Fruit and seed set in Mayapple (*Podophyllum peltatum*): influence of intraspecific factors and local enhancement near *Pedicularis canadensis*

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The breeding system and determinants of fruit and seed production in a population of 114 patches of Mayapple (*Podophyllum peltatum* L.) were examined. Experimental crosses indicated that Mayapple patches are self-incompatible (clones) and that fruit and seed set were pollinator limited. Mayapple flowers are nectarless yet depend primarily on infrequent visits by nectar-searching bumblebees for pollination. The proportion of flowers setting fruit and ovules setting seed in Mayapple clones was inversely associated with the distance to neighboring clones and the distance to *Pedicularis canadensis* L. plants. Clones within 45 m of *P. canadensis* plants (which are heavily visited by bumblebees) showed significant increases in fruit and seed production compared with a similar group of more distant clones. This effect is interpreted as evidence for a facilitative interaction between Mayapple and *P. canadensis*.

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Nous avons examiné le système reproducteur et les déterminants de la production de fruits et de graines dans une population de 114 parcelles de la pomme de mai (*Podophyllum peltatum* L.). Des croisements experimentaux ont indiqué que les parcelles de pomme de mai sont autoincompatibles (clones) et que la nouaison (fruits et graines) était limitée par les pollinisateurs. Les fleurs de la pomme de mai sont sans nectar et pourtant dependent surtout des visites espacées de bourdons en quête de nectar pour la pollinisation. La proportion de fleurs aboutissant à la nouaison et celle d'ovules se transformant en graines chez les clones de pomme de mai étaient inversement associées à la distance qui les sépare des clones avoisinants et aussi à la distance des plants du *Pedicularis canadensis* L. Les clones situés à moins de 45 m d'individus du *P. canadensis* (qui sont assidûment visités par les bourdons) ont montré des augmentations significatives dans la production de fruits et de graines en comparaison avec un groupe semblable de clones plus éloignés. Cet effet est interpreté comme preuve à l'appui d'une interaction de facilitation entre la pomme de mai et le *P. canadensis*.

[Traduit par la revue]

Introduction

Female reproductive success often varies widely among individual plants in natural populations (e.g., Schaal 1975, 1984; Handel 1983; Venable 1984). That differential pollinator visits among individual plants may be an important source of variability in fruit and seed set is often discounted (e.g., Bawa and Beach 1981). Nevertheless, several studies indicate that in some plant species seed set may be limited by insufficient pollination (see Bierzychudek 1981; Rathcke 1983). Pollinator-mediated variation in female reproductive success should be particularly important in plant species that depend on pollinators for pollen transfer but do not offer attractive floral rewards. In such species, individuals may often receive insufficient pollen and variation in seed and fruit set within a population likely reflect both intraspecific and interspecific factors that influence pollinator activity.

In this study we examined variation in fruit and seed set in a population of Mayapple (*Podophyllum peltatum* L., Berberidaceae), a perennial herb with nectarless flowers, found in deciduous woods throughout eastern North America (Gleason and Cronquist 1963). Individual Mayapple plants form discrete colonies or patches consisting of one to several thousand aerial stems. Stems may be asexual (with a single leaf) or sexual (with a pair of leaves), the latter bearing a single, open flower (3–4 cm in diameter) at the point where the stem branches.

Studies of the breeding system generally show that patches are self-incompatible clones, which depend upon infrequent visits by bumblebees for pollination (Swanson and Sohmer

1976; Rust and Roth 1981), although a putative agamospermous population from western New York State has also been reported (Bernhardt, 1975, as cited by Swanson and Sohmer, 1976). Extremely low levels of seed set have been found in some Mayapple populations, with most clones failing to set a single fruit (Swanson and Sohmer 1976; Sohn and Policansky 1977). In other populations, seed set can be quite variable both between clones and between years (Rust and Roth 1981; T. M. Laverty, unpublished). Thus pollinator visits may be an important source of variation between clones in female reproductive success.

We examined two intraspecific factors that should be important in determining fruit and seed set for a clonal, self-incompatible, entomophilous species: the number of flowers in the clone and the distance to potential pollen donors in neighboring clones (Handel 1983). In addition, field observations of pollinator activity suggested that interspecific associations with nectar-rich plant species might result in increased pollination of some Mayapple plants. Such facilitative interactions have rarely been described in plant communities (but see Thomson 1978, 1981) and there are no studies showing that the reproductive success of species that are generally unattractive to pollinators can be increased by association with heavily visited species.

