for every 100 inflorescences added; Table 3). Fruit set could not be explained by the *M. albus* treatment level in either year (Table 2; Fig. 3c), nor could it be explained by the number of *M. albus* inflorescences at the site (Table 3).

Relative importance of *M. albus* and other environmental factors in predicting reproduction

V. vitis-idaea

The number of *M. albus* inflorescences, canopy cover, flower richness, and mean temperature were identified as
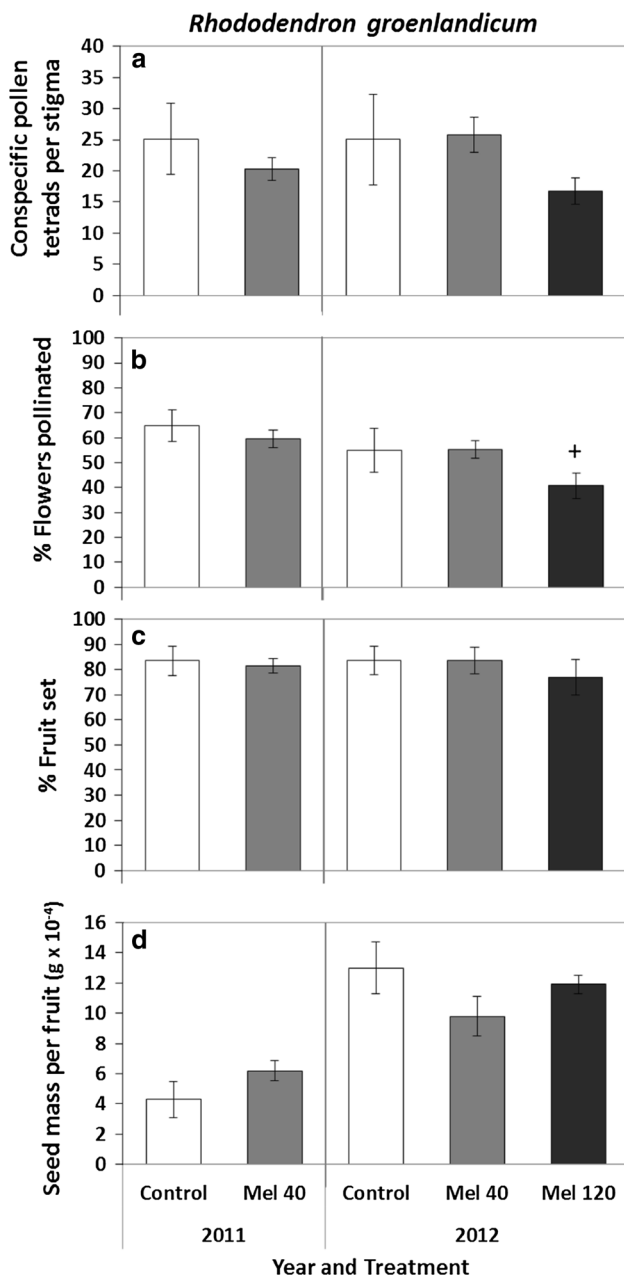
Fig. 3 *R. groenlandicum* conspecific pollen loads on stigmas (**a**), percent flowers pollinated (**b**), percent flowers setting fruit (**c**), and number of seeds per fruit (**d**) in sites without *M. albus* (*Control*), Mel 40 and Mel 120 sites during the summers of 2011 and 2012. *Bars* are mean ± SE of site-level averages for each treatment in each year. The Mel 120 treatment was only conducted in 2012. *$p < 0.05$, +$p < 0.1$ (for differences between treatment means). For abbreviations, see Figs. 2 and 3

important in explaining the variation among sites in percent *V. vitis-idaea* flowers pollinated (Table 4). *M. albus* had a lower cumulative parameter weight compared to the other three variables, all three of which were positively related to % flowers pollinated (Table 4). *M. albus* inflorescence

number was important in explaining % *V. vitis-idaea* flowers pollinated in black spruce sites, but not in mixed deciduous and white spruce sites (Appendix 4). The number of *M. albus* inflorescences was not identified as being as important as the other environmental variables for any of the other three *V. vitis-idaea* response variables across all sites (Table 4) or in the two different habitat types.

R. groenlandicum

The number of *M. albus* inflorescences at a site outweighed the importance of all the other vegetation and weather variables in explaining conspecific pollen loads and the percent pollinated *R. groenlandicum* flowers (Table 4). *R. groenlandicum* fruit set, however, was better explained by canopy cover, flower richness, and hours of rain, which were all negatively related to fruit set (Table 4). The *R. groenlandicum* seed mass per fruit was best explained by the percent canopy cover and average temperature at the sites, both of which had positive relationships with the seed mass per fruit (Table 4). The number of *M. albus* inflorescences was not identified as important in explaining the response variables when we divided the sites by habitat type.

