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Effects of invasive plant species on pollinator service and reproduction in native plants at Acadia National Park

Technical Report NPS/NER/NRTR--2007/096



ON THE COVER

A native mason bee (*Osmia* sp.) on lowbush blueberry.

Photograph by: Alan Stubbs

Effects of invasive plant species on pollinator service and reproduction in native plants at Acadia National Park

Technical Report NPS/NER/NRTR--2007/096

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Abstract

Invasive plant species can have profound negative effects on natural communities by competitively excluding native species. *Berberis thunbergii* (Japanese barberry), *Frangula alnus* (glossy or alder buckthorn) and *Lythrum salicaria* (purple loosestrife) are invasive species known to reduce native plant diversity and are thus of great concern to Acadia National Park. Pollinators visit them for nectar and pollen. The effects of invasive plant species on pollinator behavior were investigated by comparing pollinator visitation to co-flowering native and invasive species with visitation to native species growing alone. The effect of invasives on pollination of native plants was studied by comparing fruit set in patches of the native species growing near invasives with patches far from invasive species in Acadia National Park. The co-flowering pairs were as follows: in the spring native *Vaccinium angustifolium* (lowbush blueberry) was paired with *B. thunbergii*; in early summer native *Viburnum nudum* (wild raisin) was paired with *F. alnus*; in late summer native *Spiraea alba* (meadowsweet) was paired with *L. salicaria*.

We investigated whether these invasives competed with native plants for pollinators in Acadia and thus negatively affected native plant reproduction. Our objectives were to determine: 1) the influence, if any, of each invasive on pollinator visitation to a co-flowering native species, 2) factors that might affect visitation, 3) invasive pollen transfer to native plants, and 4) whether invasives influence native plant reproduction (fruit set).

Our findings indicate that at times the number of flower visitors to natives was lower or the species composition of visitors different when invasives were present, that invasives sometimes attracted more pollinators, that generally the invasives were more rewarding as far as nectar and pollen availability for pollinators, and that generally native plant fruit set and seed set was not significantly lowered in the presence of the invasive. In fact, in one year fruit set of *S. alba* was significantly greater in the presence of *L. salicaria*. The number of invasive pollen grains on native stigmas was extremely low; on average less than one grain per stigma. These fruit set and pollen deposition findings indicate that native plant reproduction was not adversely affected in the short term by these invasive species and that therefore competition between the native and invasive species for pollinators did not occur.

Native bee populations monitored in 2004-2005 at sites with and without *B. thunbergii* and/or *F. alnus* indicated a greater abundance of native bees at sites with these invasives present. Native bees collected from the native and invasive plants were compared with historical records to assess whether invasive plants favor different bee species than those that formerly predominated on Mount Desert Island. This does not appear to be the case. Several species of bumble bees (*Bombus* spp.) as well as nine solitary bee species were found that were not documented by the Procter surveys of 1917-1940. Collecting of native bees was limited to the study plants, which may, in part, explain why some bee species documented in the Procter Surveys were not found in the present research.

A field guide for identification of native bumble bees has been produced to help Park Natural Resource personnel monitor the status of native bee populations in Acadia. Other educational materials were also developed, aimed at educating Park visitors by exposing them to: 1) the role

of native plants and their bee pollinators in terrestrial ecosystems; 2) the effects of invasive plants on native plant-pollinator mutualisms; 3) the need for conserving native bees and other pollinators; and 4) conservation strategies for protecting and enhancing native plant-pollinator mutualisms in the Park.

Based on the present findings, Acadia Park Resource Management personnel should continue to closely monitor these invasive species, especially *L. salicaria* so that their populations do not overrun the native flora of the Park. However, *B. thunbergii* and *F. alnus* appear at least in the short time-frame of this research to have no negative effect, and perhaps even to benefit the co-flowering native species by attracting, at times more pollinators to them, and to benefit native bee populations by providing additional needed food resources.

Executive Summary

Invasive plant species can have profound negative effects on natural communities. *Berberis thunbergii* (Japanese barberry), *Frangula alnus* (glossy or alder buckthorn) and *Lythrum salicaria* (purple loosestrife) are invasive species known to reduce native plant diversity. These invasives are of great concern in Acadia National Park, but are highly attractive resources for pollinators. To determine if these invasive species affect pollinator behavior and thus native plant reproduction, we conducted studies from 2001-2005 testing four major hypotheses: 1) that these invasive species influence pollinator visitation to native plants; 2) that these invasives affect pollen transfer to native plants, 3) that these invasives influence native plant reproduction (fruit set), and 4) that native bee diversity and abundance is influenced by these invasive plant species.

The effects of invasive plant species on pollination of native plants and their native pollinators were investigated, with studies that compared pollinator visitation to native and invasive species and studies that compared native fruit set in patches of the native species near populations of its paired co-flowering invasive species to native fruit set at sites where the invasive was absent. The co-flowering pairs were as follows: in the spring native *Vaccinium angustifolium* (lowbush blueberry) was paired with *B. thunbergii*; in early summer native *Viburnum nudum* (wild raisin) was paired with *F. alnus*; in late summer native *Spiraea alba* (meadowsweet) was paired with *L. salicaria*. We found that the presence of invasive plants sometimes influenced insect visitation to native plants, but we found no adverse effect of invasive plants on reproduction of native species.

Native bees collected from patches of native and invasive plants were compared with historical records to assess whether invasive plants favor different bee species than those that formerly predominated on Mount Desert Island. This does not appear to be the case. However, several species of bumble bees (*Bombus* spp.) as well as nine solitary bee species were found that were not documented by the Procter surveys of 1917-1940. Collecting of native bees was limited to the study plants, which, in part explains why some bee species documented in the Procter Surveys were not found. Much more extensive collecting throughout the flowering season and from other regions of the Park would be necessary to determine if any species have been extirpated from Acadia National Park since 1940.

A field guide for identification of native bumble bees has been produced to aid Park Natural Resource personnel in monitoring the status of native bee populations in Acadia. Other educational materials were also developed, including a Power-Point presentation that can be used for educating Park visitors by exposing them to: 1) the role of native plants and their bee pollinators in terrestrial ecosystems; 2) the effects of invasive plants on native plant-pollinator mutualisms; 3) the need for conserving native bees and other pollinators; and 4) conservation strategies for protecting and enhancing native plant-pollinator mutualisms in the Park.

Based on the present findings, Acadia Park Resource Management personnel should continue to closely monitor these invasive species, especially *L. salicaria* so that their populations do not overrun the native flora of the Park. However, *B. thunbergii* and *F. alnus* appear at least in the short time-frame of this research to benefit both the co-flowering native species by attracting, at

times more pollinators to them and to benefit native bee populations by providing additional needed food resources. Therefore, until suitable native plant replacements can be found, perhaps their removal need not at present be a high priority, at least from the perspective of pollination patterns. Although native bee populations do fluctuate, the fact that native bee populations were lower in 2005 than 2004 is of some concern. Further monitoring may be warranted to determine if populations are stable or declining.

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Introduction

Invasive plant species can severely impact natural ecosystems (Nature Conservancy 1996; Pimentel 2002) by displacing native plant species. Furthermore, they can attract pollinators away from native flowers, thus influencing seed set and reproductive ecology of the native species. This in turn may have potentially broad effects on the demographics of native species and thus on ecosystem structure. To date, the implications of invasive plant species for pollination of native plants has unfortunately received little attention (NAS 2004; Totland et al. 2006).

Introduced plant species can have profound negative effects on natural communities and can constitute a substantial proportion of the insect-pollinated flora of a region, with major community-level effects. Ginsberg (1981) found that introduced flower species predominated in early summer while native species predominated in late summer in central New York State. Interestingly, visitors to the introduced early-summer weeds were primarily native bee species, while visitors to the native goldenrod species in late summer were primarily honey bees, an introduced species. In a more recent study, Stout et al. (2002) found that two exotic bee species frequently visited an invasive lupine in Tasmania, whereas native bees rarely did.

At least 25% of the flora at Acadia National Park is exotic (non-native); 14 of these are extremely aggressive invasive species (Reiner and Gregory 2000; Reiner and McLendon 2002). In order to assess the impact of invasive plant species on native plant reproduction and the pollinators of native plants, we examined three invasives thought to be adversely limiting pollination of native flowering species in Acadia. These invasive species were *Berberis thunbergii* (Japanese barberry), *Frangula alnus* = *Rhamnus alnus* (glossy or alder buckthorn) and *Lythrum salicaria* (purple loosestrife). These species are known to be highly invasive, and to spread aggressively into natural communities, potentially altering ecosystem function. For example, Ehrenfeld (1997, 1999) indicated that *B. thunbergii* threatened the native flora of small to moderate-sized forest reserves in central and northern New Jersey, and adjacent areas of New York and Pennsylvania.

Invasive species often produce highly nutritive nectar and/or pollen and are highly attractive to pollinators (Pellet 1947; Schrenk 1981; Grabas and Laverty 1999). Therefore, they can potentially attract pollinators away from native species, thus influencing the reproduction of these species, and the structure of natural communities.

Pollinators and their host plants form Keystone Mutualisms making them essential to maintaining the biodiversity and hence the integrity and sustainability of most terrestrial ecosystems (LaSalle and Gauld 1993; Kearns and Inouye 1997; Shepherd et al. 2003; Committee on the Status of Pollinators 2006). Insufficient pollination can have serious implications for the population dynamics of plant species (Buchmann and Nabhan 1996; Shepherd et al. 2003; Committee on the Status of Pollinators 2006). In fact, some rare and endangered plant species rely solely on native bees for their continued reproductive success (Geer et al. 1995; Buchmann and Nabhan 1996; Kwak et al. 1996; Nabhan 1996).

To date, the effect of invasive plants on pollinators has been mostly limited to work regarding the honey bee, which is itself, nonnative and at times an invasive species. Barthell et al. (2001) investigated honey bees as pollinators of yellow star-thistle (*Centaurea solstitialis* L.), another invasive plant. They found that the number of honey bee visitors to the yellow star-thistle was significantly higher than the numbers of native bees (Barthell et al. 2001).

The magnitude of effects of invasive species on native plant reproduction via pollination is currently unknown in the National Parks. Therefore we proposed to assess the impact of invasive flowering plants on native flowering plants and their pollinators in Acadia National Park, which is unique among national parks in having baseline data on its insect fauna (Procter 1946). Native wild bees, in particular, are essential to maintaining ecosystem health at Acadia because of their importance as pollinators.

Plants that require out-crossing rely on vectors, such as animal pollinators, to play flower “matchmaker.” Pollinators can determine which flowers are visited, which plants mate, the distance of pollen dispersal, species of pollen being deposited, and how much out-crossing actually takes place (Waddington 2001). If the introduction of an invasive species alters the behavior of pollinators, it could have a significant impact on the fecundity of the native plants. Visitation rates to native flowers may be reduced as pollinators visit the invasive, or may be enhanced by the increased concentration of resources (Ohashi and Yahara 2001). The pollinator community may partition resources such that more or less efficient pollinators are visiting one species preferentially over other species. If there is pollinator limitation or reduced pollen flow between the interspecific individuals, this could have a negative impact on the fecundity of the native plant. Not only can the quantity of pollen being deposited on stigmas be affected, so can the quality of the pollen load (mixed or uniform). Foreign pollen deposited on the stigma of another species, Improper Pollen Transfer, IPT, (Waser 1983, Rathcke 1984) can affect seed set by clogging the stigmas and/or have an allelopathic effect on native pollen, which have been shown for native-native and native-invasive pairings (Thomson et al. 1981; Campbell and Motten 1985; Galen and Gregory 1989; Brown and Mitchell 2001).

Historically, wild native species pollinated much of our native flora. Because these native species have coevolved with the native flora, they generally are superior pollinators (Tepedino 1979; Buchmann and Nabhan 1996; Stubbs and Drummond 1997). Habitat destruction, habitat fragmentation, and pesticide use, especially herbicides which remove flowering plants that provide them with nectar and pollen, have severely reduced native bee populations (Aizen and Feinsinger 1994; Buchmann and Nabhan 1996; Westrich 1996; Stubbs et al. 1997; Shepherd et al. 2003; Committee on the Status of Pollinators 2006). Adequate floral resources are extremely critical to maintaining healthy populations of pollinators. And conversely, adequate populations of pollinators are extremely critical for maintaining healthy populations of native plants.

Overall, invasive species might interfere with pollination of native species by attracting pollinators away from the native species, and/or by lowering reproductive output due to increasing the likelihood of the deposition of foreign pollen on the stigmas of the native flowers species (Waser 1983; Rathcke 1984). On the other hand, invasive species might enhance pollination by attracting larger numbers of pollinators into the area.

The effects of invasive plant species on pollinator faunas and on pollination of native plants was studied by comparing insect visitation to native and invasive species and by comparing fruit set in patches of the native species near populations of its paired co-flowering invasive plants to fruit set in patches where the invasive was absent. The co-flowering pairs were as follows: in the spring native *Vaccinium angustifolium* (lowbush blueberry) was paired with *B. thunbergii*; in early summer native *Viburnum nudum* (wild raisin) was paired with *F. alnus*; in late summer native *Spiraea alba* (meadowsweet) was paired with *L. salicaria*.

Four major hypotheses were tested for each of the three pairs of co-flowering species:

Hypothesis 1: The presence of the invasive species influences pollinator visitation to the native species.

H₀: There is no difference in pollinator visitation to the native species at sites where the invasive species is present, compared to sites where the invasive species is not present.

H₁: Pollinator visitation to the native species is lower at sites with the invasive species present than at sites without the invasive species present.

H₂: Pollinator visitation to the native species is higher at sites with the invasive species present than at sites without the invasive species present.

Hypothesis 2: The presence of the invasive species influences pollen transfer to stigmas of the native species.

H₀: There is no difference in the amount of pollen transferred to stigmas of the native species at sites with the invasive species present, compared to sites without the invasive species present.

H₁: Pollen transfer to stigmas of the native species is lower at sites where the invasive species is present than at sites without the invasive species present.

H₂: Pollen transfer to stigmas of the native species is greater at sites with the invasive species present than at sites without the invasive species present.

Hypothesis 3: Invasive plant species influence reproduction (fruit set) of native plants.

H₀: There is no difference in fruit set of native plants at sites with invasive species present compared to sites without invasive species present.

H₁: Fruit set of native plants is lower at sites with invasive species present than at sites without invasive species present.

H₂: Fruit set of native plants is greater at sites with invasive species present than at sites without invasive species present.

Hypothesis 4: Native bee diversity and abundance is influenced by invasive plant species.

H₀: There is no difference in native bee diversity and abundance at sites where the invasive species is present, compared to sites where the invasive species is not present.

H₁: There is greater native bee diversity and abundance at sites where the invasive species is present, compared to sites where the invasive species is not present.

H₂: There is less native bee diversity and abundance at sites where the invasive species is present, compared to sites where the invasive species is not present.

To address these hypotheses our research objectives were: 1) to determine whether invasive plants influence native pollinator visitation to native plants, 2) to determine whether competition

(as measured by a reduction in fruit set resulting in a reduction in fecundity) for pollinators existed between the native and invasive plant, 3) to ascertain factors that might influence the pattern of pollinator visitation to native plants, 4) to determine the potential for invasive pollen contamination on the stigmas of the native plants, and 5) to determine if invasive plant species influence native bee abundance and diversity.

Bee foraging behavior, abundance, and diversity were assessed on both the native and invasive species. Studies were conducted to address the effects of competition, if present, and improper pollen transfer on fruit set and seed production in the native species.

Study Area

Field studies were conducted on Mount Desert Island (Maine, U.S.A. [44.375° N, 291.625° E]) in Acadia National Park. Acadia encompasses about 47,000 acres of granite covered mountains and coastal shoreline. Acadia receives approximately 47 inches of precipitation during the year. Much of the eastern portion of the Park was consumed by fire in 1947 and is covered by deciduous forest containing mostly early successional species, such as birches (*Betula*), aspens (*Populus*), maples (*Acer*) and white-cedar (*Thuja occidentalis* L.). Common understory plants include bunchberry (*Cornus canadensis* L.), starflower (*Trientalis borealis* Raf.), and big-leaved aster (*Aster macrophyllus* L.). Most of the study plots were established in this burned area, although some were in an unburned area. Exotic species comprise 25% of the flora of the Park (Reiner and Gregory 2000; Reiner and McLendon 2002).

Vegetation maps of the entire Park constructed by USGS staff in 1999 were used to identify the habitat types of the study sites. Plant community classification follows NVCS vegetation associations or groups of associations. The *V. angustifolium* and *B. thunbergii* sites (Figure 1) were found in a variety of habitats, with the majority found in woodland deciduous upland or forested upland (conifer, deciduous, and mixed) areas. *Viburnum nudum* and *F. alnus* sites (Figure 2) were found mostly in woodland deciduous upland areas, and the remaining in conifer and mixed forested upland habitats. Many of the *S. alba* and *L. salicaria* sites (Figure 3) were found in either mixed or coniferous forested upland. Others were found in deciduous or mixed woodland uplands, graminoid wetlands; one site was in a forb wetland. Appendix Table 1 provides Universal Transverse Mercator (UTM) coordinates and elevation for the study sites.



Figure 1. Map of the study sites for invasive *Berberis thunbergii* (Bt) and native *Vaccinium angustifolium* (Va and Vac).



Figure 2. Map of the study sites for invasive *Frangula alnus* (Fa) and native *Viburnum nudum* (Vn and Vnc).



Figure 3. Map of the study sites for invasive *Lythrum salicaria* (Ls) and native *Spiraea alba* (Sa and Sac).

Methods

Study plants

Each of the highly invasive species was paired with a native species that flowers at the same time and requires pollinators in order to achieve satisfactory seed set (Dickinson and Phipps 1986, Wolfe and Barrett 1987, Stubbs et al. 1992). Appendix Figure 1 shows the study plant pairs.

Spring flowering (Mid-May - Early June):

Berberis thunbergii (Japanese barberry), barberry family (Berberidaceae), native to Japan, can be found in the understory of varying forest habitats (Haines and Vining 1998; Ehrenfeld 1999; Richberg et al. 2001). The plant consists of multiple woody branches of a red-brown color on the outside and yellowish wood on the inside. The stems are armed with simple sharp spines presumed to deter herbivores, and the leaves are typically obovate and serrated. Japanese barberry is one of the first plants to “leaf out” and flower in the spring (Silander and Klepeis 1999; Richberg et al. 2001). Several species of birds, including *Dumetella carolinensis* (gray catbird) feed on its fruits.

Vaccinium angustifolium is an economically important member of the heath family (Ericaceae) and is native to northeastern North America, including Maine (Gleason and Cronquist 1991; Haines and Vining 1998). Serrated deciduous leaves form in early spring on the reddish twigs, and leaf-out is followed by the formation of clusters of white bell-shaped flowers at the terminal end of the twigs. Flowers persist from late-May to early June, and cross-pollination by insect vectors is required for substantial fruit set (Stubbs et al. 1992). *Vaccinium angustifolium* is a food source for more than 24 species of birds and mammals in Acadia (Martin et al. 1961 used in conjunction with Amphibians, Reptiles, Mammals of Acadia Check List and Birds of Acadia National Park Check List, Acadia National Park 2002).

Early Summer flowering (Mid-June - Mid-July):

Frangula alnus, which is synonymous with *Rhamnus frangula* L., usually occurs as a woody shrub or small tree. It is native to Europe and Asia and is a member of the Rhamnaceae, or buckthorn family (Gleason and Cronquist 1991; Medan 1994; Richberg et al. 2001). The leaves are opposite and shiny and the primary stem or trunk is gray in color. Similar to the *B. thunbergii*, *F. alnus* also sprouts leaves early in the season (Richberg et al. 2001). Flowering in Acadia generally begins about a week prior to *V. nudum* in June, peaks in early July and at times sporadically continues into September. Its fleshy fruits are highly attractive to some birds.

Viburnum nudum, moschatel family (Adoxaceae), is a multi-stemmed shrub of wet soils that reaches heights up to approximately four meters (Gleason and Chronquist 1991, Haines and Vining 1998). It is native to eastern North America (Gleason and Cronquist 1991). Opposite ovate leaves of varying serration appear in the spring (Gleason and Cronquist 1991). The inflorescence is a cyme often several hundred millimeters in diameter of small open flowers found at the terminal end of the branches (Miliczky and Osgood 1979a). Unlike *F. alnus*, flowering ceases by mid-July.