Methods

Study area and experimental crosses

We studied plants and pollinators in a strip of beech–maple woodland (1.1 × 0.5–0.8 km) on Amherst Island (44°07′ N; 76°45′ W) at the northeast end of Lake Ontario. The long axis of the wood ran from northeast to southwest, with the northern boundary formed by
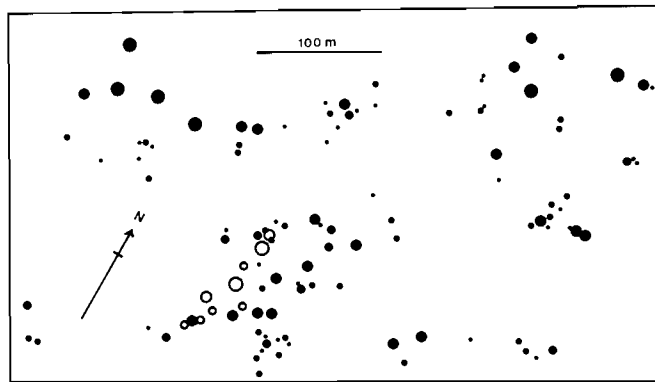
FIG. 1. Map of the central portion of the study area showing the location of Mayapple (closed circles) and *Pedicularis* (open circles) patches. Circle diameter indicates patch size: five classes for Mayapple (1−10, 11−50, 51−100, 101−500, and >500 flowers); three classes for *Pedicularis* (10−50, 51−100, 101−300 flowering spikes). Locations of nine remote Mayapple patches are not shown.

the crest of a low ridge. About three quarters of the wood was on a gentle slope; the lower one quarter formed a flat, wetter area along the base of the slope. The wood was flanked on all sides by fields, and a gravel road separated the eastern border from the adjacent field.

We studied all of the Mayapple patches observed in the wood (110 patches, assumed to be clones), as well as four additional patches along the roadside. A total of nine patches of *Pedicularis canadensis* (Scrophulariaceae), a prolific nectar-producing species, occurred in a part of the study area (see Fig. 1). Other plants in bloom at the time of the study were *Acteae rubra* (Ait.) Willd., *Phlox divaricata* L., *Ribes* spp., *Smilacina racemosa* (L.) Desf., *Tiarella cordifolia* L., and *Viola* spp. These species were not considered in detail, primarily because their flowers were seldom visited by bumblebees. Bees commonly visited *Ribes*, but these plants were widely distributed throughout the study area, in contrast to the *Pedicularis* plants.

Observations of pollinator activity, experimental crosses, and censuses of stems in each Mayapple patch were completed from May 15 to May 26, 1985. Numbers of fruits per patch and seeds per fruit were counted and interpatch distances were measured from June 22 to July 30. All fruits were collected from patches setting fewer than five fruits; five or ten fruits were sampled in small and large (> 100 fruits) patches, respectively.

We studied the breeding system by selecting four large Mayapple patches (all with >300 flowers) and tagging and bagging 50 flower buds in different areas of each patch. Treatments 1, 2, and 3 assessed self-compatibility (Table 1). Treatment 3 used pollen from bagged flowers in different parts of the patch to test whether each patch was a clone. Treatment 4 examined whether plants could set seed without receiving pollen. Pollen for the outcrossed treatment (5) was obtained from one of the three other patches. Comparison of treatment 1 (autogamy) with treatment 5 (outcrossed) tested for dependence on insect pollination. Comparison of treatments 5 and 6 (open-pollinated flowers that set fruit) determined whether seed set was limited by pollinator visits. Because flowers are partially protandrous, bagged flowers were crossed 2−3 days after anthesis (flowers last 6−9 days). Pollination bags were removed when fruits began to swell and fruits were harvested about 8−10 weeks after flowering. Fifteen flowers from each patch were also collected to determine ovule numbers. Pollinator activity was assessed during 16.5 h of observation at various times over the day and 1 h at night.