Discussion

The existing body of literature addressing the effects of invasive plants on native plant pollination and reproduction has documented a diversity of competitive (Chittka and Schürkens 2001; Brown et al. 2002; Kandori et al. 2009; Flanagan et al. 2010), facilitative (Nielsen et al. 2008; Tepedino et al. 2008; Da Silva et al. 2013) and neutral effects (Bartomeus et al. 2008a). Our study confirms the complexity of invasive plant impacts on pollination within a plant community. We found that addition of *M. albus* increased pollinator diversity in our sites and tended to increase pollinator visitation rates to native *V. vitis-idaea* and *R. groenlandicum*. We saw a facilitative effect of *M. albus* on the seed production of *V. vitis-idaea* in 2012 and no strong effect on *R. groenlandicum* reproduction. However, there was a weak competitive effect on *R. groenlandicum* pollen loads and percent flowers pollinated at the highest *M. albus* densities.

Along with other multi-species studies and plant-pollinator network studies (Moragues and Traveset 2005; Jakobsson et al. 2009; Bartomeus et al. 2008b; Albrecht et al. 2014), we suggest that the identity of shared pollinators between specific invasive and native pairs or identity of new pollinators attracted to the invaded sites are likely determining factors in the reproductive responses of native plants. Our study also indicates that site environmental conditions and resource limitations to plant reproduction

Table 4 Modeled Akaike's information criterion (AIC) average parameter estimates (*b*) and relative variable importance (cumulative parameter weights; $\sum \omega_i$) for candidate variables explaining differences in total pollen deposited on stigmas, % flowers well pollinated (≥ 10 pollen grains), % flowers setting fruit, and seeds per fruit (total number seeds for *V. vitis-idaea* and seed mass for *R. groenlandicum*) for focal species across all sites

Species	Explanatory variables	Response variables							
		Conspecific pollen		% Flowers pollinated		% Fruit set		Seeds or seed mass per fruit	
		$\overline{b}$	$\sum \omega_i$	$\overline{b}$	$\sum \omega_i$	$\overline{b}$	$\sum \omega_i$	$\overline{b}$	$\sum \omega_i$
V. vitis-idaea	No. *M. albus* inflorescences	–	0.23	-8×10^{-5}	0.58	–	0.19	–	0.26
	Canopy cover (%)	*0.12*	*0.67*	*0.003*	*0.86*	–	0.28	*0.09*	*0.86*
	Shrub cover (%)	–	0.42	–	0.33	–	0.30	–	0.35
	No. *V. vitis-idaea* flowers	–	0.26	–	0.39	*2.25*	*0.88*	–	0.34
	No. All flowers	–	0.26	–	0.40	*−2.30*	*0.90*	–	0.30
	Flower richness	–	0.41	*0.09*	*0.68*	*16.45*	*0.84*	*3.40*	*0.72*
	Average temperature	–	0.24	*0.06*	*0.67*	–	0.28	–	0.40
	Hours of rain	–	0.24	–	0.22	*−0.13*	*0.86*	–	0.23
R. groenlandicum	No. *M. albus* inflorescences	*−0.01*	*0.68*	*−0.01*	*0.71*	–	0.54	–	0.19
	Canopy cover (%)	–	0.24	–	0.25	*−0.31*	*0.99*	*7 × 10⁻⁶*	*0.83*
	No. *R. groenlandicum* inflorescence	–	0.22	–	0.23	–	0.21	–	0.28
	No. All flowers	–	0.24	–	0.24	–	0.23	–	0.20
	Flower richness	–	0.30	–	0.23	*−5.93*	*0.71*	–	0.20
	Average temperature	–	0.32	–	0.36	–	0.31	*3 × 10⁻⁴*	*0.91*
	Hours of rain	–	0.29	–	0.24	*−0.04*	*0.56*	–	0.40

Values in *italic* indicate well-supported variables $\sum \omega_i > 0.55$) and average parameter values for these variables were taken over models with a difference in AIC adjusted for small sample size <2

further complicate the generalizations that can be made from the existing corpus of experimental studies on invasive plant impact on native plant reproduction. We discuss here how both pollinator identity and site environmental conditions may have influenced our results.