Mid- to late summer flowering (Mid-July - September):

Lythrum salicaria, a perennial herbaceous plant of the loosestrife family (Lythraceae), generally requires wet soils and an open canopy to thrive. It is native to Eurasia. Purple loosestrife grows to a height of slightly over 3 m, and has a characteristic square stem. Leaves are opposite and lack a petiole. The primary inflorescence is an indeterminate spike (flowers attached directly to the stem) usually several hundred millimeters in length (Judd et al. 1999; Dalby 2001). The purple flowers are medium-sized, with bees the most common visitors. Capsules at the base of the spike release tiny seeds as the upper flowers are still opening in August; one plant can produce several million seeds annually (Dalby 2001). This high seed output, along with asexual vegetative spread has contributed to *L. salicaria* becoming one of the most invasive weeds in the northeastern United States and Canada (but see Farnsworth and Ellis 2001; also, Hager and McCoy 1998; Hager and Vinebrooke 2004).

Spiraea alba, a member of the rose family (Rosaceae), is native to eastern North America (Gleason and Cronquist 1991; Haines and Vining 1998). The shrubs consist of simple arching red-brown branches. Typically found in rhizomatous clusters numbering anywhere from a few to several hundred, *S. alba* is common along roadsides, in fields, or in other open areas (Haines and Vining 1998). *Spiraea alba* produces serrated obovate leaves in the spring. Like *F. alnus*, *S. alba* has a prolonged flowering period - with flowering commencing in mid-July and lasting into mid-September. Small pentamerous white, sometimes pinkish, flowers comprise a panicle-like cyme (>2° of branching from central axis) that varies in range from a few to several hundred mm in length.

Pollinator visitation to co-flowering native and invasive species

To determine the effect, if any, of invasive plants on pollinator visitation to native plants (Major Hypothesis 1) pollinator visitation studies were conducted in 2002-2003.

Three treatment groups were established: 1) Experimental native plant plots, which were in the presence of the invasive species, 2) Invasive plant plot, which was located in or near the Experimental native plot, and 3) Control native plant plots that were at least 1 km from the closest known location for the paired invasive. (Most native bees do not generally fly further than 0.5 km from their nest site (Free 1993).) At each Control native plant study site one 4 m² study plot was established. One or two 4 m² plots were established at the sites having native and the co-flowering invasive present together. Depending on the proximity of the invasive species to the Experimental native plant, the invasive was either in the same 4 m² plot as the native or in a separate 4 m² plot nearby. The 4 m² study plots were initially established in 2001 for the spring and early summer co-flowering species and for the mid- to late summer species in 2002. Severe grazing of the native species by deer necessitated, however, that many new plots be established in 2002 and 2003.

In 2002 and 2003 ten minute observations were made on all study plant species and all floral visitors to the study plots were recorded. Sampling periods for *V. angustifolium* and *B. thunbergii* were late-May to early-June, late-June to early-July for *V. nudum* and *F. alnus*, and late-July to late-August for *S. alba* and *L. salicaria*. These times coincided with the dates when both plants were flowering. Two to eight observations per study plot were taken during the

flowering period. Tables 1 - 6 provide the sampling dates and times for each plot, as well as the environmental conditions and visitation numbers for the most important pollinator groups.

Based on preliminary sampling in 2001, most observations were conducted between 0800 and 1600 hours because that was the time of highest insect visitation to study plants. Some pollinators, such as members of the families Andrenidae (soil-nesting bees) or Halictidae (sweat bees), were difficult to identify on the wing beyond the family or genus level. Others, like *Bombus ternarius* Say (orange-belted bumblebee), were distinct and could be identified to the species-level. Individuals were collected outside study plots to identify pollinators to the species level while avoiding destructive sampling of the pollinator community in 2002. A few voucher specimens were collected from inside the plots in 2003. Specimens will be curated at Acadia National Park Headquarters Museum.

Environmental factors

Environmental factors that can affect pollinator visitation were also measured. Temperature, humidity, and average wind speed were all recorded using a Kestrel 3000®, a hand held weather monitoring device, at the beginning of each sampling period. Canopy cover was determined using a convex spherical densitometer each time the plots were sampled. Visual estimates of percent of the plot in sun were also made at the time of sampling.

All plant species within each plot were identified and percent cover for each was estimated using a modified Daubenmire scale (Daubenmire 1959). Four 15 m transects, one in each cardinal direction from the midpoint (1 m) of each side of the plot, were established to determine the overall plant species composition of the study sites. Presence of plant species in three meter increments was recorded.

Soil samples for each study site were also collected by digging down into the soil approximately 15-20 cm at each of the four corners of the plots, and taking an equal representation from each. In certain cases, this depth could not be reached or a sample could not be taken at some corners due to shallow soil and a rock barrier. Here, soil samples constituted only those corners from which samples could be obtained. The Soils Laboratory, Maine Agricultural and Forestry Experiment Station, University of Maine, analyzed the soil samples for % organic matter, pH, and macronutrients.

Floral rewards- floral display

Ohashi and Yahara (2001) showed that pollinator visitation increased in areas of higher floral density. Therefore floral density was recorded for each observation period as it could affect pollinator visitation. Floral densities were estimated by measuring the length of five branches or stems, and either counting the numbers of total and open flowers (*V. angustifolium*, *B. thunbergii*, *F. alnus*) or visually estimating the percent of open flowers on a cluster (*V. nudum*, *L. salicaria*, *S. alba*) each time the plots were sampled. Each time a plot was sampled for visitation, the percentage cover of any other co-flowering species in the study plot was recorded.

Floral rewards- nectar and pollen

Nectar and pollen availability studies were conducted to determine if the invasive species was more or less rewarding than the co-flowering native species (factors that might influence visitation). Floral rewards for each species were measured to ascertain a level of flower attractiveness. Plants with higher quality floral rewards (e.g. copious nectar) generally are more attractive to pollinators (Ohashi and Yahara 2001).

Collecting 10 flowers from each study plot, and, using forceps, tapping the flower with a dissecting needle over a grid-lined Petri dish, ascertained pollen availability. The pollen grains were then counted using a dissecting microscope at 30x (Stubbs and Drummond 1997).

Nectar volume and sugar concentration were measured using two methods. In 2002, nectar was extracted and volume measured using 5 ul micro-capillary tubes (Dafni 1992). Overall nectar sucrose concentration was measured with a field refractometer (model Atago N-50E) calibrated for the 0-50% sucrose range. Nectar was extracted from three flowers each time the plot was sampled to obtain three readings unless the volume was too small to read on the refractometer. In those cases, multiple flowers were sampled until an adequate volume was obtained. For the *S. alba* – *L. salicaria* co-flowering pair in 2002 and for all pairs in 2003, filter paper wicks were secured on small pins and inserted into flowers when nectar removal by microcapillary was difficult (McKenna and Thomson 1988). Multiple wicks were used when copious amounts of nectar were present. The overall sugar concentrations from the wicks were calculated using a sucrose standard curve and sucrose:hexose ratios were determined (Dafni 1994).

Floral rewards- nectar replenishment

A nectar replenishment experiment (see Castellanos et al. 2002) was performed because it was hypothesized that a plant that replenishes nectar more efficiently after frequent visitation by pollinators would be more attractive to pollinators. Three plots from each treatment group were chosen, and three flowers per plant per plot (nine total flowers for each treatment) were bagged for one of two treatments: 1) hourly or 2) daily (twice per day) nectar removal. Open flowers were randomly selected. At 0800 hours, nectar was extracted from all flowers. Pollinators were excluded from visitation to these flowers by a mesh bag tied around the stem; the nectar removed from the flowers during this initial extraction was called the standing crop. Every hour for six hours, nectar was removed from flowers in the hourly treatment. During the last sampling time, the nectar from all flowers was removed again. Comparisons were made between total nectar taken from flowers of both treatments following removal of the standing crop.

Fruit and seed set

To assess the impact of invasive species on reproductive output (Major Hypothesis 3), we measured fruit set in 2002 and 2003 at Control (invasive absent) and Experimental (invasive present) sites. In both years, prior to flowering, randomly selected stems of the native and invasive species were tagged and non-opened flowers counted. The number of non-opened flowers per stem was recorded. Approximately 50% of the stems were bagged with Delnet[®] pollinator exclusion bags (item P520) to ascertain the importance, if any, of selfing and if native pollinators were necessary for fruit production. Approximately one to two weeks after flowering ceased, any bags on stems were removed and the fruits counted and recorded for all tagged

stems. (See Appendix Tables 2 - 4 for sites and dates.) Percentage fruit set was determined by dividing the number of fruits per stem by the number of flowers.

In 2002 fruits on tagged stems were monitored throughout the summer to see if differences existed in the time to ripening. Animal predation (birds, humans, etc.) can affect fruit set so approximately two weeks after bloom, we examined all marked stems and counted developing fruits. Every one to two weeks thereafter, fruits were monitored because pollinator limited plants are thought to take longer to develop and ripen (Free 1993) In late summer to early fall, fruits were counted for the final time and harvested.

To further assess the impact of invasive species on reproductive output (Major Hypothesis 3), we measured seed set. Pollinator limited native plants have generally fewer fruits, smaller fruits, and fewer seeds (Free 1993, Delaplane and Mayer 2000). Harvested fruits were frozen (*V. angustifolium*) or stored dry (*S. alba*), until seed counts of mature plump seeds could be made.

Seed set in harvested fruits from tagged stems was measured and compared between the Control and Invasive study sites for *V. angustifolium* in 2002 and 2003. *Viburnum nudum* sets only one seed per fruit; thus seed set was not measured for this species. In 2003 seed set was measured in *S. alba* from dehiscent follicles collected from Control and Experimental sites.

Pollen transfer (PT) studies were conducted to determine if invasive pollen (improper pollen, IP) adversely affected native plant fruit and seed set (Major Hypotheses 2 and 3). Foreign pollen, such as that of an invasive, deposited on the stigma of another species, (Waser 1983, Rathcke 1984) can adversely affect seed set by clogging the stigmas or have an allelic effect on native pollen reducing fruit and/or seed set in native-invasive pairings (Brown and Mitchell 2001).

Improper pollen transfer (IPT) was assessed two ways. First, to determine whether foreign invasive pollen was deposited by pollinators, ten stigmas from each native plant plot were collected during the flowering period and stained using a fuchsin gel (Dafni 1992). Using reference collection material to compare to the prepared slides of the stained stigmas, the quantity and identity of pollen grains on native plant stigmas was determined by counting the number of native, invasive, or other foreign pollen grains on the stigma using a light microscope. Stigmas were collected in 2002 and 2003, but those from 2002 were unusable due to loss in storage.

Second, field studies examining the effect of IPT on native fruit set were conducted in 2002 and 2003. Prior to hand pollinating native plant stigmas in the field with either conspecific pollen (proper pollen, PP) or invasive species (improper pollen, IP), a preliminary trial was done for each native species. Open flowers were collected and individual stigmas dusted with multiple anthers removed from donor plants with forceps. These dusted stigmas were examined under a dissecting scope, with an OptiVISOR® (# 10 lens), which is a precision binocular headband magnifier, and a hand lens to determine if this technique would deposit at least 20 grains of pollen on the stigma. Generally it required the anthers of two to four flowers to detect sufficient pollen on the stigma. After hand pollinating with two to four invasive flowers an OptiVISOR® and/or a hand lens was used in the field studies to ascertain if sufficient invasive pollen was

deposited on each individual stigma. If not, the stigma was dusted with more anthers until sufficient pollen could be detected.

The locations and dates for pollen transferal (hand pollination) to stigmas and fruit set counts for the paired co-flowering study plants are given in Appendix Tables 5 - 7 for the two years of these studies. In 2003 an additional study using *F. alnus* as the invasive pollen with *S. alba* was performed because this invasive continued flowering while *S. alba* was flowering. For the additional study with *S. alba* stigmas dusted with glossy buckthorn, the study sites were Great Meadow, Jessup Trail and a site near SAC 8. These plants were treated on 7 July 2003 and fruit set assessed 10 August 2003.

For all native plants used in the IPT hand pollination studies, approximately one week before flower bud break the stems were tagged and bagged with Delnet[®] to prevent pollinators from visiting any flowers that might open. When it appeared that sufficient flowers were open on the stems, bags were removed. On stems that were to receive a pollen dusting all unopened flowers were removed so that only even-aged open flowers remained on a plant. The remaining open flowers were counted. Then open flowers received their respective treatment (see below). In both 2002 and 2003 generally two to four weeks after flowering ceased, fruit set was assessed on tagged stems and percentage fruit set calculated.

In 2002, three hand pollination treatments were performed for lowbush blueberry: 1) native flowers hand pollinated with invasive (IP) and bagged with Delnet[®] mesh bags, 2) native hand pollinated with conspecific native pollen (PP) and bagged, and 3) native not hand pollinated not bagged. In 2002 for *V. nudum* and *S. alba* a fourth hand pollination treatment was added: hand pollinated with PP and unbagged.

In 2003, the PP versus IP treatments were as follows for all native species: 1) native hand pollinated with native (PP) unbagged, 2) native hand pollinated with native (PP) and bagged, 3) native not hand pollinated unbagged, 4) native hand pollinated with invasive (IP) and bagged, and 5) native hand pollinated with invasive (IP) unbagged. Fruit set from these treatments were compared to open pollinated fruit set for each native species at the study Experimental and Control sites.

Flowering stems or branches for the donor pollen were collected the morning of the treatment application and placed in containers of water to keep them fresh. All *V. angustifolium* stems were collected from patches of flowering *V. angustifolium* along the Loop Road in Acadia. All *B. thunbergii* stems were collected from a heavy infestation at Compass Harbor. All *V. nudum* were collected from plants along Rt. 3 and along the Park Loop Road. In 2002 *F. alnus* branches were collected from Jessup Trail and along Rt. 3 near the Dairy Bar. In 2003 all *F. alnus* were collected from a heavy infestation in Orono. All *S. alba* was collected along the Loop Road and Rt. 233 on Mt. Desert Island. In 2002 donor *L. salicaria* was collected from Orono, Trenton, and Frankfort and in 2003 from Orono and Frankfort, ME.

Pollen transfer studies were also used to assess the possibility of pollinator limitation. Dieringer (1992) defined pollinator limitation as the reduction of fruit and/or seed production below the level that is physiologically possible as a consequence of pollinator behavior, such as low

visitation rate or improper pollen transfer. Comparing fruit set for native species in which additional proper pollen was applied onto the stigma to nondusted open pollinated species addressed this question. If fruit set was significantly greater when additional proper pollen was applied to open pollinated flowers than without additional pollen applied, then pollinator limitation might also be indicated.

As the floral arrangement of each study native plant is very different, dusting varied between species. For *V. angustifolium* dusted with conspecific or *B. thunbergii* pollen, 2-8 *V. angustifolium* flowers per stem received a dusting. For *V. nudum* there are five clusters on each inflorescence. In 2002, one cluster per inflorescence was removed. Then the stigmas of 5-8 flowers were dusted per cluster. Two clusters were dusted with the invasive *F. alnus*: one bagged; one not. Two clusters were dusted with *V. nudum*: one bagged, one not. In 2003, on each study plant four inflorescences were used per plant, one for each treatment. One cluster of *V. nudum* per inflorescence was tagged with string, which was the cluster that received treatment. Seven to fifty-one *Viburnum* flowers per cluster were dusted in 2003. In 2002 and 2003 for *S. alba* 8-14 stigmas were dusted on four clusters per plant. Two clusters were dusted with the invasive *L. salicaria*: one bagged, one not. Two clusters were dusted with *S. alba*: one bagged, one not. Methods for dusting *S. alba* with *F. alnus* were the same as described above for *V. angustifolium* hand pollinated with *B. thunbergii*.

Additional native bee observations

Observations and results from 2002-2003 suggested that *B. thunbergii* and *F. alnus* might, at times, be contributing to maintaining the overall well-being of native bee communities. Therefore, native bee abundance and diversity was observed and recorded approximately bimonthly from mid-May to mid-July in 4 m² plots of *V. angustifolium* and *V. nudum* for one minute per monitoring period and for five minutes along a transect of variable length (generally 80 – 100 meters) in 2004-2005 at several sites with and without the invasive *B. thunbergii* and/or *F. alnus* present (Major Hypothesis 4). Figure 4 shows these study sites.

Additional collections of native bees were also randomly made in 2004 and 2005 from the study plants. Each bee was individually caught in a Petri dish as it visited a study plant. Approximately 15 hours of collecting time was spent per plant species per year.

Data analyses

For pollinator visitation studies any differences in pollinator visitation rates were determined using a Mann-Whitney Wilcoxon Rank Test ($P \leq 0.05$) and comparing each treatment plant group (Invasive, Native Experimental, and Native Control) against each other (Zar 1984; Quinn and Keough 2006).

To ascertain if there were site differences in floral availability the list of plant species present was condensed down only to those which co-flowered with the study plant pair, were entomophilous (attractive to insects), and were present in 20% or more of the plots for a given pair of study plants. The total number of times that a species was present was calculated (each increment over all four transects gave a total of 20 possible times). These numbers were then divided by 20 to yield a proportion of increments in the plot containing the species. These were entered into a spreadsheet and then analyzed by cluster analysis with Clustan (www.clustan.com);



Figure 4. Map of study sites for native bee observations in 4 m² plots and transects (2004-2005).

Van Sickle 1997) and MeanSim6 (Wishart 1999). A Euclidean dissimilarity matrix was formed using Clustan, and MeanSim6 was used to determine any significance after 10000 repetitions were used. This analysis is a randomization procedure (Manly 1991) that results in the sampling of the data 10000 times (or the number of times desired by the analyst), reshuffling the dissimilarity matrix each time before calculating a within and between treatment variance of the dissimilarity distance matrix. The frequency distribution of F ratios are compared to the one derived from the original data to determine whether it is greater than one would expect by chance (result of the 10000 randomizations).

Data analyses for the weather conditions were performed using Mann-Whitney Rank Tests ($P \leq 0.05$) on the plot averages of the readings taken from the sampling times for each year of the visitation studies.

The nonparametric Kruskal -Wallis (Zar 1984; Quinn and Keough 2006) was initially used to determine statistical significance ($P \leq 0.05$) for IPT treatments. If a significant difference resulted among treatments then individual Mann-Whitney Wilcoxon tests (Zar 1984; Quinn and Keough 2006) were used to determine which treatments were different. Fruit set data were analyzed with the Mann-Whitney Wilcoxon test. Bee abundance data for 2004 - 2005 were analyzed with the Mann-Whitney Wilcoxon test.

Results

Pollinator visitation

Pollinators were more abundant at *V. angustifolium* control sites than at *V. angustifolium* with *B. thunbergii* present in 2002 (Figure 5). The trend was similar in 2003, but was not statistically significant (Figure 5). For the other two native species, pollinator abundance did not differ in between sites without and with the invasive present (Figures 6 and 7).

Overall, the average number of visitors per ten minutes per study plot was not consistently different to the native plant species than to their co-flowering paired invasive (Figures 6 and 7). More pollinators visited *S. alba* and *L. salicaria* in 2003 than in 2002 (Figure 7). Pollinators, overall, were more abundant for the mid to late summer co-flowering study plants.

Bees (Apoidea), beetles (Coleoptera), flies, (Diptera) and ants (Formicidae) were the major pollinating/visiting insect groups observed. Insects that were recorded as part of the total visitors to the study plants, but not included as separate groups in Tables 1 - 6 were wasps, thrips, Lepidoptera, and Collembola. Table 7 provides a list of the major pollinators/visitors collected from the study plants. (Note that some of the species listed in Table 7 were also at times observed visiting other species of study plants, but as they were not collected and pinned they were not included in the table). Overall, 13 species of native bees were collected that were not previously documented in the Procter Surveys (Procter 1946). These include a species of *Bombus* (bumble bees) as well as solitary bee species not documented by the Procter surveys of 1917-1940 (Procter 1946). Appendix Figure 2 shows examples of the Megachilidae, one of the major native bee families in Acadia.

The presence of an invasive apparently influenced the composition of the pollinator community visiting native species. For example, there were more bees (Apoidea) at sites that contained *B. thunbergii* than at the *V. angustifolium* control sites (Tables 1 and 2). Another striking difference in pollinator community structure was that beetles were the most prevalent pollinators of *V. nudum* at control sites (see Procter et al. 1996 and Mawdsley 2003 for the importance of beetles as pollinators), but bees were the prevalent flower visitors at the experimental sites (Tables 3 and 4).

Apparently beetles did not visit *F. alnus* regularly, but bees were highly attracted to it (Tables 3 and 4). Very few honey bees, were observed and those mostly were at sites where *L. salicaria* was present.