Variables measured

We mapped the location of all Mayapple and *Pedicularis* patches within the study area and measured distances between them. Mayapple patches were defined as groups of sexual and asexual stems growing closely together with no other stems within at least 3 m. Typical patches were roughly circular in shape around the base of

TABLE 1. Summary of experimental treatments to determine the breeding system of Mayapple

Treatment*	Protected from insects	Anthers removed	Pollination type	Seed set due to:
1	Yes	No	None	autogamy
2	Yes	No	Hand, self	selfing
3	Yes	Yes	Patch, self	geitonogamy
4	Yes	Yes	None	apomixis
5	Yes	Yes	Outcrossed	xenogamy
6	No	No	Open	insects

*Sample size for treatments 1−5 in each patch = 10 flowers; treatment 6 was based on unbagged flowers in each patch.

trees. These were assumed to be clones, although it is possible that some patches may have been composed of two or more intermingled clones.

We related interpatch differences in two dependent variables (the proportion of flowers producing fruits and the proportion of ovules setting seed) to three independent factors: Mayapple patch size, characteristics of neighboring patches, and proximity to *Pedicularis* plants. Patch size was expressed as the number of flowers in each patch; several variables were calculated for the other factors (see below). Transformations were applied where distributions of these independent variables were skewed. The proportion of variation in the dependent variables explained by each independent variable was analysed using the general linear modelling program GLIM (release 3.77: Baker and Nelder 1985).

Because bees tend to move short distances between flowers and patches (Levin 1981), the distance from a Mayapple clone to its neighbors should influence the probability of receiving outcrossed pollen and hence fruit and seed set. The number of flowers in neighboring patches could also influence the movements of pollinators. We treated these two possibilities as separate variables: the mean distance (metres) to the five nearest neighbors regardless of their size and the total number of flowers in the five nearest neighbors. Two compound variables incorporated both size and distance effects. The first was calculated as the sum of the products of 1/distance^2 and the number of flowers in the patch for the 10 neighboring patches which maximized this value. The second, which embodied the idea of angles subtended by neighboring clones, was computed in a similar fashion to the angle variable for *Pedicularis* (see below).

The effect of *Pedicularis* on Mayapple seed and fruit set was assessed as the mean distance from each Mayapple clone to all nine *Pedicularis* patches in the study area, as well as the inverse and inverse square of this distance. A compound variable for the *Pedicularis* effect included both the distance to, and size of (total spikes in patch), each *Pedicularis* patch and was calculated as the product of 1/distance^2 and the number of spikes.

Another compound variable was derived by assuming the number of bees visiting a *Pedicularis* patch was proportional to the number of its flowering spikes and that departure angles of bees leaving the patch were random. The incidence of bees encountering a Mayapple patch after leaving *Pedicularis* should then be related to the size of the Mayapple patch and to its distance from the *Pedicularis* patch (i.e., to the angle on the *Pedicularis* patch subtended by the diameter of the Mayapple patch). This angle variable was calculated as follows:

$$\text{angle}_i = \sum_1^j N_j \tan^{-1}((D_i/2)/(S_{ij} + D_i/2))/\pi,$$ where D_i is the diameter

of the Mayapple patch, N_j is the number of spikes in the *j*th *Pedicularis* patch, and S_{ij} is the distance between the border of the Mayapple patch and the *j*th *Pedicularis* patch.

We also made a more detailed assessment of the effect of *Pedicularis* by comparing levels of fruit and seed set in 16 Mayapple patches growing within 45 m of *Pedicularis* plants with levels in 16 more distant patches. For this comparison we controlled intraspecific

TABLE 2. Summary of fruit and seed set (mean ± SD) in experimental treatments, ovule numbers, and frequency of pollinator visits in four mayapple patches

Character	Patch				
	1	2	3	4	All*
Fruit and seed set					
Treatments 1−4	0	0	0	0	0
Treatment 5, outcrossed					
Fruit set (%)	100	100	100	100	100
Seeds/fruit ± SD	22.0±6.9	37.8± 7.0	30.2±12.4	46.7± 8.1	34.2±3.3
Treatment 6, open-pollinated					
Fruit set (%)	1.1	17.4	31.1	52.5	25.5±6.9
Seeds/fruit ± SD	7.0±3.3	2.4± 1.5	25.2±17.3	18.8± 8.2	13.4±3.3
Ovules					
Ovules/flower ± SD	36.7±8.1	48.3±14.3	41.5± 9.3	51.8±11.1	44.6±2.1
Seeds/ovule (%) in outcrossed fruits (treatment 5)	60.3	78.2	72.8	90.1	75.4±3.9
Seeds/ovule (%) in open-pollinated fruits (treatment 6)	19.2	5.0	60.7	36.3	30.3±7.6
Pollinators					
Pollinator frequency (visits · flower^{-1} · h^{-1})	0	0.035	0.051	0.141	0.057±0.06
Minimum distance to *Pedicularis* (m)	1620	704	19	<1	