M. albus effect on pollination and reproduction of two boreal shrubs

The addition of *M. albus* did little to change pollen loads or pollination rates of *V. vitis-idaea*. Seed production per berry, however, did increase in the presence of the highest *M. albus* abundance level. A higher seed set without evidence of higher pollen loads suggests that there is an increase in the proportion of outcross pollen being delivered by pollinators when higher densities of *M. albus* are introduced. This explanation is consistent with previous hand-pollination experiments in which cross-pollinated *V. vitis-idaea* plants produced more seeds than self-pollinated plants (Jacquemart and Thompson 1996; Fröborg 1996; Jacquemart 1997), but did not have higher fruit set (Jacquemart and Thompson 1996; Jacquemart 1997).

The shift in the pollinator community composition in the presence of *M. albus* provides a mechanism through which the outcrossing rates may change. Densely flowered clonal plants like *V. vitis-idaea* are subject to high levels of within-genet pollen transfer due to the foraging strategies of bumblebees in particular (Jacquemart and Thompson 1996). Other pollinating guilds such as butterflies tend to take longer flights between plants than *Bombus* spp. (Proctor et al. 1996) thereby increasing outcross potential. Butterflies, syrphid flies, other flies, and wasps were observed visiting the native focal species only at sites where *M. albus* was added. Other studies have documented changes in pollinator behaviors (e.g., changes in distance traveled between plants) as a result of non-native plant invasions (Ghazoul 2004), which could also explain a possible shift in outcrossing rates.

The modest decline in conspecific pollen loads and pollination rates of *R. groenlandicum* flowers with greater numbers of *M. albus* flowers is suggestive of a greater overlap in pollinator community and a shift by more effective *R. groenlandicum* pollinators to visiting *M. albus* when it is at high densities. Indeed a high proportion of pollinator guilds are shared between *R. groenlandicum* and *M. albus* (plant-pollinator networks are explored in Schneller et al., in prep). Despite a potential for reduced conspecific pollen flow, we did not observe an associated decline in fruit or seed set. Resource limitation is likely to play a major role in limiting sexual reproduction in these boreal communities

(Grainger and Turkington 2013) and pollination rates beyond a minimum threshold may not result in changes in fruit and seed set.

The magnitude of the *M. albus* effect on *V. vitis-idaea* fruit set and *R. groenlandicum* seed mass per fruit was greater in 2012 compared to 2011. In 2011 it rained for almost twice as many hours as in 2012 (173 vs. 97 h during the experimental period), which likely allowed for a greater amount of time for pollinator activity in the second year (Kuchko 1988; Tuell and Isaacs 2010). It may also have affected which types of pollinators are active (Corbett et al. 1993). Other studies have found it difficult to disentangle the role of variations in weather in *V. vitis-idaea* fruit set (Jacquemart 1997; Krebs et al. 2009), with factors like late spring frosts having a potential effect on both flowers and insect populations. Similarly, we cannot determine whether the warmer conditions in the second year of our study reduced pollinator limitation or resources limitation for *V. vitis-idaea* fruit set and *R. groenlandicum* seed production. *V. vitis-idaea* fruit set was negatively related to the number of heterospecific flowers and positively related to the number of conspecific flowers, which is consistent with pollen limitation. Further, seed production for *V. vitis-idaea* increased only under the highest level of *M. albus* addition, suggesting that this variable is pollinator limited in a warm year.

Relative importance of *M. albus* and other environmental variables in explaining reproduction

M. albus inflorescence number was more important for explaining *R. groenlandicum* pollination than were the other biotic and abiotic variables we measured. The importance of *M. albus* did not persist in subsequent *R. groenlandicum* reproduction. Similarly, the number of *M. albus* inflorescences was only important in explaining the percent flowers pollinated for *V. vitis-idaea,* while fruit set was more influenced by the environmental conditions. This finding is consistent with Totland et al. (2006), who documented non-native *Phacelia tanacetifolia* affecting pollinator visitation to a native boreal plant species (*Melampyrum pratense*), but not reproductive success. Totland et al. (2006) similarly attributed this finding to the high resource limitations on reproduction in boreal forest habitats.

Our finding that *M. albus* had far greater importance in explaining pollination rates of *V. vitis-idaea* in black spruce sites than in mixed deciduous-spruce sites further supports the important role of resource availability in mediating relationships between invasive and native boreal plant reproduction. Black spruce sites tend to have lower soil temperatures (Viereck et al. 1992) and lower densities of native flowers than the mixed deciduous-spruce sites. The reduced floral resources and the lower temperatures for ground-nesting pollinators likely limit the number of pollinators in black spruce sites, and the addition of *M. albus* may act as a distraction for the few pollinators present.

Our study sets the stage for further investigation of the pollination of native plants in the face of accelerating rates of invasion in boreal forest ecosystems.

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