Environmental factors

Environmental readings were analyzed to test whether any of these factors may confound the visitation rates to the plants. Tables 1 - 6 provide averages, standard deviations and stand errors of the mean for temperature, wind speed, relative humidity, and canopy cover. Temperature was significantly lower for samplings of the control plots for both *V. nudum* and *S. alba* in 2002 (Tables 3 and 5). If temperature had an effect, it could have possibly increased or decreased visitation rate in the control plots. Also, there were no significant differences in 2003 for temperature. Wind speed in *B. thunbergii* plots was significantly lower than in control

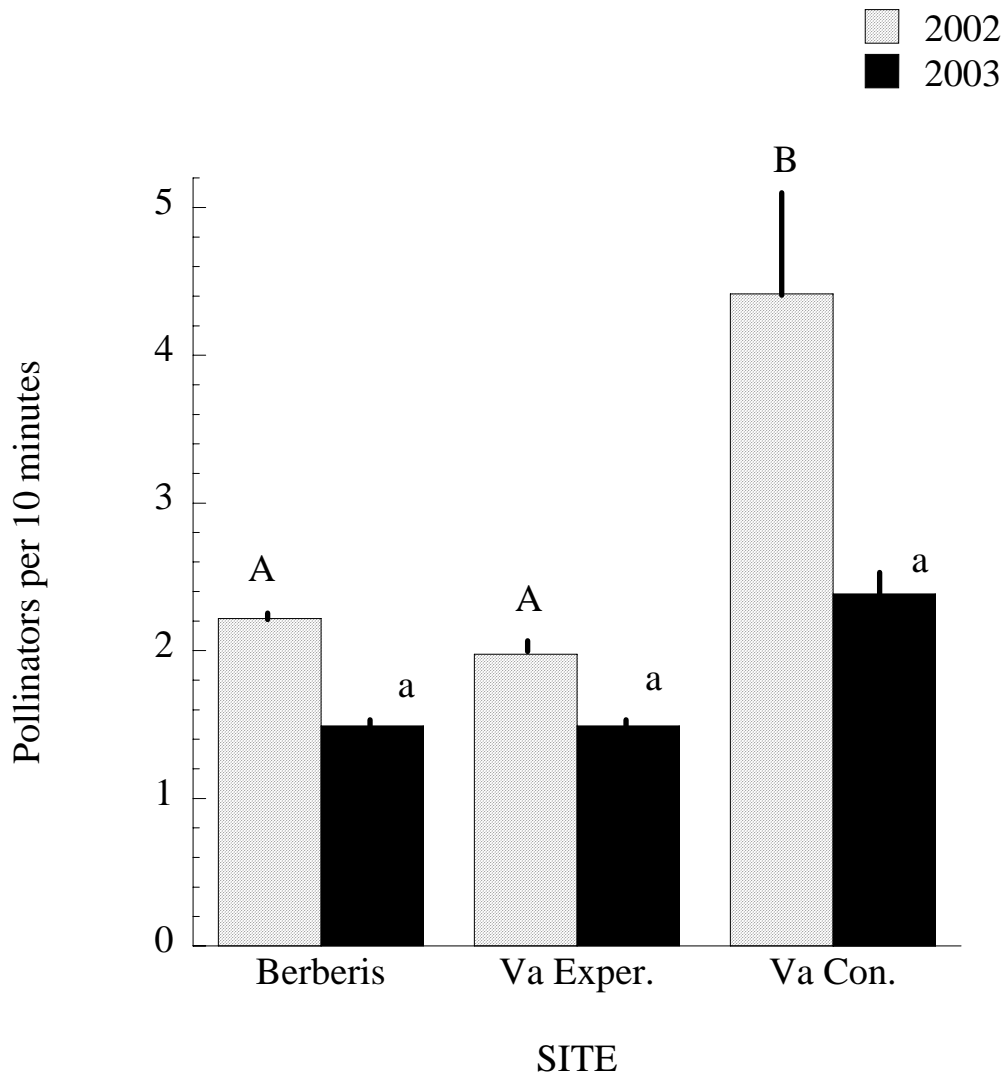


Figure 5. Mean number of pollinators + SE per 10 minute observation per site visiting the invasive *Berberis thunbergii* and native *Vaccinium angustifolium* at sites with (Exp. = Experimental) and without (Con. = Control) the invasive. N = 10, 11, and 6 in 2002 and 12, 12, and 11 in 2003. Bars with identical letters did not exhibit significant differences. Upper case letters indicate 2002 and lower case letters 2003.

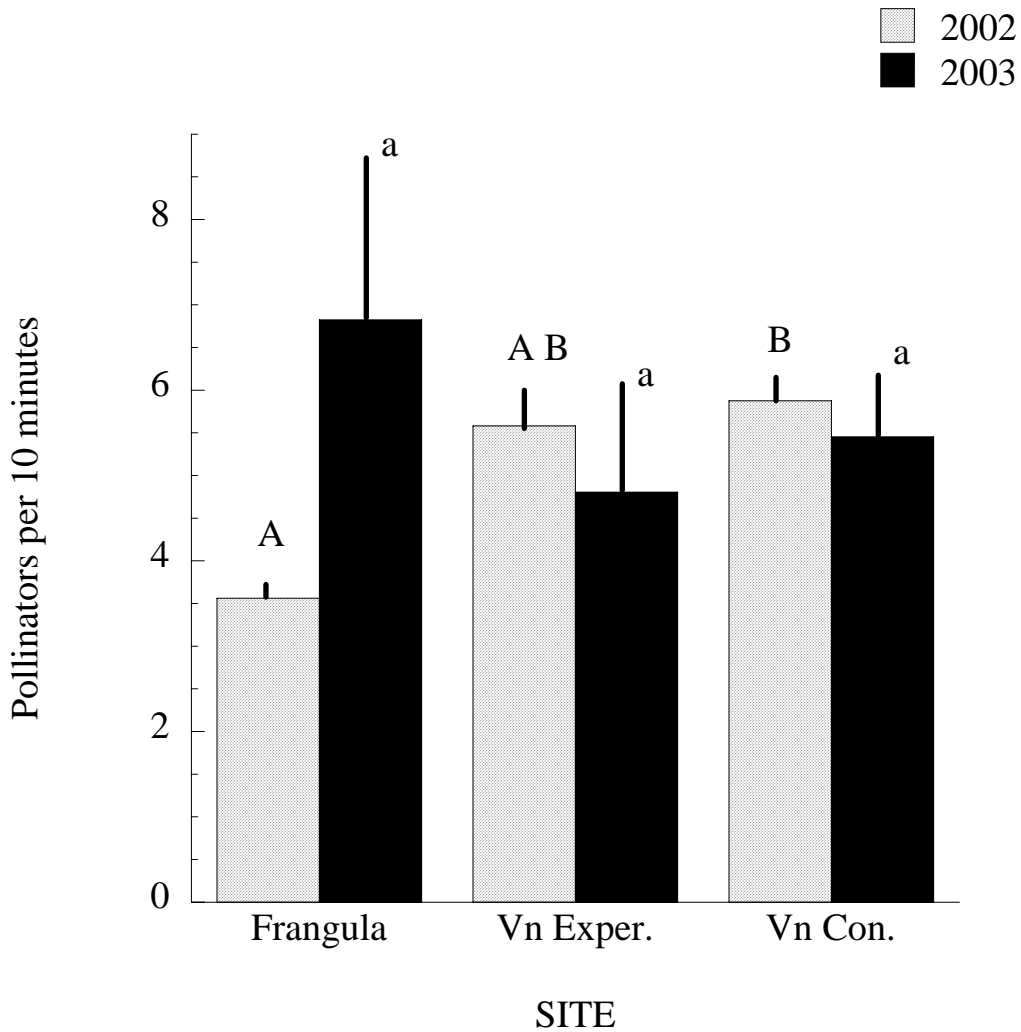


Figure 6. Mean number of pollinators + SE per 10 minute observation per site visiting the invasive *Frangula alnus* and native *Viburnum nudum* at sites with (Exp. = Experimental) and without (Con. = Control) the invasive. N = 12, 12, and 8 in 2002 and 11, 11 and 11 in 2003. Bars with identical letters did not exhibit significant differences. Upper case letters indicate 2002 and lower case letters 2003.

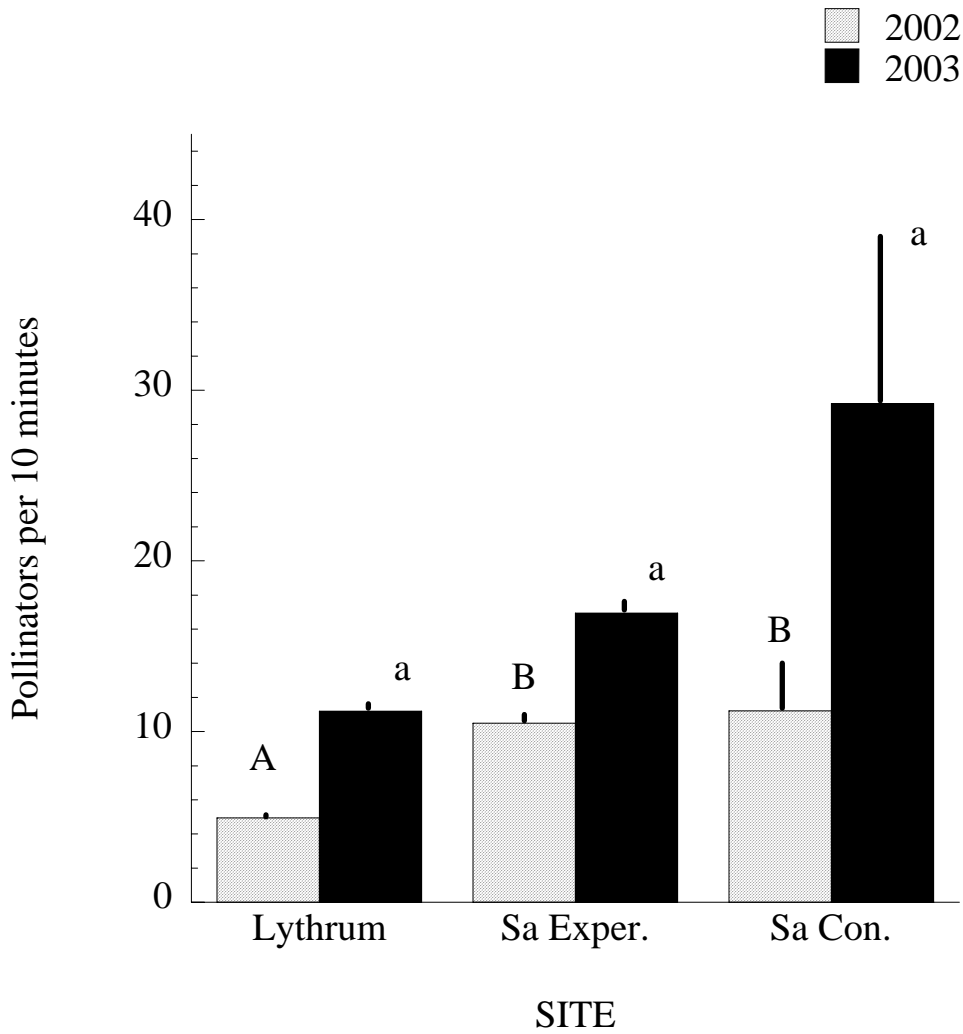


Figure 7. Mean number of pollinators + SE per 10 minute observation per site visiting the invasive *Lythrum salicaria* and native *Spiraea alba* at sites with (Exp. = Experimental) and without (Con. = Control) the invasive. N = 13, 13, and 7 in 2002 and 13, 13, and 8 in 2003. Bars with identical letters did not exhibit significant differences. Upper case letters indicate 2002 and lower case letters 2003.

Table 1. Summary of sampling dates, number of 10-minute observations, average environmental conditions, average number of flowers per stem, average percentage open flowers, average total insect pollinator visitation, and average number of bees (Apoidea), beetles (Coleoptera), flies (Diptera), and ants (Formicidae) to *B. thunbergii* and *V. angustifolium* for each study plot in 2002.

Plot	Dates	N	Temp (°C)	% RH	Wind (km)	% Closure Canopy	Flowers	%		Apoidea	Coleoptera	Diptera	Formicidae
								Flowers Open	Pollinators				
Bt2	5/21-6/3	4	22.79	32	1.66	88.75	3.47	42	2.75	1.5	0	0	0.5
Bt3	5/21-5/31	3	20.16	35	1.90	92.3	1.4	100	0	0	0	0	0
Bt5	5/23-6/1	3	19.06	32.7	1.08	91.95	14.53	58	3.67	0	0.33	0	0
Bt6	5/21-5/31	2	19.88	39.4	1.61	96.72	2.4	100	0.5	0	0	0.5	0
Bt7	5/21-5/30	3	17.17	46.2	1.93	92.82	12.8	7	1	0	0	0.67	0.33
Bt8	5/21-6/3	4	20.43	43.2	1.54	95.37	14.3	57	0	0	0	0	0
Bt9	5/21-6/3	4	22.28	63	3.54	56.16	13.4	66	3.25	1.75	0.25	0.25	0
Bt10	5/22-6/4	3	19.55	42.4	2.01	89.18	13.8	75	2.33	0.33	0	1	0.67
Bt11	5/21-5/27	3	18.02	51.8	4.54	15.08	15.6	90	5.67	3.33	0	0.67	1
Bt12	5/25-6/4	3	14.04	34.7	2.09	89.7	7.8	92	3	0	0.33	0.33	0.33
AVG		3.20	19.34	42.04	2.19	80.80	9.95	68.70	2.22	0.69	0.09	0.34	0.28
SD		0.63	2.53	9.73	1.04	25.83	5.61	29.39	1.83	1.14	0.15	0.36	0.35
SE		0.20	0.80	3.08	0.33	8.17	1.77	9.29	0.58	0.36	0.05	0.11	0.11
Va2	5/21-6/3	4	22.79	32	1.72	61.45	8.2	59	2.75	1.75	2	0.25	0.25
Va3	5/21-5/31	3	21.36	33.8	1.96	87.36	4	98	0	0	0	0	0
Va5	5/23-6/1	3	19.06	32.7	1.08	75.23	4.73	72	3.75	2		0.25	0.25
Va6	5/21-5/31	2	20.28	38.4	1.48	81.12	4.6	97	1.5	1	0	0.5	0
Va7	5/21-5/30	3	17.17	46.2	1.93	28.34	7.7	76	3.33	1.33	0	0	1.67
Va8	5/21-6/3	4	20.30	48	2.22	82.34	11	36	0	0	0	0	0
Va9	5/21-6/3	4	22.24	46.3	1.72	53.82	9.2	54	1	0.5	0	0.25	0
Va10	5/22-6/4	3	20.46	39.5	1.93	89.18	14.2	24	0	0	0	0	0
Va11	5/21-5/27	3	18.02	51.8	4.54	73.84	7.4	88	2	1.67	0	0	0
Va12	5/25-6/4	3	13.57	32.8	2.25	75.23	3	94	0.67	0	0	0	0.67
Va13	5/22-6/4	4	19.07	43	1.69	48.01	11.13	65	6.75	3.75	0	1.75	0.5
AVG		3.27	19.48	40.41	2.05	68.72	7.74	69.36	1.98	1.09	0.20	0.27	0.30
SD		0.65	2.59	7.07	0.89	18.84	3.49	24.74	2.07	1.18	0.63	0.52	0.51
SE		0.16	0.63	1.71	0.22	4.57	0.85	6.00	0.50	0.29	0.15	0.13	0.12
Vac1	5/21-6/3	4	15.49	35	5.79	72.28	8.5	68	7	4.25	0.25	0.5	0.5

Plot	Dates	N	Temp (°C)	% RH	Wind (km)	% Closure Canopy	Flowers	% Flowers					
								Open	Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
Vac2	5/21-6/4	4	17.03	42.3	3.28	74.45	13.6	72	3.75	2.25	0	0	1
Vac3	5/22-6/3	4	16.91	38.5	2.49	3.9	6.1	52	4.25	2.75	0	0.5	0.25
Vac4	5/21-5/25	4	20.15	29.4	2.00	66.43	24.8	53	2.25	1	0.25	0	0.5
Vac5	5/21-6/3	4	16.17	35.7	2.30	85.02	9.47	75	3.25	1.75	0		1
Vac6	5/22-6/3	4	18.13	34.5	1.98	60.75	4.6	83	6	2.25	0.5	0.25	2
AVG		4.00	17.31	35.91	2.97	60.47	11.18	67.17	4.42	2.38	0.17	0.25	0.88
SD		0.00	1.65	4.30	1.46	28.89	7.36	12.38	1.77	1.09	0.20	0.25	0.63
SE		0.00	0.67	1.75	0.60	11.79	3.00	5.06	0.72	0.45	0.08	0.10	0.26

Table 2. Summary of sampling dates, number of 10-minute observations, average environmental conditions, average number of flowers per stem, average percentage open flowers, average total insect pollinator visitation, and average number of bees (Apoidea), beetles (Coleoptera), flies (Diptera), and ants (Formicidae) to *B. thunbergii* and *V. angustifolium* for each study plot in 2003.

Plot	Dates	N	Temp (°C)	% RH	Wind (km)	% Closure Canopy	% Flowers						
							Flowers	Open	Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
Bt2	5/26-6/3	3	16.13	56	1.72	70.72	8.2	43	0	0	0	0	0
Bt3	5/21-6/3	3	19.56	40	1.29	31.55	9.07	46	1.33	0.67	0	0	0.33
Bt5	5/29-6/6	3	17.89	57	1.50	65.78	22.13	52	5	0	0	0	0
Bt6	5/21-5/27	4	16.67	57	1.45	58.37	12.35	33	0.25	0.25	0	0	0
Bt7	6/4-6/9	3	19.63	62.67	0.69	53.36	23.73	60	0.67	0	0	0	0.33
Bt8	6/2-6/6	3	20.89	34	2.78	74.71	14.2	67	2.33	1	0.33	0.33	0
Bt9	5/26-6/2	3	16.85	63	0.97	48.97	22.07	33	3.33	1.33	0	0.67	0
Bt10	6/6-6/10	3	18.18	7	0.80	79.3	15.73	28	1	0	0.33	0.67	0
Bt11	5/22-5/27	3	13.71	69.67	1.24	7.8	21.73	12	0	0	0	0	0
Bt12	6/2-6/9	3	16.78	53.33	3.06	54.08	20.87	59	1	0	0	0	0
AVG		3.10	17.63	49.97	1.55	54.46	17.01	43.30	1.49	0.33	0.07	0.17	0.07
SD		0.32	2.07	18.46	0.79	21.52	5.83	16.98	1.62	0.50	0.14	0.28	0.14
SE		0.10	0.66	5.84	0.25	6.81	1.84	5.37	0.51	0.16	0.04	0.09	0.04
Va2	5/26-6/3	3	15.87	56	2.46	37	12.6	45	3	1.33	0.33	0.67	0.67
Va3	5/21-6/3	3	20.32	40	1.13	31.37	7.1	40	0.33	0.33	0	0	0
Va5	5/29-6/6	3	19.56	52.33	1.61	45.33	7.27	55	6	4	0	0	2
Va6	5/21-5/27	4	17.03	58	1.13	47	14.9	68	2.25	2	0	0.26	0
Va7	6/4-6/9	3	19.09	58.67	1.61	9.01	7.6	34	0.33	0	0	0	0.33
Va8	6/2-6/6	3	20.5	36.67	3.86	53.04	4.53	54	0.67	0.33	0	0	0.33
Va9	5/26-6/2	3	17.18	56.67	1.13	35.1	7.07	37	1.33	1	0	0	0
Va10	6/6-6/10	3	19	73.33	0.80	53.82	4.8	46	0.67	0.67	0	0	0
Va11	5/22-5/27	3	13.39	72.67	1.45	48.88	14.6	69	0.33	0.33	0	0	0
Va12	6/2-6/9	3	17.06	54.67	1.77	59.71	5.33	53	0	0	0	0	0
AVG		3.10	17.9	55.90	1.69	42.03	8.58	50.10	1.49	1.00	0.03	0.09	0.33
SD		0.32	2.22	11.71	0.89	14.65	3.95	12.02	1.85	1.23	0.10	0.22	0.63
SE		0.10	0.70	3.70	0.28	4.63	1.25	3.80	0.59	0.39	0.03	0.07	0.20
Vac1	5/19-6/2	5	18.66	46.4	2.41	46.44	17.88	42	6.8	5.8	0.2	0.8	0
Vac2	5/21-5/26	3	18.06	43	1.77	43.68	6.13	25	0.33	0.33	0	0	0
Vac3	5/26-6/6	3	16.26	64	1.93	16.47	6.27	51	2.67	2.33	0	0	0

Plot	Dates	N	Temp (°C)	% RH	Wind (km)	% Closure Canopy	% Flowers						
							Flowers	Open	Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
Vac4	5/30-6/6	3	16.56	64	2.90	31.55	6.47	67	0.33	0.33	0	0	0
Vac5	5/21-5/26	3	15.33	55.5	1.13	49.05	4.4	44	0.33	0.33	0	0	0
Vac8	5/27-6/6	3	18.82	51	1.45	1.13	13.87	65	5	3	0	0	0.33
Vac9	5/27-6/6	3	19.71	54.67	2.25	2	11.73	52	3.67	1	0	0.33	2
Vac10	5/27-6/3	3	17.07	49.33	2.90	44.98	4.93	63	1.33	0.67	0	0	0.67
Vac11	6/3-6/9	3	16.59	65.67	4.07	31.46	11.73	66	1	1	0	0	0
AVG		3.22	17.45	54.84	2.31	29.64	9.27	52.78	2.38	1.64	0.02	0.13	0.33
SD		0.67	11.22	8.23	1.12	18.87	4.70	14.14	2.34	1.82	0.07	0.28	0.67
SE		0.22	3.74	2.74	0.37	6.29	1.57	4.71	0.78	0.61	0.02	0.09	0.22

Table 3. Summary of sampling dates, number of 10-minute observations, average environmental conditions, average number of flowers per stem, average percentage open flowers, average total insect pollinator visitation, and average number of bees (Apoidea), beetles (Coleoptera), flies (Diptera), and ants (Formicidae) to *F. alnus* and *V. nudum* for each study plot in 2002.

Plot	Dates	N	Temp (^o C)	% RH	Wind (km)	% Closure		% Flowers		Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
						Canopy	Flowers	Open	Flowers					
Fa1	6/24-7/2	3	25.93	44.33	1.01	86.71	22.5	40	3	2	0	0.67	0	
Fa2	6/25-7/2	3	24.44	57.33	0.68	89.44	19	26.67	2	1.33	0	0	0.33	
Fa7	6/24-6/29	3	26.75	41	1.77	10.75	14.67	68.52	2.67	1.67	0.67	0	0.33	
Fa8	6/29-7/2	3	24.19	61	1.37	13.39	20.33	38.33	8.33	1.33	0	0	6	
Fa9	6/24-6/27	2	28.31	34	1.77	34.06	15.5	16.25	4	2	0	0	1.5	
Fa10	6/29-7/2	3	26.06	52.33	2.41	23.4	16.67	52.33	5.33	2	0.33	0.33	1.67	
Fa11	6/29-7/2	3	27.65	52.67	0.00	57.46	18.67	39.68	2.67	0	0	0	2.67	
FaX	7/3	2	32.25	71	1.45	16.64	11.5	20.5	0.5	0	0	0	0.5	
AVG		2.75	26.95	51.71	1.31	41.48	17.36	37.79	3.56	1.29	0.13	0.13	1.63	
SD		0.46	2.57	11.80	0.74	32.37	3.49	17.12	2.38	0.84	0.25	0.25	1.98	
SE		0.16	0.91	4.17	0.26	11.44	1.23	6.05	0.84	0.30	0.09	0.09	0.70	
Vn1	6/24-7/2	3	26.09	46	0.64	88.66	45.8	82.2	6	2.5	1	1	0	
Vn2	6/25-7/2	3	24.43	60.67	0.69	83.72	59.73	34.07	3.67	0.33	1.67	0.33	1	
Vn7	6/24-6/29	3	25.86	46.5	1.69	10.75	78.9	13.3	5	3.33	0.67	0.33	0.33	
Vn8	6/29-7/2	3	25.61	53.5	1.29	21.97	56	67.9	9	3	1.33	2	0.33	
Vn9	6/24-6/27	2	28.64	34.5	1.37	53.82	60.8	95.6	9	3.5	0	0	5.5	
Vn10	6/29-7/2	3	25.85	54	2.57	54.47	50.4	47.8	4.33	1	0.33	1.33		
Vn11	6/29-7/2	3	27.19	57	0.00	57.46	45.2	68	1.67	0.33	0.33	0	0	
VnX	7/3	2	31.94	72.5	1.45	18.59	49.8	29	6	5.5	0.5	0		
AVG		2.75	26.95	53.08	1.21	48.68	55.83	54.73	5.58	2.44	0.73	0.62	1.19	
SD		0.46	2.36	11.27	0.78	29.33	11.03	28.35	2.52	1.80	0.56	0.74	2.14	
SE		0.16	0.84	3.99	0.27	10.37	3.90	10.02	0.89	0.63	0.20	0.26	0.76	
Vnc1	6/29-7/3	3	24.22	71.33	0.80	70.29	44.27	56	6.00	0.33	1.67	0.67	2.67	
Vnc2	6/27-7/1	3	22.67	64.67	1.29	23.57	46.93	51.87	8.67	0.00		1	7.67	
Vnc3	6/29-7/4	3	24.89	63.67	0.00	95.81	57.33	86.2	5.33	0.67		4.33		
Vnc4	6/29-7/4	3	25.91	63	0.00	91	61.84	80.4	4.00	0.00	2.67	0.33	1	
Vnc5	6/29-7/4	3	23.32	66.67	0.80	90.13	66.2	21.53	3.33	0.00	1.67	0.33	0	
Vnc6	6/25-7/1	3	25.17	53	1.17	61.19	49.1	33.1	5.33	0.00	2.33	0.67	0.66	
Vnc7	6/27-7/1	3	25.41	55.67	0.64	59.11	37.67	69.87	9.67	1.33	3.67	1	3	

Plot	Dates	N	Temp (⁰ C)	% RH	Wind (km)	% Closure		% Flowers		Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
						Canopy	Flowers	Open						
Vnc8	6/25-6/30	3	27.19	51.5	2.98	88.83	48.4	56	4.67	0.33	2.00	1	0	
AVG		3.00	24.85	61.19	0.96	72.49	51.47	56.87	5.88	0.33	2.34	1.17	2.14	
SD		0.00	1.44	7.03	0.94	24.41	9.54	22.11	2.21	0.47	0.76	1.31	2.72	
SE		0.00	0.51	2.49	0.33	8.63	3.37	7.82	0.78	0.17	0.27	0.46	0.96	

Table 4. Summary of sampling dates, number of 10-minute observations, average environmental conditions, average number of flowers per stem, average percentage open flowers, average total insect pollinator visitation, and average number of bees (Apoidea), beetles (Coleoptera), flies (Diptera), and ants (Formicidae) to *F. alnus* and *V. nudum* for each study plot in 2003.

Plot	Dates	N	Temp ($^{\circ}$ C)	% RH	Wind (km)	% Closure		% Flowers		Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
						Canopy	Flowers	Open	Flowers					
Fa1	6/22-6/25	3	22.43	72.67	0.00	58.07	18.67	47.83	2.67	2.33	0	0	0	
Fa2	6/24-6/30	3	22.71	72.67	0.53	69.85	26.67	33.52	0.33	0	0	0	0.33	
Fa3	6/21-6/24	4	20.77	72	0.37	81.19	8.35	68.36	1.5	1.5	0	0	0	
Fa4	6/22-6/25	3	22.74	68	0.00	75.4	11.47	46.21	1	0.67	0	0.33	0	
Fa5	6/24-6/30	3	24.78	61.33	0.27	47.93	18.4	41.53	10.67	6.33	2.33	0.33	0.67	
Fa7	6/19-6/24	4	23.22	54	1.58	1.5	24.1	28.11	4.75	1	0	0	3.25	
Fa8	6/25-6/30	3	28.96	45.33	1.08	2.17	39.67	45.89	13.67	2.67	0	0.33	10.67	
Fa9	6/22-6/25	3	24.26	56	1.29	21.06	11.4	37.61	4	0.33	0	0	3.33	
Fa10	6/24-6/29	3	27	46	1.24	14.39	23.67	25.14	16.33	0.67	0	0	15.33	
Fa11	6/24-6/29	3	27.44	51	0.85	19.33	13.07	16.26	13.33	5.33	0.67	0	6	
AVG		3.20	24.43	59.90	0.72	39.09	19.55	39.05	6.83	2.08	0.30	0.10	3.96	
SD		0.42	2.61	10.93	0.56	30.87	9.40	14.55	6.04	2.16	0.74	0.16	5.27	
SE		0.13	0.82	3.46	0.18	9.76	2.97	4.60	1.91	0.68	0.24	0.05	1.67	
Vn1	6/22-6/25	3	21.63	69.33	0.00	70.72	49.3	55.8	1	0	1	0	0	
Vn2	6/24-6/30	3	22.44	70.67	0.21	69.51	60.53	53.33	2	0.67	1	0	0.33	
Vn3	6/21-6/24	4	20.68	72	0.37	78.61	66.85	54.95	1.75	1.25	0.25	0.25	0	
Vn4	6/22-6/25	3	22.74	68	0.00	73.41	55.93	63.67	4	1.33	2	0.67	0	
Vn5	6/24-6/30	3	26.43	59.33	0.21	47.58	50.8	31.8	7.33	4	2	1	0	
Vn7	6/19-6/24	4	23.22	54	1.58	1.5	68.35	76.8	6	3	1	1	1	
Vn8	6/25-6/30	3	27.02	46.33	1.34	0.35	50.8	40.73	2.33	1	0	0	1.33	
Vn9	6/22-6/25	3	23.63	54.67	2.04	62.57	73.07	74.07	16.67	7.33	0.67	1.33	6	
Vn10	6/24-6/29	3	26.72	49	0.48	54.69	62.47	63.27	6	1.33	0	0.33	4.33	
Vn11	6/24-6/29	3	27.44	51	0.85	19.33	47.4	51.67	1	0.33	0.33	0	0.33	
AVG		3.20	24.2	59.43	0.71	47.83	58.55	56.61	4.81	2.02	0.83	0.46	1.33	
SD		0.42	2.48	9.77	0.72	29.95	9.02	13.80	4.75	2.22	0.73	0.50	2.11	
SE		0.13	0.78	3.09	0.23	9.47	2.85	4.36	1.50	0.70	0.23	0.16	0.67	
Vnc1	6/30-7/2	3	27.44	45.33	1.01	54.08	47.73	65.33	10.67	1.33	2.67	2.67	3	
Vnc2	6/24-6/29	3	24.65	60	0.97	10.92	55.4	42.07	3.67	0.67	0.33	0.67	2	
Vnc3	6/30-7/2	3	24.54	51.33	0.43	71.67	70.33	97.67	7.67	1.67	3.67	1.67	0.67	

Plot	Dates	N	Temp (⁰ C)	% RH	Wind (km)	% Closure		% Flowers		Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
						Canopy	Flowers	Open	Flowers					
Vnc4	6/30-7/2	3	23.54	51.33	0.48	82.25	69.93	87.33	2.67	0.33	0.67	0.33	1	
Vnc5	7/2	1	22.67	45	1.45	54.6	57	79	4	0	3	0	1	
Vnc6	6/27-6/30	3	27.61	56.67	6.28	15.34	59.3	72.5	1.67	0.33	0.67	0	0.33	
Vnc7	6/27-6/30	3	27.32	53.67	1.17	21.84	55.13	85.33	9	1.67	5.33	1	0	
Vnc8	6/25-6/28	3	24.37	61	1.93	80.6	47.8	39	1	0.67	0.33	0	0	
Vnc9	6/21-6/24	3	25.98	50	0.21	12.31	55.07	40.73	8	1.67	2.67	1.67	0.67	
Vnc10	6/30-7/2	3	24.78	47.67	0.97	58.11	44.87	24.47	2.67	0	1.67	0.67	0.33	
Vnc11	7/5-7/6	2	27.31	53.5	0.32		66.2	61	9	4.5	0	3.5	0	
AVG		2.73	25.47	52.32	1.38	46.17	57.16	63.13	5.46	1.17	1.91	1.11	0.82	
SD		0.65	1.74	5.37	1.70	28.57	8.73	23.75	3.45	1.29	1.70	1.16	0.94	
SE		0.19	0.53	1.62	0.51	8.61	2.63	7.16	1.04	0.39	0.51	0.35	0.28	

Table 5. Summary of sampling dates, number of 10-minute observations, average environmental conditions, average number of flowers per stem, average percentage open flowers, average total insect pollinator visitation, and average number of bees (Apoidea), beetles (Coleoptera), flies (Diptera), and ants (Formicidae) to *L. salicaria* and *S. alba* for each study plot in 2002.

Plot	Dates	N	Temp ($^{\circ}$ C)	% RH	Wind (km)	% Closure		% Flowers					
						Canopy	Flowers	Open	Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
Ls1	7/25-8/12	5	24.27	50	1.38	56.55	173.88	38.44	3.4	2.2	0	0.8	0.4
Ls2	7/25-8/12	5	24.38	47.4	1.16	44.14	153.1	60	2	1.2	0	0.4	0.2
Ls3	7/28-8/12	3	26.44	53	0.48	34.58	234.8	69	3	2	0	0.33	0.67
Ls5	8/10-8/19	3	27.02	60	0.00	67.99	233.27	46.13	8.67	6.67	0	0.67	0.67
Ls6	7/26-8/15	4	23.49	62	0.16	50.7	288.55	45.05	6.5	5.75	0	0	0.5
Ls7	7/26-8/18	5	24.89	70.4	0.61	44.41	275.7	41.55	8.6	7.4	0.8	0.2	0
Ls8	7/27-8/19	4	27.75	56.75	0.32	53.65	192.7	37.15	5	4.5	0	0.25	0
Ls9	7/15-8/23	7	26.39	50.67	0.68	0	162.58	44.78	3	2.14	0.14	0	0
Ls10	7/16-8/23	6	26.35	44.67	0.72	0.99	104.53	24.27	4.83	3.17	0.33	0.33	0.67
Ls11	7/15-8/23	6	26.67	53.17	1.13	12.48	98.1	64.3	3.5	2.5	0.17	0.5	0.33
Ls12	7/18-8/23	6	26.24	48.67	1.24	0	182.2	68	5.67	3.83	0.83	0.5	0
Ls13	7/13-8/23	6	25.84	48	0.71	1.09	127.47	17.73	6.67	2.17	0.83	0.83	1
Ls14	7/16-8/23	6	25.25	54.67	0.32	15.99	169.5	28.9	3.67	3	0	0	0.67
AVG		5.08	25.77	53.80	0.69	29.43	184.34	45.02	4.96	3.58	0.24	0.37	0.39
SD		1.26	1.23	7.07	0.43	25.07	59.89	16.46	2.15	1.95	0.35	0.29	0.33
SE		0.35	0.34	1.96	0.12	6.95	16.61	4.57	0.60	0.54	0.10	0.08	0.09
Sa1	7/25-8/12	5	24.27	50	1.38	56.55	140.56	47.12	7.4	1.6	3.2	0	2.4
Sa2	7/25-8/12	5	24.38	47.4	1.16	44.14	131	26.5	9.4	2.4	2.2	1.4	1
Sa3	7/28-8/12	3	26.44	53	0.48	34.58	142.8	25	5.67	2.33	0.33	0.67	1
Sa5	8/10-8/19	3	27.02	60	0.00	67.99	143.53	14.33	4	1	0.33	0.67	0.67
Sa6	7/26-8/15	4	23.93	58.5	0.45	55.03	118.13	32.33	54	1.25	0.5	0.5	50
Sa7	7/26-8/18	5	24.29	71.4	0.74	53.04	116.4	36.07	7.6	1.6	0.2	0.4	3.4
Sa8	7/27-8/19	4	27.75	56.75	0.32	55.12	141.78	21.47	6	1.75	0	0	0
Sa9	7/15-8/23	7	26.49	50.83	0.64	0	99.33	52	8.58	5.29	0.86	0.43	1
Sa10	7/16-8/23	6	26.72	46.5	1.05	5.46	100.6	23.27	5	2.67	0	0.5	1.5
Sa11	7/15-8/23	6	26.57	56	0.93	5.72	82.1	34.2	7.84	3.5	0.33	0.5	3.17
Sa12	7/18-8/23	6	25.86	49.5	1.17	0	141.2	57	4.33	2.33	0.67	0.67	0
Sa13	7/13-8/23	6	24.88	47.83	1.40	13.69	91.45	28.75	9.5	5	0.5	1	2.5
Sa14	7/16-8/23	6	25.25	54.33	0.43	24.53	130	59.4	9.17	2.5	0.5	0.33	2.33

Plot	Dates	N	Temp (°C)	% RH	Wind (km)	% Closure		% Flowers					
						Canopy	Flowers	Open	Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
AVG		5.08	25.68	54.00	0.78	31.99	121.45	35.19	10.65	2.56	0.74	0.54	5.31
SD		1.26	1.25	6.81	0.44	24.82	21.77	14.38	13.16	1.33	0.92	0.37	13.47
SE		0.35	0.35	1.89	0.12	6.88	6.04	3.99	3.65	0.37	0.26	0.10	3.74
Sac1	7/25-8/17	4	25.19	48	0.97	61.01	106.6	5.55	5	0	1	0	2.75
Sac2	7/24-8/17	4	26.25	41.25	1.50	47.06	80.87	38.67	7	0.5	2.25	0	1.25
Sac3	7/15-8/17	4	23.33	71.25	1.17	33.71	56.2	33.8	7.42	0.5	5.67	0.75	0
Sac7	7/13-8/23	8	22.67	61.13	1.63	17.81	77.12	33.6	7.51	0.63	5.25	0.5	0
Sac8	7/17-8/21	7	24.22	50.47	0.82	1.19	111.8	29.03	6.15	1.86	0.57	1.71	0.29
Sac9	7/16-8/21	8	24.86	47.71	0.64	20.93	79.53	46.57	7.64	2.13	1.88	1.5	0
Sac10	7/13-8/22	7	22.73	63.43	1.22	19.33	90.86	26.29	37.85	2.29	32.57	1	1
AVG		6.00	24.18	54.75	1.14	28.72	86.14	30.50	11.22	1.13	7.03	0.78	0.76
SE		0.72	0.92	4.04	0.08	7.61	7.15	4.85	4.45	0.35	4.32	0.25	0.38

Table 6. Summary of sampling dates, number of 10-minute observations, average environmental conditions, average number of flowers per stem, average percentage open flowers, average total insect pollinator visitation, and average number of bees (Apoidea), beetles (Coleoptera), flies (Diptera), and ants (Formicidae) to *L. salicaria* and *S. alba* for each study plot in 2003.

Plot	Dates	N	Temp		Wind (km)	% Closure		% Pollinators					
			(⁰ C)	% RH		Canopy	Flowers	FlowersOpen	Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
Ls1	7/25-8/3	3	24.89	60	2.25	37.27	175.87	16.93	6.33	5.67	0	0	0.67
Ls2	7/25-8/3	3	23.57	64.33	0.85	44.98	178.07	35.87	3	2	0	1	0
Ls3	7/25-8/3	3	23.52	62.33	1.13	40.73	168.47	28.73	11.67	10	0	0.33	0
Ls5	8/11-8/13	3	22.35	91	0.00	91.17	160.2	29	5.67	4.67	0	1	0
Ls6	8/11-8/13	3	22.78	94	0.00	49.49	193.87	33.67	8	7.67	0	0.33	0
Ls7	8/11-8/13	3	23.29	96.67	0.00	31.72	142	26.5	17.33	10.67	0	1	5.67
Ls8	8/11-8/13	3	22.59	91.33	0.00	25.48	259.33	32	10	8	0.33	0.33	0.67
Ls9	7/26-8/15	3	27.35	51.67	1.24	0	129.67	34.73	11	7.33	0.33	1.33	2
Ls10	7/26-8/15	3	28.26	43.67	1.61	1.04	143.47	25.33	11	8.67	0.67	1.33	0
Ls11	7/26-8/15	3	26.71	52.67	0.85	5.07	163.07	39.8	15.67	13	0	1	0
Ls13	7/26-8/15	3	27.82	48	1.08	2.99	142.4	28.93	15.67	12.33	0	1.33	0
Ls14	7/26-8/15	3	29.06	46.67	0.27	4.81	171.8	30.4	19	11.67	0	4	0
AVG		3.00	25.18	66.86	0.77	27.90	169.02	30.16	11.20	8.47	0.11	1.08	0.75
SD		0.00	2.49	20.48	0.74	27.32	33.93	5.87	4.97	3.29	0.22	1.03	1.66
SE		0.00	0.72	5.91	0.21	7.89	9.79	1.69	1.44	0.95	0.06	0.30	0.48
Sa1	7/25-8/3	3	24.89	60	2.09	39.17	104.4	39.67	13.33	2.67	2.33	5	2.67
Sa2	7/25-8/3	3	23.57	64.33	0.85	44.98	88.6	15.4	17	2.33	8.67	1.33	3.33
Sa3	7/25-8/3	3	25.56	66	1.29	31.63	104.07	27.73	23.33	3.67	9.67	3.67	4.67
Sa5	8/11-8/13	3	22.35	91	0.00	75.31	101.67	35.33	7.33	0.33	0	1.33	3.67
Sa6	8/11-8/13	3	22.71	92.33	0.00	68.12	113.93	32.33	14.67	2.67	2.67	1.67	7
Sa7	8/11-8/13	3	22.5	93.67	0.00	53.04	113.53	35.27	20.67	2	0.33	2	16
Sa8	8/11-8/13	3	23.17	95.33	0.00	51.48	163.13	21.4	22	1.33	0.67	2.33	15.33
Sa9	7/26-8/15	3	27.35	53.33	1.40	0	87.87	40.2	14.33	4	1.33	4.33	1.33
Sa10	7/26-8/15	3	28.87	42.67	1.01	0.61	88.6	28.27	15.33	5	1	3.67	4.67
Sa11	7/26-8/15	3	25.56	57	0.80	5.72	80.6	35.93	18.67	7.67	3.33	2.33	2.67
Sa13	7/26-8/15	3	28.93	48	1.50	17.81	81.33	26.53	20.67	8	0.33	4.33	5
Sa14	7/26-8/15	3	26.87	47.33	0.32	67.08	114.13	40.87	16	3	0	4.33	5
AVG		3.00	25.19	67.58	0.77	37.91	103.49	31.58	16.94	3.56	2.53	3.03	5.95
SD		0.00	2.40	20.03	0.71	26.86	22.54	7.92	4.45	2.34	3.29	1.33	4.77
SE		0.00	0.69	5.78	0.21	7.75	6.51	2.29	1.29	0.67	0.95	0.38	1.38
Sac5	7/18-7/28	3	24.02	55.33	2.74	0.78	90	25.33	19.67	1.33	5.33	2.67	5.67
Sac6	7/25-8/4	3	23.32	57.67	1.24	24.79	91.93	23.4	63	1.33	51.33	2	5
Sac7	7/15-7/21	3	25.02	61	0.80	3.73	93.8	31.3	20	4.33	6.67	3.67	0

Plot	Dates	N	Temp		Wind (km)	% Closure Canopy	%						
			(°C)	% RH			Flowers	FlowersOpen	Pollinators	Apoidea	Coleoptera	Diptera	Formicidae
Sac8	7/25-7/29	3	27.17	57.33	1.29	1.13	116.87	34	28.33	11.67	4.33	5.67	0.67
Sac9	7/25-7/29	3	27.48	55.33	0.85	1.21	120.8	24.33	73.33	6.67	2.67	1	0
Sac10	7/15-7/24	3	24.18	63.67	1.61	16.47	91.6	42.1	4.67	8	62.33	1	0
Sac11	7/23-7/25	2	21.11	97.5	1.29	5.46	47.9	34.5	20.33	0	0	1.5	0
Sac12	7/25-7/29	3	26.02	43	1.93	0.09	76.07	29.5	20.67	9.67	3	2.33	1
AVG		2.88	24.79	61.35	1.47	6.71	91.12	30.56	31.25	5.38	16.96	2.48	1.54
SD		0.35	2.11	15.82	0.63	9.05	22.83	6.32	23.86	4.30	24.86	1.57	2.38
SE		0.13	0.75	5.59	0.22	3.20	8.07	2.23	8.44	1.52	8.79	0.55	0.84

Table 7. Species of insects collected from native and invasive study plants (2001-2005).
 * indicates a species of bees not found in the Procter surveys.

Species	Study plant collected on
Hymenoptera (Apoidea)	
Andrenidae (Miner bees)	
* <i>Andrena alleghaniensis</i>	<i>Frangula alnus</i>
<i>Andrena clarkella</i>	<i>Frangula alnus</i>
<i>Andrena crataegi</i>	<i>Frangula alnus</i>
* <i>Andrena cressonii</i>	<i>Frangula alnus</i>
	<i>Vaccinium angustifolium</i>
* <i>Andrena dunningi</i>	<i>Berberis thunbergii</i>
<i>Andrena hirticincta</i>	<i>Frangula alnus</i>
* <i>Andrena ilicis</i>	<i>Frangula alnus</i>
<i>Andrena lata</i>	<i>Berberis thunbergii</i>
<i>Andrena milwaukeensis</i>	<i>Berberis thunbergii</i>
<i>Andrena miranda</i>	<i>Viburnum nudum</i>
* <i>Andrena rugosa</i>	<i>Berberis thunbergii</i>
	<i>Vaccinium angustifolium</i>
<i>Andrena sigmundi</i>	<i>Frangula alnus</i>
<i>Andrena thaspis</i>	<i>Vaccinium angustifolium</i>
<i>Andrena vicina</i>	<i>Vaccinium angustifolium</i>
	<i>Frangula alnus</i>
	<i>Viburnum nudum</i>
<i>Andrena sp.</i>	<i>Viburnum nudum</i>
	<i>Vaccinium angustifolium</i>
	<i>Berberis thunbergii</i>
	<i>Frangula alnus</i>
	<i>Spiraea alba</i>
Apidae (Apid bees, honeybees, bumblebees, cuckoo bees)	
<i>Apis mellifera</i>	<i>Lythrum salicaria</i>
<i>Bombus bimaculatus</i>	<i>Spiraea alba</i>
	<i>Frangula alnus</i>
* <i>Bombus impatiens</i>	<i>Berberis thunbergii</i>
<i>Bombus perplexus</i>	<i>Spiraea alba</i>
<i>Bombus (Psithyrus) ashtoni = Psithyrus ashtoni</i>	<i>Spiraea alba</i>
* <i>Bombus (Psithyrus) insularis = Psithyrus insularis</i>	<i>Frangula alnus</i>
<i>Bombus ternarius</i>	<i>Spiraea alba</i>
<i>Bombus vagans</i>	<i>Spiraea alba</i>
	<i>Lythrum salicaria</i>
	<i>Spiraea alba</i>
	<i>Frangula alnus</i>
<i>Ceratina dupla dupla</i>	<i>Vaccinium angustifolium</i>
<i>Nomada spp.</i>	<i>Vaccinium angustifolium</i>
	<i>Frangula alnus</i>

Colletidae (Polyester and yellow-faced bees)

Hylaeus modestus

Frangula alnus

Spiraea alba

Colletes inaequalis

Vaccinium angustifolium

Berberis thunbergii

Halictidae (Halictid and sweatbees)

**Agapostemon sericeus*

Spiraea alba

Agapostemon viresecens

Spiraea alba

Augochlorella striata = *Augochlorella aurata*

Spiraea alba

Vaccinium angustifolium

Halictus confusus

Spiraea alba

Halictus rubicundus

Spiraea alba

Halictus sp.

Berberis thunbergii

**Lasioglossum (Lasioglossum) forbesii*

Vaccinium angustifolium

**Lasioglossum (Lasioglossum) fuscipenne*

Spiraea alba

Lasioglossum (Lasioglossum) sp.

Spiraea alba

**Lasioglossum (Dialictus) illinoensis* = *Dialictus illinoensis*

Spiraea alba

Lasioglossum (Dialictus) zephyrus = *Dialictus zephyrus*

Frangula alnus

Lasioglossum (Dialictus) sp. = *Dialictus sp.*

Frangula alnus

Frangula alnus

Viburnum nudum

Lasioglossum (Evylaeus) cinctipes = *Evylaeus arcuatus*

Frangula alnus

Lasioglossum (Evylaeus) truncatum = *Evylaeus truncatum*

Spiraea alba

Lasioglossum (Evylaeus) sp. = *Evylaeus sp.*

Spiraea alba

Vaccinium angustifolium

Megachilidae (Mason and leaf-cutting bees)

**Megachile gemula*

Spiraea alba

Megachile inermis

Spiraea alba

Megachile melanophaea

Spiraea alba

Megachile relativa

Frangula alnus

Osmia atriventris

Vaccinium angustifolium

Chrysididae (Parasitic wasps)

Chrysis sp.

Spiraea alba

Vespidae (Vespid wasps)

Dolichovespula maculata

Vaccinium angustifolium

Berberis thunbergii

Dolichovespula sp.

Spiraea alba

Berberis thunbergii

Eumenes sp.

Frangula alnus

Euodynerus foraminatus

Vaccinium angustifolium

<i>Polistes</i> sp.	<i>Spiraea alba</i>
<i>Vespula</i> sp.	<i>Spiraea alba</i>
<i>Vespula vulgaris</i>	<i>Vaccinium angustifolium</i>
	<i>Berberis thunbergii</i>
	<i>Spiraea alba</i>
	<i>Frangula alnus</i>
Formicidae (Ants)	
<i>Camponotus pennsylvanicus</i>	<i>Viburnum nudum</i>
<i>Formica aserva</i>	<i>Viburnum nudum</i>
<i>Formica glacialis</i>	<i>Frangula alnus</i>
<i>Formica</i> sp.	<i>Frangula alnus</i>
<i>Myrmica rubra</i>	<i>Frangula alnus</i>
	<i>Spiraea alba</i>
	<i>Viburnum nudum</i>
Diptera (Flies)	
Syrphidae	<i>Viburnum nudum</i>
	<i>Spiraea alba</i>
	<i>Berberis thunbergii</i>
Hemiptera (True bugs)	
Miridae	
<i>Lygus lineolaris</i>	<i>Spiraea alba</i>
Coleoptera (Beetles)	
Cerambycidae (Long-horned flower beetles)	<i>Spiraea alba</i>
<i>Brachyleptura champlaini</i>	<i>Spiraea alba</i>
<i>Cosmosalia chrysocoma</i>	<i>Viburnum nudum</i>
<i>Judolia montivagans</i>	<i>Spiraea alba</i>
<i>Stictoleptura canadensis</i>	<i>Spiraea alba</i>
<i>Strangalepta abbrevia</i>	<i>Spiraea alba</i>
<i>Trachysida mutabilis</i>	<i>Viburnum nudum</i>
<i>Trigonarthris proxima</i>	<i>Viburnum nudum</i>
<i>Typocerus velutinus</i>	<i>Viburnum nudum</i>
Alleculidae (Comb-claw beetles)	
<i>Isomira quadristriata</i>	<i>Viburnum nudum</i>
Curculionidae (Snout beetles)	
<i>Anthonomus</i> sp. Prob. <i>subfasciatus</i>	<i>Spiraea alba</i>
Elateridae (Click beetles)	
<i>Agriotes quebecensis</i>	<i>Viburnum nudum</i>
<i>Agrotiella bigeminata</i>	<i>Viburnum nudum</i>
<i>Prosternon</i> sp. Prob. <i>fallax</i>	<i>Vaccinium angustifolium</i>
<i>Sericus brunneus</i>	<i>Viburnum nudum</i>

Lampyridae (Lightning bugs, fireflies)	<i>Berberis thunbergii</i>
<i>Pyractomena angulata</i>	<i>Spiraea alba</i>
Scarabaeidae (Scarab and flower beetles)	
<i>Serica</i> sp. Prob. <i>tristis</i>	<i>Berberis thunbergii</i>
<i>Trichiotinus assimilis</i>	<i>Viburnum nudum</i>
Oedemeridae	
<i>Asclera ruficollis</i>	<i>Berberis thunbergii</i>
Mordellidae	
<i>Mordellistena</i> sp. Prob. <i>scapularis</i>	<i>Spiraea alba</i>
<i>Mordellistena ancilla</i>	<i>Spiraea alba</i>
Cantharidae	
<i>Cantharis rectus</i>	<i>Frangula alnus</i>
Dermestidae (Dermestid beetles)	
<i>Anthrenus</i> sp.	<i>Spiraea alba</i>

V. angustifolium plots in 2003 and control *S. alba* plots had a significantly higher average wind speed than either the *L. salicaria* or experimental *S. alba* in both years. Canopy cover was significantly higher in control *V. nudum* in 2002 but in 2003 significantly lower in control *V. angustifolium* and *S. alba* than in their respective co-paired experimental plots.

Analysis of the transect data for each plant group showed that there were no significant differences between *V. angustifolium* and *B. thunbergii* with respect to other vegetation in and near the study plots. Plants common to both experimental and control plots were *Maianthemum canadensis*, *Aralia nudicaulis*, *Amelanchier* spp., and *Veronica chamaedrys*. The vegetation for *F. alnus* and *V. nudum* again showed no significant differences. Plants common to all treatment groups were *Rubus hispidus*, *R. allegheniensis*, *Hieracium* spp., *Potentilla tridentata*, *Rosa virginiana*, *Ranunculus acris*, and *V. dentatum*. However, there were significant differences between Invasive and Control plots and between Experimental and Control plots for *S. alba* ($P < 0.001$). Neither *Myosotis* spp. nor *Impatiens capensis*, were found at any Control sites. Appendix Table 7 provides a list of the 208 plant species found in the transects and/or plots at the study sites.

Soil analyses indicated only differences between the Control and Experimental *V. nudum* sites. PH was higher, organic matter less and calcium higher at the Experimental than Control *V. nudum* sites (Mann-Whitney $P \leq 0.05$).

Flower rewards- display

Berberis thunbergii had considerably more flowers on a stem than *V. angustifolium* at either the Experimental or Control sites in 2002 (Tables 1 and 2). *Lythrum salicaria* had larger flower clusters than *S. alba* both years but it is difficult to make a comparison between any of these unrelated species because they are morphologically different. More importantly, for all three native plant species, there were no significant differences between Control and Experimental plots for any given year. Comparisons of percent of flowers open on a stem or a cluster were difficult to make because of morphological differences, especially for buckthorn (flowers could be individually counted) and wild raisin (flowers in large clusters). Again, there were no significant differences for any native species comparisons between Control and Experimental plots (See Tables 1- 6).

Floral rewards- nectar and pollen availability

Floral reward data from 2003 (Table 8) indicates that nectar rewards were comparable between *V. angustifolium* and *B. thunbergii*. However only trace quantities of nectar for *V. nudum* were recorded.

Likewise the flowers of *S. alba* had considerably less nectar than *L. salicaria*, which produced four times more nectar on average. Quantity of pollen was extremely variable, but there was approximately eight times more pollen produced per flower for *B. thunbergii* than for native *V. angustifolium* (Table 8). *Frangula alnus* and *L. salicaria* on average produced about twice as much pollen as their co-flowering native species (Table 8). *Spiraea alba* and *L. salicaria* nectar had the highest sucrose content (Table 8).

Table 8. Average floral rewards in invasive and native plants in 2003.

Plant species	Nectar (μ L)/flower	% Sucrose Av.	# Pollen grains
<i>V. angustifolium</i>	0.31	13	34
<i>B. thunbergii</i>	0.46	5	242
<i>V. nudum</i>	<0.01	4	143
<i>F. alnus</i>	0.46	14	18
<i>S. alba</i>	0.05	> 50	111
<i>L. salicaria</i>	0.2	> 50	222

Although the differences were not significant due to high variability, the nectar replenishment studies showed the following trends: 1) that *V. angustifolium*, *B. thunbergii*, and *F. alnus* tended to produce more nectar during the hourly removal regime (Figure 8) and 2) that hourly removal, in contrast, reduced overall nectar production of *S. alba* and *L. salicaria* (Figure 8). No nectar could be extracted from *V. nudum* in the replenishment study.

Fruit and Seed Set

Pollinators were necessary for good fruit set for both the native species and the invasive species. Fruit production was significantly less for stems that had been bagged to exclude pollinators than from stems that were unbagged and hence open for insects to pollinate them, for all plant species investigated (Figures 9 and 10).

Native plant fruit set was never adversely affected in the presence of its paired co-flowering invasive species in either year (Figure 11). The only significant difference in fruit set was for *S. alba* in 2003 (Figure 11B) where fruit set was actually higher at sites where the invasive *L. salicaria* was present.

Native plant stigmas hand pollinated with invasive improper pollen (IP) and bagged had generally significantly less fruit set than open pollinated IP dusted stigmas (Figures 12 -15). For example, in 2003, fruit set for *V. angustifolium* with improper pollen on unbagged flowers was 26 % compared to 78% with proper pollen dusted on unbagged flowers (Figure 12). Likewise for *S. alba* in 2002, fruit set was 26 % for improper pollen on unbagged flowers versus 90% for flowers dusted with proper pollen (Figure 14). A major exception was *V. nudum* in 2002 for which there was no difference among treatments due to the high variance (Figure 13).

It appears that there may be some pollinator limitation as fruit set of the unbagged native species without dusting with conspecific pollen was generally lower than those open pollinated stems that received additional pollen. For example in 2003 for *V. nudum* in 2003 fruit set was significantly higher when additional pollen was added; it was 16 to 30 % higher (Figure 13). Likewise for *S. alba* the trend suggests some pollinator limitation for as fruit set was higher when dusted with additional proper pollen (Figure 14).

The presence of the co-flowering invasive species did not affect time to ripening. The time to ripening for unbagged stems was not different between Experimental and Control sites for *V. angustifolium*. Ripening began on 16 July and by 24 July, 25 ripe blueberries were recorded at Control sites and 43 ripe berries at Experimental sites. For *V. nudum*, ripe fruits were first recorded on 14 August at both Control and Experimental sites. Similarly ripening for *S. alba* began on the same date at both Experimental and Control sites, September 9, 2002.

The invasive *B. thunbergii* did not adversely affect seed set of open pollinated blueberry in either 2002 or 2003. *Vaccinium angustifolium* seed set in 2002 was similar at Control and Experiment sites (Mann Whitney U, $P = 0.7911$). The mean number of *V. angustifolium* seeds at Control sites was 22.1 seeds ($n = 6$ sites, range 3 - 62 seeds, $SD = 6.498$, $SE = 2.653$). The mean number of *V. angustifolium* seeds at Experimental sites was 21 seeds ($n = 4$ sites, range 3-43 seeds, $SD = 6.863$, $SE = 3.431$). Similarly, total number of seeds per berry did not differ between sites with and without *B. thunbergii* (Mann Whitney U, $P = 0.9528$). The mean number of

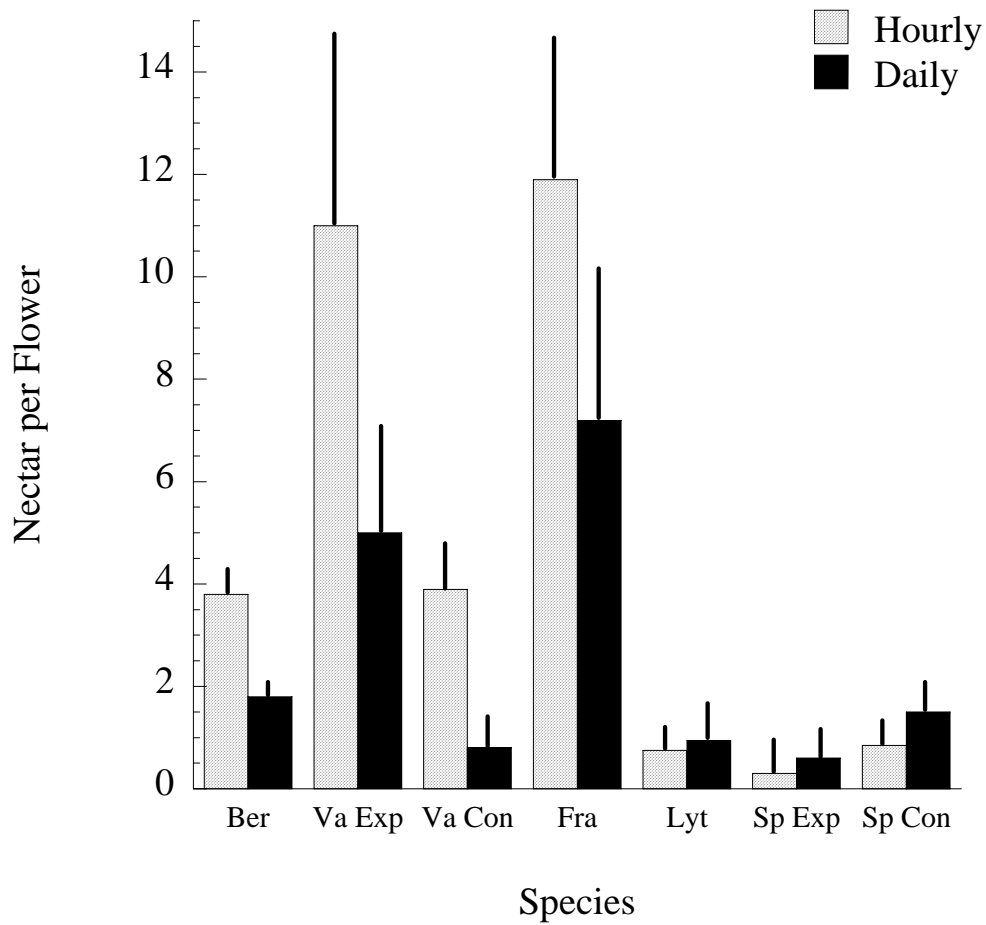


Figure 8. Mean + SE microliters of nectar replenished in *Berberis thunbergii* (Ber), *Vaccinium angustifolium* experimental and control (Va Exp, Va Con), *Frangula alnus* (Fa), *Lythrum salicaria* (Lyt) and *Spiraea alba* experimental and control (Sp Exp , Sp Con) flowers following extraction of standing crop either hourly or daily.

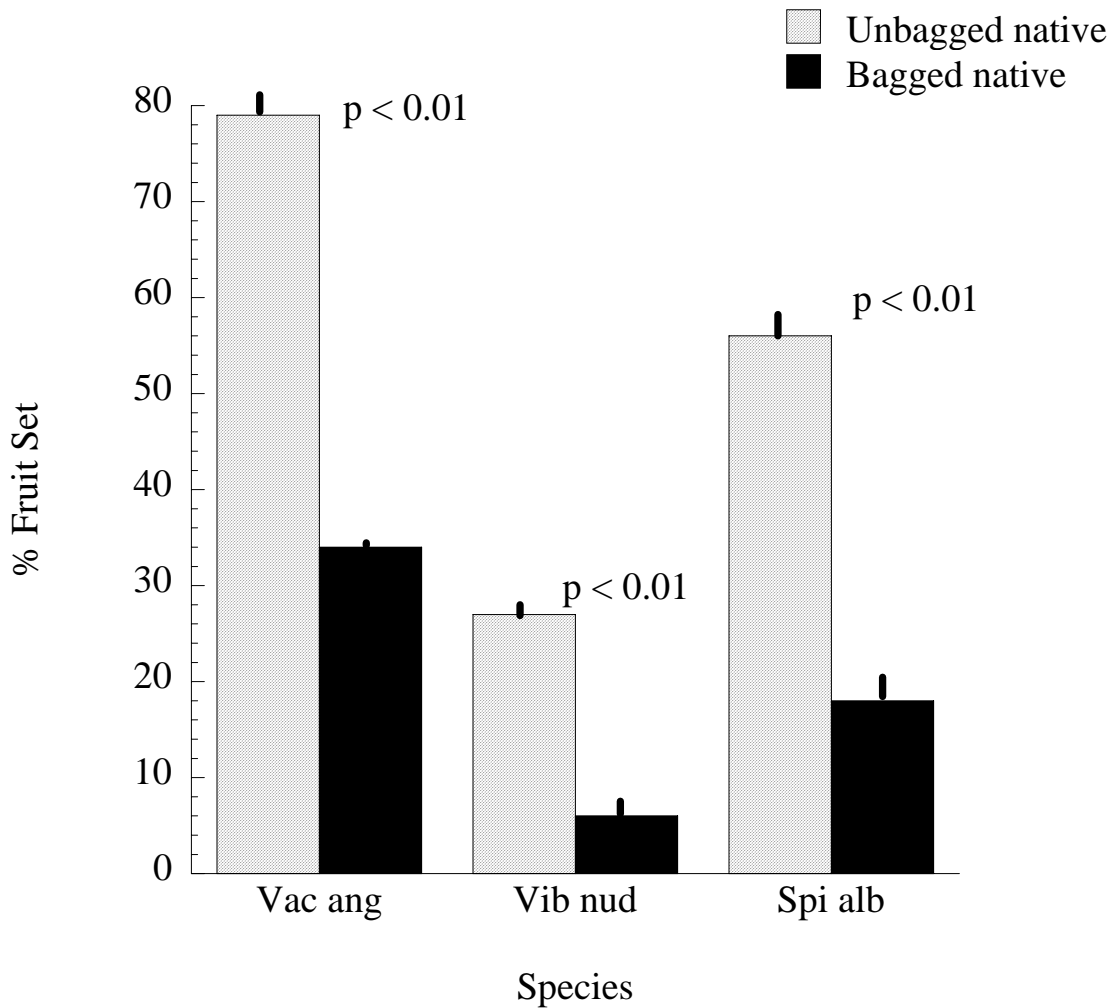


Figure 9. Mean + SE fruit set for unbagged (open pollinated) versus bagged (pollinators excluded) native *Vaccinium angustifolium* (n = 24; 23 stems respectively), *Viburnum nudum* (n = 33; 33 stems respectively), and *Spiraea alba* (n = 22; 19 stems respectively) in 2002.

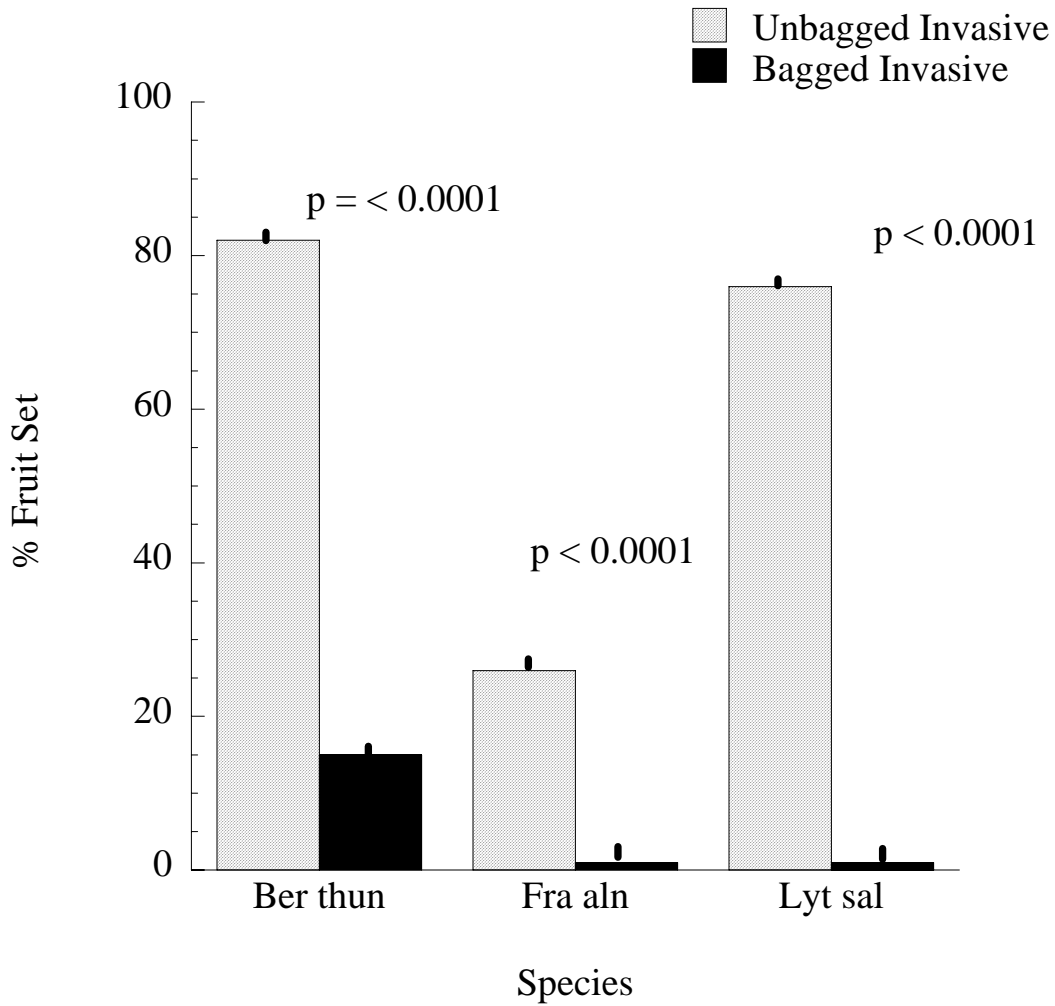


Figure 10. Mean + SE percentage fruit set for unbagged (open pollinated) versus bagged (pollinators excluded) invasive *Berberis thunbergii* (n = 13; 10 stems respectively), *Frangula alnus* (n = 23; 23 stems respectively), and *Lythrum salicaria* (n = 25; 25 stems respectively) in 2002.

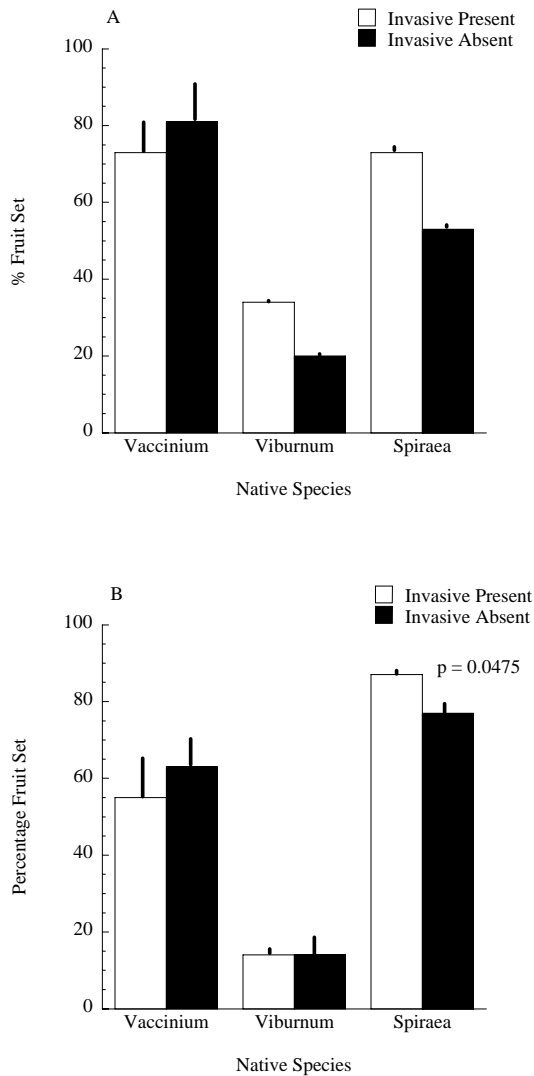


Figure 11. Mean percentage fruit set per stem + SE: (A) open pollinated native *Vaccinium angustifolium* at sites with and without *Berberis thunbergii* (n = 9; 16 stems respectively), *Viburnum nudum* at sites with and without *Frangula alnus* (n = 33; 14 stems respectively) and *Spiraea alba* at sites with and without *Lythrum salicaria* (n = 29; 22 stems respectively) in 2002 and (B) native *Vaccinium angustifolium* at sites with and without *Berberis thunbergii* (n = 9; 10 sites respectively), *Viburnum nudum* at sites with and without *Frangula alnus* (n = 7; 8 sites respectively), and *Spiraea alba* at sites with and without *Lythrum salicaria* (n = 11; 9 sites respectively) in 2003.

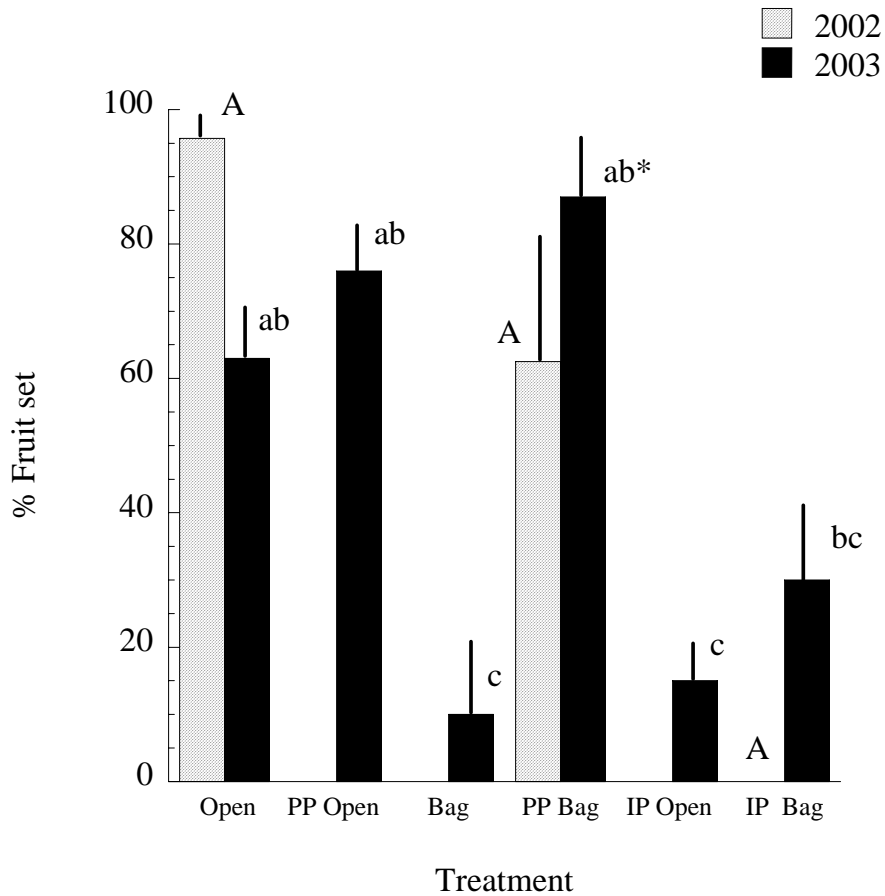


Figure 12. Mean + SE percentage fruit set per stem for native *Vaccinium angustifolium* for open pollinated, stigmas dusted with PP (Proper Pollen- *V. angustifolium* pollen) and stigmas dusted with IP (Improper Pollen- invasive *Berberis thunbergii* pollen) in 2002. N = 2, 4, and 3 stems respectively. Mean + SE percentage fruit set for native *V. angustifolium* stigmas: open pollinated; dusted with PP open pollinated; not dusted with pollen bagged; dusted with PP bagged; dusted with IP open pollinated; and dusted with IP bagged in 2003. N = 6, 5, 4, 4, 4, and 6 sites respectively in 2003. Bars with identical letters above did not exhibit significant differences. * indicates P = 0.055 for PP bagged versus IP bagged. Upper case letters indicate 2002 and lower case letters 2003.

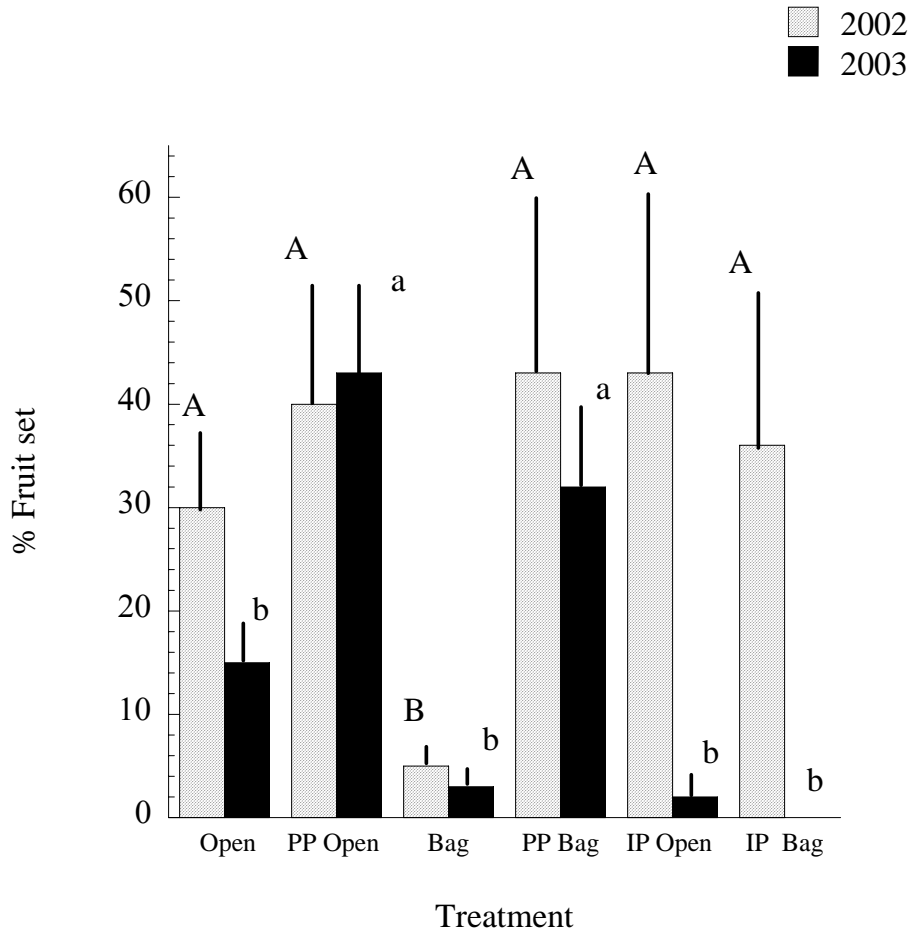


Figure 13. Mean + SE percentage fruit set per for native *Viburnum nudum* stigmas: open pollinated; dusted with PP (Proper Pollen- *V. nudum* pollen) open pollinated; not dusted with pollen bagged; dusted with PP bagged; dusted with IP (Improper Pollen- invasive *Frangula alnus* pollen) open pollinated; and dusted with IP bagged in 2002 and 2003. N = 7, 8, 16, 9, 8, and 7 stems respectively in 2002. N = 6 sites for all treatments in 2003. Bars with identical letters above did not exhibit significant differences. Upper case letters indicate 2002 and lower case letters 2003.

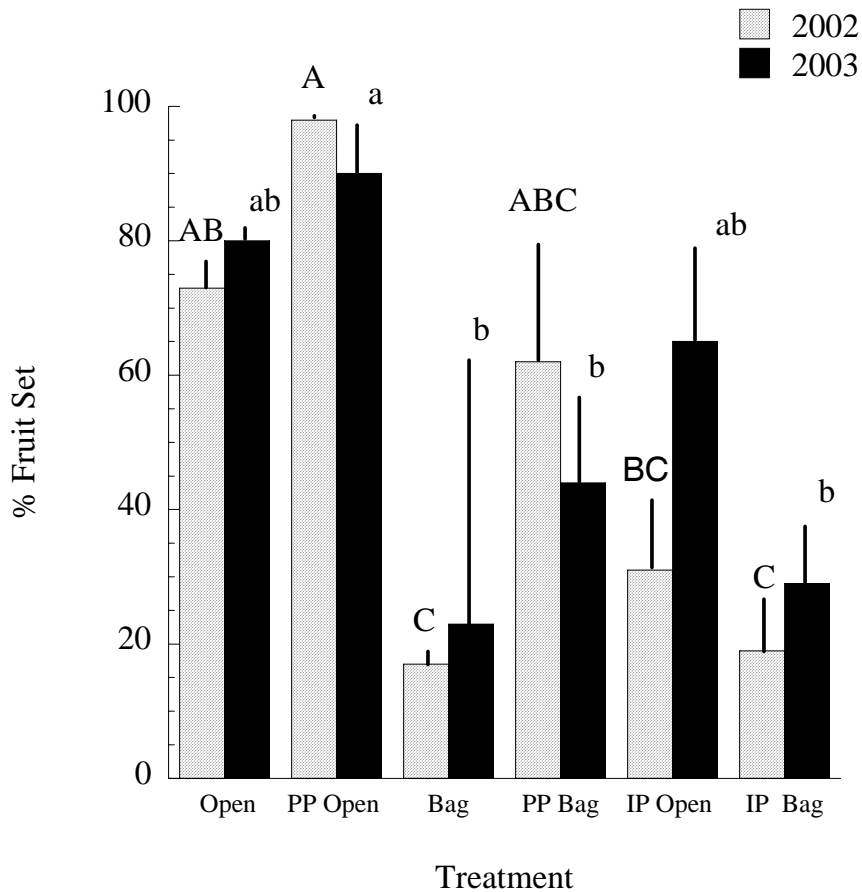


Figure 14. Mean + SE percentage fruit set for native *Spiraea alba* stigmas: open pollinated; dusted with PP (Proper Pollen- *S. alba* pollen) open pollinated; not dusted with pollen bagged; dusted with PP bagged; dusted with IP (Improper Pollen- invasive *Lythrum salicaria* pollen) open pollinated; and dusted with IP bagged in 2002 and 2003. N = 5, 6, 9, 6, 3, and 4 stems respectively in 2002. N = 7, 8, 5, 5, 8, and 4 sites respectively in 2003. Bars with identical letters above did not exhibit significant differences. Upper case letters indicate 2002 and lower case letters 2003.

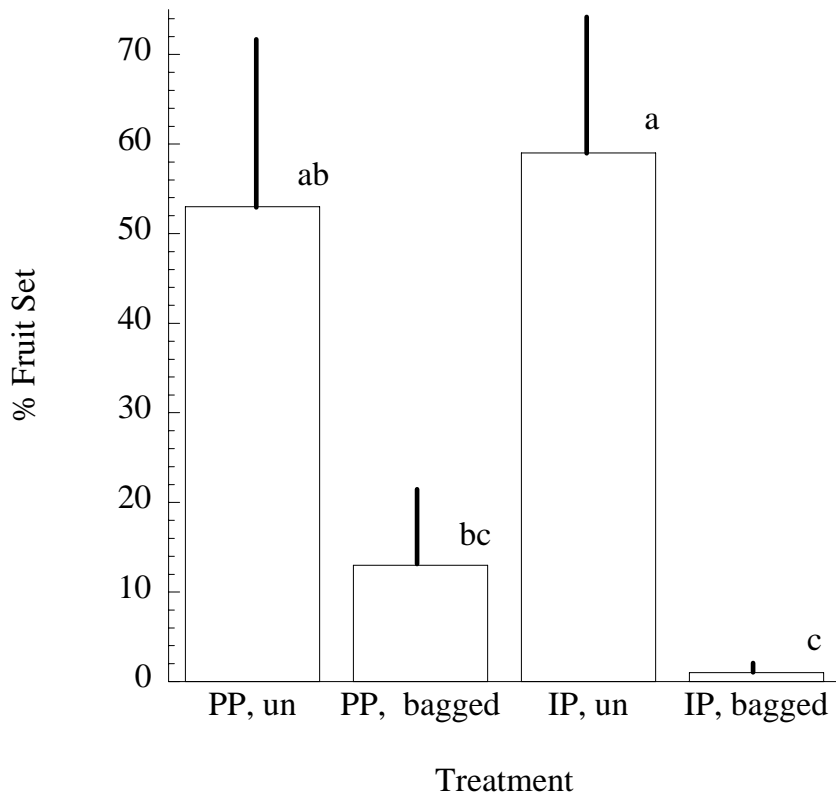


Figure 15. Average + SE percentage fruit set per stem for native *Spiraea alba* for stigmas unbagged and bagged dusted with PP (Proper Pollen- *S. alba* pollen) and stigmas dusted with IP (Improper Pollen- invasive *Frangula alnus* pollen) in 2003. Bars with identical letters above did not exhibit significant differences. N = 4, 4, 4, and 3 stems respectively.

V. angustifolium seeds per berry at Control sites was 24.3 seeds (n = 88 berries, SD = 11.86, SE = 1.287) versus 23.9 seeds at Experimental sites (n = 88 berries, SD = 11.313, SE = 1.206). In 2003, *V. angustifolium* seed set was again similar at Control and Experiment sites (Mann Whitney U, P = 0.8715). The mean number of *V. angustifolium* seeds at Control sites was 27.5 seeds (n = 8 sites, range 10 - 45 seeds, SD = 8.017, SE = 2.834) and 28.6 seeds at Experimental sites (n = 5 sites, range 3 - 48 seeds, SD = 14.925, SE = 6.675). Also when examined by treatment, total number of seeds per berry) similar results were again obtained (Mann Whitney U, P = 0.9528). The mean number of *V. angustifolium* seeds per berry at Control sites was 20.1 seeds (n = 37 berries, SD = 9.6, SE = 1.58). The mean number of *V. angustifolium* seeds at Experimental sites was 20.2 seeds (n = 39 berries, SD = 11.1, SE = 1.78).

The importance of pollinators for good seed set in *V. angustifolium* was demonstrated by the fact that for the few fruits that did set seed in the exclusion study in 2002 the average number of seeds was 1.5 per berry (n = 6 fruits) and in 2003 for the 3 fruits produced with pollinators excluded the average number of seeds per berry was 0.3 as compared to the 20 – 27 seeds per berry for open pollinated flowers (see above).

Seed set in *S. alba* in 2003 was similar at Control and Experiment sites (Mann Whitney U, P = 0.9828). The mean number of *S. alba* seeds per dehiscent follicle was 2.8 seeds (n = 20, range 0-5 seeds, SD = 1.71, SE = 0.388) at Control sites and 2.7 seeds per dehiscent follicle (n = 10, range 0-15 seeds, SD = 1.41, SE = 0.448) at Experimental sites.

Examination of the stigmas of the prepared slides indicated very little invasive pollen was deposited on the respective co-flowering native. Also there was no significant difference in the average number of *V. angustifolium* pollen grains on Control and Experimental *V. angustifolium* stigmas. There was also no difference in the amount of non-*B. thunbergii* foreign pollen on *V. angustifolium* stigmas. In general most stigmas had no invasive pollen on them. For example, about one *B. thunbergii* pollen grain was found for every three blueberry stigmas examined. This pattern applied to the other two sets of plants, as well. The presence of other foreign pollen was in general slightly greater than that of the invasives for all three native study plants examined.

Additional native bee sampling

Native bee abundance was the same for the one minute counts in the 4 m² plot in 2004 for sites with or without the invasive(s) present, but greater at sites with the invasive present in the 4 m² plots in 2005 (Figure 16). Furthermore, native bee abundance was greater at sites with the invasive(s) present for transect counts in both years (Figures 17). In 2004 two genera (*Colletes* and *Augochorella*) were observed only at sites with the invasive present. In 2005 bee numbers were reduced compared to 2004, but again abundance was greater at sites with these invasives present. Again in 2005 *Colletes* was only observed at sites with *B. thunbergii*, but no *Augochorella* were observed.

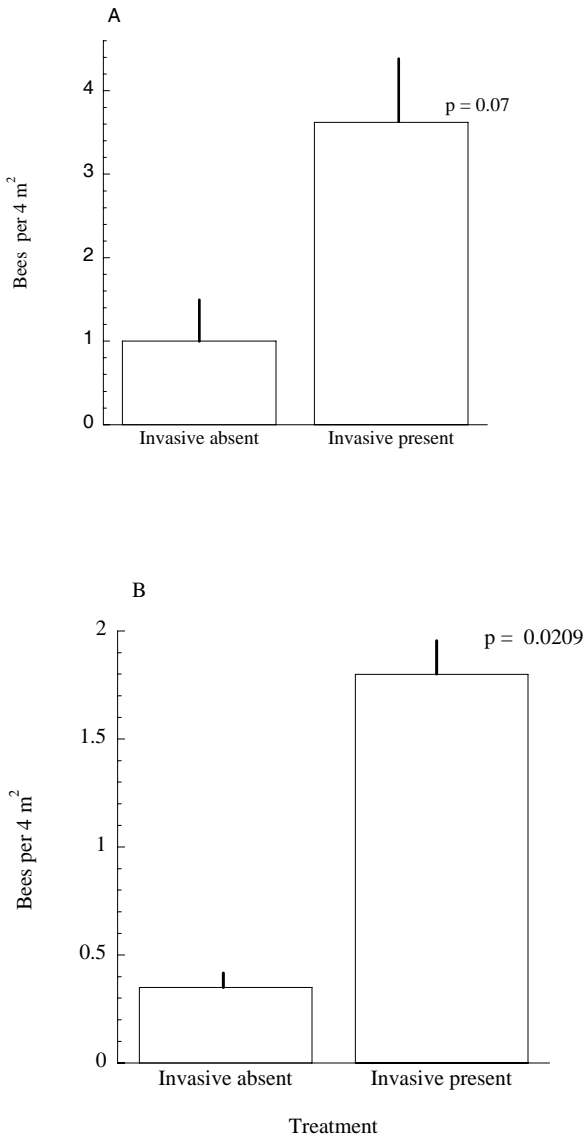


Figure 16. Average + SE number of native bees observed per 4 m² per one minute per site at 5 sites with and 5 sites without the invasive *Berberis thunbergii* and/or *Frangula alnus* in 2004 (A) and 2005 (B). N = 5 and 5 for both years.

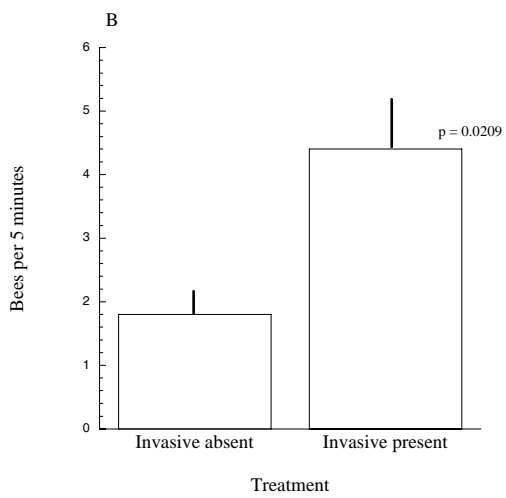
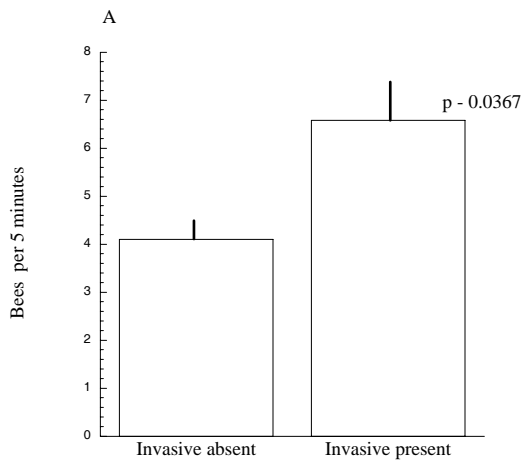


Figure 17. Average number of native bees observed per five minute transect per site at 5 sites with and 5 sites without the invasive *Berberis thunbergii* and/or *Frangula alnus* in 2004 (A) and 2005 (B). N = 5 and 5 for both years.

Discussion

Invasive plant species had varying effects on pollinator visitation to native plants, but apparently did not adversely affect fruit set in the native species examined. Overall our results suggest that the native plants did not compete with the invasives for pollinator service.

The effect of invasives on pollinator visitation to natives varied, depending on the species involved. Generally there was no consistent pattern. In one year the invasive *B. thunbergii* was associated with lowered visitation to native *V. angustifolium*, but was not in another year. In another instance, the invasive *F. alnus* apparently modified insect species composition of visitors to the native *V. nudum*. *Frangula alnus*, also, apparently provided nectar that attracted bees, which then visited nearby patches of the native wild raisin. In this way the invasive rendered patches of the native more "visible" and thus more attractive to some flower visitors. Similarly, Geer et al. (1995) found for a rare endangered milkvetch in Utah, that rather than competing for pollinators with common sympatric milkvetches, visitation rate to the rare endangered species was enhanced in the presence of additional co-flowering species.

To date only *L. salicaria* has been studied in terms of an invasive species affecting native species fruit and seed set in North America. The fact that *L. salicaria* did not adversely affect fruit and seed set in the *S. alba* is consistent with some of the findings of Grabas and Lavery (1999) who found no significant reduction in seed of *Eupatorium maculatum* (spotted joepeeweed) due to *L. salicaria*. However, Grabas and Lavery found *E. perfoliatum* (common boneset) and *Impatiens capensis* (jewelweed) had decreased seed set in plots of medium and high *L. salicaria* densities, respectively. The pollinator overlap was low between *L. salicaria* and the *Eupatorium* species, possibly due to the high incidence of honey bees on *L. salicaria*, whereas native bees were more prevalent on the native plant species (Grabas and Lavery 1999).

Grabas and Lavery (1999) also showed that some bees visited both *L. salicaria* and *E. maculatum* on the same foraging trip. This was also the case in the present research especially for some bumble bee species who visited all three species pairs. The fact that an insignificant amount of invasive pollen was deposited on native stigmas and that fruit and seed set were not negatively affected at sites where the invasives were present suggest that this sharing of foragers was of little consequence for the native plants under study in 2002 - 2003 in Acadia.

The present findings are in marked contrast to findings by Brown et al. (2002), who studied pollinators on *L. salicaria* and a conspecific native, *Lythrum alatum* Pursh (winged loosestrife). They found that *L. salicaria* lowered visitation rates to *L. alatum*, and that seed set was reduced in the native. Brown and Mitchell (2001) found that foreign pollen from *L. salicaria* on stigmas of *L. alatum* lead to a reduction in seed set, as well, and that pollen was often transferred between the two species in the field. In the Brown et al. (2002) study decreased visitation and deposition of foreign pollen reduced fitness of the native conspecific plant. However, one major difference between the Brown et al. (2002) study and the present study is that in Acadia honey bees were not abundant. Thus they would not significantly take-over the pollinating role of native bees and other pollinators. This lack of honey bees, coupled with deer browsing native vegetation, may in part explain why native pollinators visited the co-flowering invasives in

Acadia. In some studies native pollinators rarely visited the exotic invasive (e.g. *Lupinus arboreus* in Tasmania; Stout et al. 2002). However, native bees were abundant on alien plants in central New York (Ginsberg 1981).

Our seed set findings are consistent with those of Totland et al. (2006). Although Totland et al. (2006) found that *Phacelia tanacetifolia*, an invasive in Norway, had a strong negative effect on pollinators, drawing them away from the native *Melampyrum pratense*, fruit and seed set in the native were not significantly reduced.

Nectar volume apparently was not a factor in invasive species attracting pollinators away from native species. Based on nectar alone, *F. alnus* should have had higher bee visitation rates than *V. nudum* because the latter was a poor nectar producer. However, when the plants were together, there were no significant differences in bee visitation. It is possible the bees were visiting both plants to obtain both pollen from *V. nudum* and nectar from *F. alnus*.

Vaccinium angustifolium and *B. thunbergii* showed that they both significantly increase their nectar yield (replenish) following repeated removal, and glossy buckthorn showed a similar, though non-significant, trend. It appears that replenishment rate did not play a role in the *V. angustifolium* and *B. thunbergii* comparison or the *S. alba*-*L. salicaria* comparison. Plants that have the ability to rapidly replenish a nectar reward removed by pollinators probably are at a competitive advantage for pollinators over plants that cannot because a flower that is full is more likely to be visited again, and have more pollen deposited on the stigma thereby resulting in greater fruit and seed set. In the early spring in Acadia when flowering plant forage for pollinators is limited to a few species, having a species replenish nectar more with increased pollinator visitation should benefit both the plants and the pollinators.

The pollinator community varied among and between plant groups. In some instances generalist species, such as the orange-belt bumble bee, *Bombus ternarius*, visited all native and invasive species. In other instances, species with a more protracted adult activity period and forage preferences, such as the blueberry bee, *Osmia atriventris*, were found to visit only one or two of the study plants. In general, most of the native bee species observed and/or collected are generalists. This finding has important implications for the management of native plants as it suggests that should a particular native bee species become extirpated other generalists could "fill in" as long as there is considerable diversity within the native bee community (Kremen et al. 2002). Also other insect pollinators, as long as overall pollinator diversity is maintained "may fill" in, as was found for the pollination of *Shorea siamensis*, a tropical tree (Ghazoul 2004). Ghazoul (2004) found that human disturbance included the introduction of an invasive species more attractive to the butterfly, which reduced butterfly pollination. Nevertheless, overall native seed set was not affected due to compensatory pollination by perhaps moths and/or birds.

Briefly mentioned in the Methods section was the fact that grazing by deer necessitated the establishment of many new study plots. It was not an objective of the present research to assess deer herbivory on native plants and their pollinators. However if continued heavy grazing persists, especially on the crucial early spring flowering species, this could affect future flowering and pollination patterns.

Also note that there were no short term adverse effects on native plant reproduction, and bee abundance and diversity was greater in areas where Japanese barberry was present in 2004 and 2005. Tolerant of these two invasives, at least in the short-term, is consistent with recommendations by Ewel and Putz (2004), who argued that alien species can be tolerated or even used to good advantage in some ecosystem restoration projects if these aliens provide essential ecological or socioeconomic services. In Acadia *B. thunbergii* and *F. alnus* may be helping to sustain native bee populations. However, recent research suggests that invasives unpalatable to deer, such as *B. thunbergii*, may result in increased tick populations and possibly increased risk of Lyme disease (Elias et al. 2006).

Overall, bee diversity on *V. angustifolium* in Acadia was lower than in the managed blueberry major growing regions of Maine, where over 40 species of bees have been collected (Stubbs et al. 1992). This difference is likely due, in part, to the present sampling being conducted in one ecoregion. Sampling on Schoodic and Isle au Haut might increase the number of species found in Acadia visiting this species. Also, this study was only for several years whereas sampling in managed *V. angustifolium* extended over 30 years (Stubbs et al. 1992) so more intensive sampling would likely yield more species.

Relatively limited sampling might also be the reason for lower pollinator diversity for *V. nudum* in Acadia than in other regions of Maine. Miliczky and Osgood (1979a), Krannitz and Maun (1991) showed that *Viburnum* species (*cassinoides* [synonym for *V. nudum* in Haines and Vining (1991)] and two *opulus* varieties, respectively) required insect pollination for measurable fruit production. Miliczky and Osgood (1979b) identified five orders and 33 families of insects collected from the blooms of *V. cassinoides*, which represented greater pollinator diversity than in the present research at Acadia. Successful pollination of *V. nudum* yields a blue drupe in August, and consistent with findings by Miliczky and Osgood (1979a) and, Krannitz and Maun (1991) we found fruit set to be generally low, but that it did increase with additional pollen applied to stigmas, suggesting pollinator limitation.

The differences in temperature, wind speed, soil PH, and soil calcium did not appear to substantially affect visitation rates. Temperature and wind speed differences were well within the range for foraging activity by pollinators. In fact, there may have been more nectar available at lower temperatures. Interestingly, sites with lower organic matter had fewer soil nesting bees and had more beetles than bees as pollinators. This is in contrast to earlier findings by Osgood (1974), who found fewer soil nesting Andrenidae and Colletidae in *V. angustifolium* fields with high organic matter compared to fields with less organic matter. Perhaps in the present study differences in soil moisture (which was not measured) contributed to fewer soil nesting bees at some sites.

Conclusions

Recently Morales and Aizen (2006) suggested that the influence of invasive plants may be limited to co-flowering plants and that particular attention should be given to monitoring possible changes in pollinator visitation rates and seed output. Interestingly, the present research did not show any short term adverse effects to the co-flowering native species in spite of effects on pollinator visitation in some cases. Based on the present findings, Acadia Park Resource management personnel should continue to closely monitoring these invasive species, especially *L. salicaria*, so that their populations do not overrun the native flora of the Park. However, *B. thunbergii* and *F. alnus* appear, at least in the short term of this study, to have only modest effects on the co-flowering native species and might, actually at times, attract more pollinators to them. *Berberis thunbergii* and *F. alnus* might also benefit native bee and other pollinator populations by providing additional needed food resources.

We found that pollinators were necessary for good fruit set for all the plants we studied, both the native and the invasive species. Fruit production for all plant species investigated was significantly less for stems that had been bagged thus excluding pollinators than from stems that were unbagged and hence open pollinated.

Native plant fruit set was never adversely affected in the presence of its paired co-flowering invasive species. The only significant difference in fruit set was for *S. alba* in 2003 where fruit set was actually higher at sites where the invasive *L. salicaria* was present. The fact that our findings showed that pollinators were essential for fruit and seed set in the native species demonstrates that conservation and protection of pollinators should be of concern to Park Resource Management.

Based on these findings Acadia Park Resource Management personnel, should as previously mentioned continue to closely monitor and when needed manage these invasive species, especially *L. salicaria*, so that their populations do not overrun the native flora of the Park. *B. thunbergii* and *F. alnus* appear at least in the short term to attract pollinators. These two invasives provide additional food resources for native bees and other pollinators.

On the basis of pollination effects alone, removal of these two invasives need not at present be a high priority. Although native bee and other insect pollinator populations do fluctuate (Williams et al. 2001; Roubik 2001) the fact that native bee populations were lower in 2005 than 2004 is of some concern. Further monitoring may be warranted to determine if populations are stable or declining and if diversity is remaining constant or changing.

As mentioned in the Results section, native bees collected from patches of native and invasive plants were compared with historical records to assess whether invasive plants favor different bee species than those that formerly predominated on Mount Desert Island. This does not appear to be the case. However several species of *Bombus* (bumble bees) as well as nine solitary bee species were found that were not documented by the Procter surveys of 1917-1940 (Procter 1946). Also, because collecting of native bees was limited to the study plants many bee species documented in the Procter Surveys were not found. Much more extensive collecting throughout

the flowering season throughout other sections of Acadia would be necessary to determine if any species have been extirpated from the Park since the 1940's. Additional collections from other ecoregions would also provide a more complete inventory of native bee species within Acadia National Park.

Recommendations

First, from the standpoint of native plant reproduction our findings indicate that Park personnel do not need to intensively manage barberry or glossy buckthorn, at least in the short term. Second, in conjunction with the growing concern with pollinator declines world-wide, our initial sampling of pollinator populations, especially native bee species, and our fruit and seed set findings which suggest possible pollinator limitation, the Park personnel may want to consider periodic monitoring of these populations.

Products

The data were compiled and analyzed in order to provide the following information and/or products:

1) The effects of invasive exotic plant species on native plant pollination and on plant-pollinator communities were determined. These effects were evaluated in different habitat types (associated with the three different invasive plant species) to assess whether the effects of invasives are consistent across habitat-types. In the short term the invasives studied did not adversely affect the reproduction of the native plants studied.

2) Diversity, abundance, and community composition of native bees and other pollinators was compiled for these selected habitats in Acadia National Park.

3) The native pollinator collection (See Table 7) will be a valuable addition and asset to the Invertebrate Collection at Acadia.

4) A model system using easily recognized native bumble bees found in Acadia (Appendix Figure 3) was developed for use in monitoring and maintaining native plant pollinator-dependent ecosystem health. Many of these species have wide geographic ranges thus this system will be adaptable to many National parks and other public lands.

5) An educational program and materials were developed; some of which were presented at the United States Botanic Garden on 24 September 2004. These materials, which include some for youth ages 4 - 12, can be used for educating Park visitors by exposing them to: 1) the role of native plants and their bee pollinators in the ecosystem; 2) effects of invasive plants on native plant-pollinator mutualisms; 3) the need for conserving pollinators; 4) conservation strategies in the Park to conserve and enhance native plant-pollinator mutualisms. "The ultimate fate of many plants may depend on preserving their mutualistic relationship with pollinators" (Kearns and Inouye 1997, p. 297). Therefore the educational materials developed from our findings may be extremely useful to other National Parks. These materials will be housed at Acadia National Park.

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Appendix Table 1. Study sites: Universal Transverse Mercator (UTM) coordinates.

Site	UTM Coordinates	Elevation (Meters)
BTVA 1	N 44° 21' 52.9" W 068° 11' 0.42"	33.53
BTVA 2	N 44° 21' 58.6" W 068° 10' 9.75"	35.36
BTVA 3	N 44° 23' 0.6" W 068° 13' 5.88"	85.34
BTVA 5	N 44° 21' 20.2" W 068° 10' 9.34"	26.82
BTVA 6	N 44° 23' 46.7" W 068° 14' 2.15"	74.07
BTVA 7	N 44° 24' 12.2" W 068° 14' 0.66"	64.31
BTVA 8	N 44° 24' 12.2" W 068° 14' 0.66"	74.07
BTVA 9	N 44° 22' 14.3" W 068° 15' 56.0"	132.28
BTVA 10	N 44° 19' 8.3" W 068° 14' 0.88"	110.03
BTVA 11	N 44° 21' 28.6" W 068° 10' 9.75"	118.62
BTVA 12	N 44° 23' 22.27" W 068° 12' 6.47"	79.4
VAC 1	N 44° 20' 9.08" W 068° 12' 1.14"	115.82
VAC 2	N 44° 20' 20.05" W 068° 12' 0.87"	52.43
VAC 3	N 44° 21' 20.44" W 068° 12' 16.3"	82.60
VAC 4	N 44° 21' 20.32" W 068° 12' 17.19"	87.78
VAC 5	N 44° 20' 20.29" W 068° 12' 12.1"	71.02
VAC 6	N 44° 19' 20.30" W 068° 11' 8.15"	39.92
VAC 8	N 44° 23' 5.6" W 068° 14' 38.5"	70.4
VAC 9	N 44° 23' 45.0" W 068° 14' 16.8"	79.85
VAC 10	N 44° 22' 52.27" W 068° 12' 47.45"	87.16
VAC 11	N 44° 20' 37.7" W 068° 10' 7.54"	54.55
FAVN 1 - 4	N 44° 22' 17.7" W 068° 12' 29.7"	41.74
FAVN 5	N 44° 22' 12.27" W 068° 12' 29.5"	41.5
FAVN 6	N 44° 21' 7.3" W 068° 11' 7.64"	38.4
FAVN 7 - 11	N 44° 21' 6.36" W 068° 11' 8.28"	49.98
FAVN 12	N 44° 21' 8.8" W 068° 12' 6.14"	35.96
FAVN Jessup FA	N 44° 22' 15.2" W 068° 12' 7.02"	31.39
FAVN Jessup VN	N 44° 22' 17.1" W 068° 12' 7.12"	30.17

Site	Location	Elevation (Meters)
VNC 1	N 44° 22' 7.07" W 068° 15' 0.96"	95.09
VNC 2	N 44° 22' 7.23" W 068° 15' 9.75"	101.19
VNC 3	N 44° 20' 49.5" W 068° 11' 0.88"	39.62
VNC 4	N 44° 20' 22.2" W 068° 10' 8.15"	61.2
VNC 5	N 44° 20' 8.2" W 068° 10' 6.6"	64.0
VNC 6 – 8	N 44° 18' 9.65" W 068° 11' 8.64"	14.32
VNC 9	N 44° 23' 45.0" W 068° 14' 21.2"	70.40
VNC 10	N 44° 19' 0.53" W 068° 11' 48.0"	41.45
VNC 11	N 44° 18' 8.53" W 068° 11' 7.86"	29.56
LSSA 1 - 3	N 44° 21' 7.01" W 068° 11' 7.71"	28.95
LSSA 5 - 7	N 44° 22' 22.34" W 068° 11' 7.01"	78.02
LSSA 9 - 14	N 44° 25' 7.52" W 068° 16' 9.76"	19.2
SAC 1 - 2	N 44° 24' 12.2" W 068° 14' 0.66"	74.07
SAC 3	N 44° 20' 54.3" W 068° 14' 38.0"	110.3
SAC 5 – 6	N 44° 19' 0.54" W 068° 11' 7.09"	35.96
SAC 7 & 10	N 44° 20' 7.33" W 068° 14' 41.5"	111.25
SAC 8 - 9	N 44° 19' 20.30" W 068° 11' 8.15"	70.4
SAC 11	N 44° 19' 22.30" W 068° 16' 2.15"	131.06
SAC 12	N 44° 23' 56.32" W 068° 12' 34.6"	122.2

Appendix Table 2. Sites and dates for fruit set studies for tagged *Berberis* and *Vaccinium*.

Site	Dates of flower count	Dates fruit set measured
BT2	5/19/02	6/13/02
BT3	5/19/02	6/13/02
BT 5	5/19/02	6/13/02
VA 5	5/21/02	6/13/02
VA 7	5/30/02	6/13/02
VA 8	6/5/02	6/13/02
VA 9	6/3/02	6/13/02
VA 11	5/30/02	6/13/02
BT 11	5/30/02	6/13/02
VAC 1	5/21/02	6/13/02
VAC 2	5/21/02	6/13/02
VAC 3-4	5/30/02	6/20/02
VAC 6	5/21/02	6/13/02
VAC 4	6/3/03	7/1/03
VAC 8	6/3/03	7/1/03
VAC 10	6/3/03	7/1/03

Appendix Table 3. Sites and dates for fruit set studies for tagged *Frangula* and *Viburnum*.

Site	Dates of flower count	Dates fruit set measured
FAVN 1	6/19/02	7/18/02
FAVN 2	6/19/02	7/18/02
FAVN 3	6/19/02	7/18/02
FAVN 4	6/19/02	7/18/02
FAVN 5	6/19/02	7/18/02
FAVN 6	-	7/18/02
FAVN 7	-	7/18/02
FAVN 8	-	7/18/02
FAVN 9	-	7/18/02
FAVN 10	-	7/18/02
FAVN 11	-	7/18/02
FAVN 12	6/14/02	7/18/02
VNC 1	6/18/02	7/18/02
VNC 2	6/18/02	7/18/02
VNC 3	6/18/02	7/18/02
VNC 4	6/18/02	7/18/02
VNC 5	6/18/02	7/18/02
VNC 6	6/18/02	7/18/02
VNC 7	6/18/02	7/18/02
FAVN 1	6/19/03	7/17/03
FAVN 2	6/19/03	7/17/03
FAVN 3	6/19/03	7/17/03
FAVN 4	6/19/03	7/17/03
FAVN 5	6/19/03	7/17/03
FAVN 6	6/19/03	7/17/03
FAVN 7	6/19/03	7/17/03
FAVN 8	6/19/03	7/17/03
FAVN 9	6/19/03	7/17/03
FAVN 10	6/19/03	7/17/03
FAVN 11	6/19/03	7/17/03

Appendix Table 4. Sites and dates for fruit set studies for tagged *Lythrum* and *Spiraea*.

Site	Dates of flower count	Dates fruit set measured
LSSA 1	7/13/02	8/14/02
LSSA 2	7/13/02	8/14/02
SAC 1	7/13/02	8/14/02
SAC 4	7/26/02	8/14/02
SAC 5	7/13/02	8/14/02
LSSA 1	7/26/02	9/5/02
	7/31/02	
LSSA 2	8/1/02	9/5/02
	8/6/02	
	8/7/02	
LSSA 3	8/1/02	9/5/02
	8/6/02	
	8/7/02	
LSSA 5	7/18/03	8/10/03
LSSA 6	7/21/03	8/10/03
LSSA 7	7/21/03	8/10/03
LSSA 8	7/21/03	8/10/03
LSSA 9	7/25/03	8/10/03
LSSA 10	7/18/03	8/10/03
LSSA 11	7/18/03	8/10/03
LSSA 13	7/18/03	8/10/03
LSSA 14	7/18/03	8/10/03
SAC 4	7/21/03	8/20/03
SAC 5	7/21/03	8/20/03
SAC 6	7/25/03	8/20/03
SAC 7	7/25/03	8/20/03
SAC 8	7/25/03	8/20/03
SAC 9	7/18/03	8/20/03
SAC 10	7/18/03	8/20/03
SAC 11	7/18/03	8/20/03

Appendix Table 5. Sites and dates for pollen transfer for tagged *Vaccinium angustifolium* flower clusters dusted with either conspecific pollen or with improper invasive *Berberis thunbergii*.

Site	Dates of flower count and pollen dusting	Dates fruit set measured
VA 2	6/3/02	6/13/02
VA 5	5/21/02	6/13/02
VA 6	5/21/02	6/13/02
VA 7	5/30/02	6/13/02
VA 8	6/5/02	6/13/02
VA 9	6/3/02	6/13/02
VAC 4	6/3/03	7/1/03
VAC 8	6/3/03	7/1/03
VAC 10	6/3/03	7/1/03

Appendix Table 6. Sites and dates for pollen transfer for tagged *Viburnum nudum* flower clusters dusted with either conspecific pollen or with improper invasive *Frangula alnus*.

Site	Dates of flower count and pollen dusting	Dates fruit set measured
VN 22	7/1/02	7/18/02
VN 23	7/1/02	7/18/02
VN 24	7/1/02	7/18/02
VN 25	7/8/02	7/18/02
VN 26	7/3/02	7/18/02
VN 27	7/1/02	7/18/02
VN 28	7/1/02	7/18/02
VN 29	7/1/02	7/18/02
VNC 21	6/27/03	7/15/03
VNC 22	6/27/03	7/15/03
VNC23	7/1/03	7/15/03
VNC 24	7/1/03	7/15/03
VNC 25	7/1/03	7/15/03

Appendix Table 7. Sites and dates for pollen transfer for tagged *Spiraea alba* flowers dusted with either conspecific pollen or with improper invasive *Lythrum salicaria*.

Site	Dates of flower count And pollen dusting	Dates fruit set measured
SA 1	7/22/02	8/14/02
SA 2	7/26/02	8/14/02
	8/13/02	9/5/02
SA 3	8/1/03	8/14/02
		9/5/02
SA 4	7/26/02	8/14/02
	8/1/02	9/5/02
SA 5	7/26/02	8/14/02
		9/5/02
SA 6	7/26/02	9/5/02
	7/31/02	
SA 7	7/26/02	9/5/02
	8/1/02	
	8/6/02	
	8/7/02	
SA 8	8/1/02	9/5/02
	8/6/02	
	8/7/02	
BTVA 11	7/18/03	8/10/03
SAC 4	7/21/03	8/10/03
SAC 5	7/21/03	8/10/03
SAC 6	7/21/03	8/10/03
SAC 12	7/25/03	8/10/03

Appendix Table 8. Plant species found in 4 m² plots and transects.

Abies balsamia
Acer pensylvanicum
Acer platanoides
Acer rubrum
Acer species
Achillea millefolium
Agrostis gigantea
Agrostis repens
Agrostis scabra
Alnus rugosa
Amelanchier species
Antennaria species
Anthoxanthum odoratum
Apocynum androsaemifolium
aquatic unknown
Aralia nudicaulis
Aster acuminatus
Aster blakei
Aster lateriflorus
Aster macrophyllus
Aster novi-belgii
Aster simplex
Aster umbellatus
Berberis thunbergii
Betula nigra
Betula papyrifera
Betula populifolia
Bidens spp.
Brachyelytrum erectum
Brasenia schreberi
Calamagrostis canadensis
Carex arctata
Carex brunnescens
Carex folliculata
Carex gynandra
Carex intumescens
Carex lacustris
Carex lurida

Carex nigra
Carex ovales (section)
Carex paleacea
Carex pennsylvanica
Carex rugosperma
Carex scoparia
Carex stipata
Carex stricta
Celastrus orbiculata
Chamaedaphne calyculata
Cirsium spp.
Comptonia peregrina
Convallaria majalis
Cornus canadensis
Cornus sericea
Cornus spp. (woody)
Corylus cornuta
Crataegus spp.
Dactylis glomerata
Danthonia spicata
Deschampsia flexuosa
Diervilla lonicera
Drosera intermedia
Drosera spp.
Dryopteris spinulosa
Dulichium arundinaceum
Eleocharis species
Epifagus virginiana
Equisetum sylvaticum
Eriocaulon parkeri
Eriophorum species
Euphorbia cyparissias
Fagus grandifolia
Fallopia japonica
Festuca filiformis
Festuca rubra
Fragaria virginiana
Frangula alnus
Fraxinus spp.
Galeopsis tetrahit

Galium sp.
Galium trifidum
Gaultheria procumbens
Gaylussacia baccata
Glyceria canadensis
Glyceria sp.
Glyceria striata
Hieracium pilosella
Hieracium spp.
Hypericum dissimulatum
Hypericum perforatum
Ilex verticillata
Impatiens capensis
Iris versicolor
Juncus militaris
Juncus sp 1.
Juncus sp. 2
Junus bufonius
Junus effusus
Kalmia angustifolia
Lactuca biennis
Leersia oryzoides
Leontodon autumnalis
Leucanthemum vulgare
Lobelia cardinalis
Lonicera canadensis
Lonicera sp.
Lupinus polyphyllus
Luzula campestris
Lycopus uniflorus
Lysimachia quadrifolia
Lysimachia terrestris
Lythrum salicaria
Maianthemum canadense
Malus sylvestris
Melampyrum lineare
Mitchella repens
mowed grass (mix)
Myosotis spp.
Myrica gale

Myrica pensylvanica
Nemopanthus mucronatus
Nuphar variegata
Nymphaea odorata
Oenothera biennis
Onoclea sensibilis
Oryzopsis asperifolia
Osmunda cinnamomea
Osmunda claytoniana
Osmunda regalis v. *spectabilis*
Panicum spp.
Parthenocissus quinquefolia
Persicaria sagittata
Phleum pratense
Photinia melanocarpa
Physocarpus opulifolius
Picea glauca
Picea rubens
Picea species
Pinus rigida
Pinus strobus
Plantago major
Poa annua
Poa compressa
Poa nemoralis
Polygala sanguinea
Populus grandidentata
Populus tremuloides
Potentilla simplex
Potentilla tridentata
Prenanthes alba
Prenanthes trifoliolata
Prunus pensylvanica
Prunus virginiana
Pteridium aquilinum v. *latiusculum*
Pyrola rotundifolia
Pyrus melanocarpa
Quercus rubra
Ranunculus acris
Ranunculus repens

Rhinanthus crista-galli
Rhododendron canadense
Rhus hirta
Rosa spp.
Rosa virginiana
Rubus allegheniensis
rubus hispidus
Rubus idaeus
Rubus pubescens
Rumex acetosella
Rumex pallidus
Salix fragilis
Salix species
Scirpus cyperinus
Solanum dulcamara
Solidago bicolor
Solidago canadensis
Solidago graminifolia
Solidago juncea
Solidago rugosa
Solidago sp.
Sorbus americana
Sorbus sp.
Sparganium spp.
Spiraea alba v. *latifolia*
Spiraea japonica
Spiraea tomentosa
Stellaria sp.
Taraxacum officinale
Thuja occidentalis
Toxicodendron rydbergii
Triadenum virginicum
Trientalis borealis
Trifolium arvense
Trifolium aureum
Trifolium pratense
Trifolium sp.
Tsuga canadensis
Typha latifolia
Vaccinium angustifolium

Vaccinium corymbosum
Vaccinium myrtilloides
Veronica chamaedrys
Viburnum acerifolium
Viburnum dentatum v. *lucidum*
Viburnum nudum v. *cassinoides*
Viburnum opulus
Vicia cracca
Viola spp.
Xanthorhiza simplicissima

Appendix Figure 1. Co-flowering paired native and invasive study plants.

Study Plants: Spring



Lowbush Blueberry
(*Vaccinium angustifolium*)



Japanese barberry (*Berberis thunbergii*)

Study Plants: Early Summer



Wild Raisin (*Viburnum nudum*)



Glossy Buckthorn (*Frangula alnus*)

Study Plants: Mid-Late Summer



Meadowsweet (*Spiraea alba*)



Purple Loosestrife (*Lythrum salicaria*)

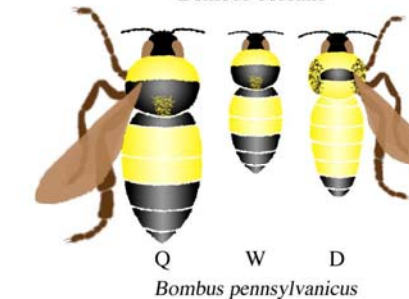
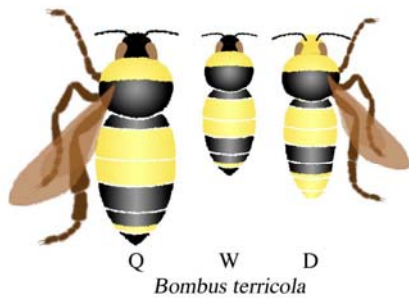
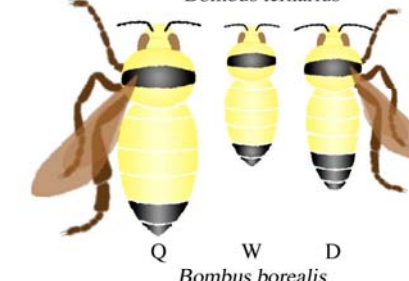
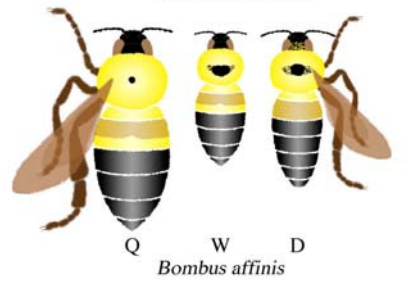
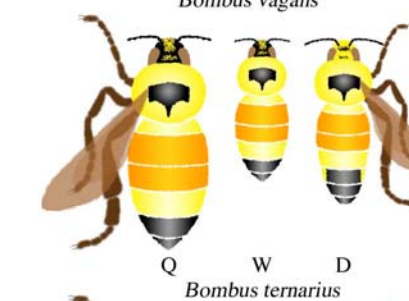
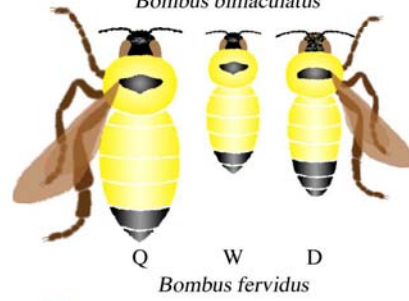
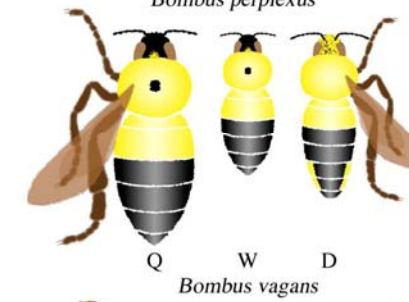
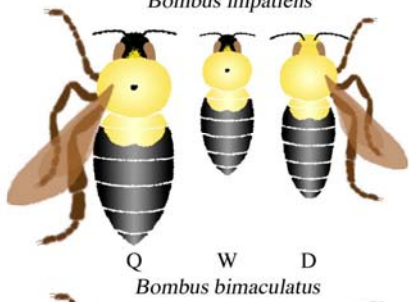
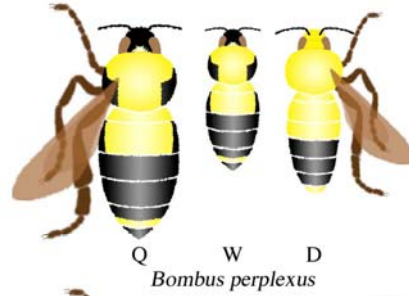
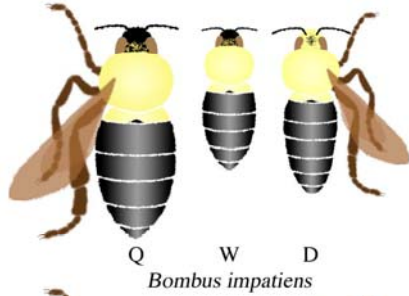
Appendix Figure 2. Pollinator community: leaf and mason bees (Megachilidae).



Appendix Figure 3. Native bumble bees of Acadia National Park.

(Note that *B. impatiens* has a bare black patch in the center of the scutum on the thorax.)

Bumblebees of Acadia National Park



As the nation's primary conservation agency, the Department of the Interior has responsibility for most of our nationally owned public land and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

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