*Mean of patches 1−4, ±SEM.

effects which were significant in GLIM analysis (patch size, and the distance to the five nearest neighbors) by matching each Mayapple patch close to *Pedicularis* with the most similar distant patch in the population. The criteria for this matching were nearest neighbor distance followed by patch size.

Results

Breeding system and pollinators

Crosses among different flowers in the same patch produced no fruit or seed; only flowers receiving pollen from another patch set fruit and seed (Table 2). This indicates that Mayapple is an obligate outcrosser and that at least the four patches used in the breeding system analysis were clones. Fruit set in hand-outcrossed flowers (treatment 5) was 100%, compared with a range of 1−52% for open-pollinated flowers (treatment 6). The mean number of seeds per fruit in hand-outcrossed and open-pollinated flowers shows that natural seed set approached maximal levels in only one of the four clones. Based on the mean number of ovules per flower for each of the four patches, the proportion of ovules setting seed in hand-outcrossed fruits ranged from 60 to 90 with a mean of 75%, while in open-pollinated fruits, seed set ranged from 5 to 61 with a mean of 30%.

Overall, the frequency of pollinator visits to Mayapple flowers was low, ranging from 0 to 0.1413 visits per flower per hour for the four experimental patches; visitor frequency also tended to increase in patches closer to *Pedicularis* (Table 2). Nine honeybees and 36 queens of eight bumblebee species were the only visitors observed and no flower visitors were seen at night. The two groups of bees differed markedly in their flower-visiting behavior. Honeybees visited an average of 14.0 ± 4.9 (SD) flowers per patch (mean flowers per patch, 363) and all collected pollen, usually "milking" four or five anthers on each flower. In contrast, bumblebees visited fewer flowers per patch (3.9 ± 2.4; Mann−Whitney, $U = 2.0$, $P <$ 0.001); none of the queens observed had pollen loads and 72% probed the flowers, apparently in search of nectar.

Although we did not systematically observe visitors to *Pedi-*

cularis flowers, individuals of long-tongued *Bombus* (*B. fervidus* and particularly *B. vagans*) were frequent visitors (see also Macior 1968). On two occasions *B. vagans* queens were seen moving from *Pedicularis* flowers to search for nectar in several nearby Mayapple flowers before returning quickly to *Pedicularis*.

Variation in fruit and seed set

Mayapple patches varied considerably in size (Figs. 1, 2A) and fruit and seed set (Figs. 2B, 2C, 2D). The median patch size was 30 flowers, median fruit set was 29.6%, and mean seed set was 16.3 ± 2.2 seeds per fruit. All patches that set 100% fruit consisted of one to five flowering stems.

Variability in the proportion of fruits per flower, and seeds per ovule among Mayapple patches was analysed using general linear models. The effect of patch size was analysed in normal error models with logit transformation of the independent variable (see Baker and Nelder 1985). Patch size had a significant inverse effect on fruit set (i.e., small clones set proportionately more fruits than did large clones: $F = 12.38$; df 1, 112; $P < 0.001$). However, patch size had no effect on seed set ($F = 2.48$; df 1, 112; $P > 0.05$).

The effects of neighboring Mayapple patches and *Pedicularis* plants were analysed in models incorporating binomial error distributions (Table 3). Intraspecific variables were added to the models followed by variables for *Pedicularis*. The mean distance to the five nearest neighbor Mayapple clones was the most important intraspecific variable, accounting for about 25% of the variation in the two dependent variables. Both fruit and seed set were lower in patches that were more distant from neighboring clones. The other independent variables for neighbor effects were not significant.

The most effective interspecific variable was the mean distance from a Mayapple patch to *Pedicularis* plants (Table 3). This variable accounted for 9 and 18% of the explained variation in fruit and seed set, respectively, and was inversely related to the dependent variables (i.e., fruit and seed set were greater in Mayapple patches close to *Pedicularis* plants). All
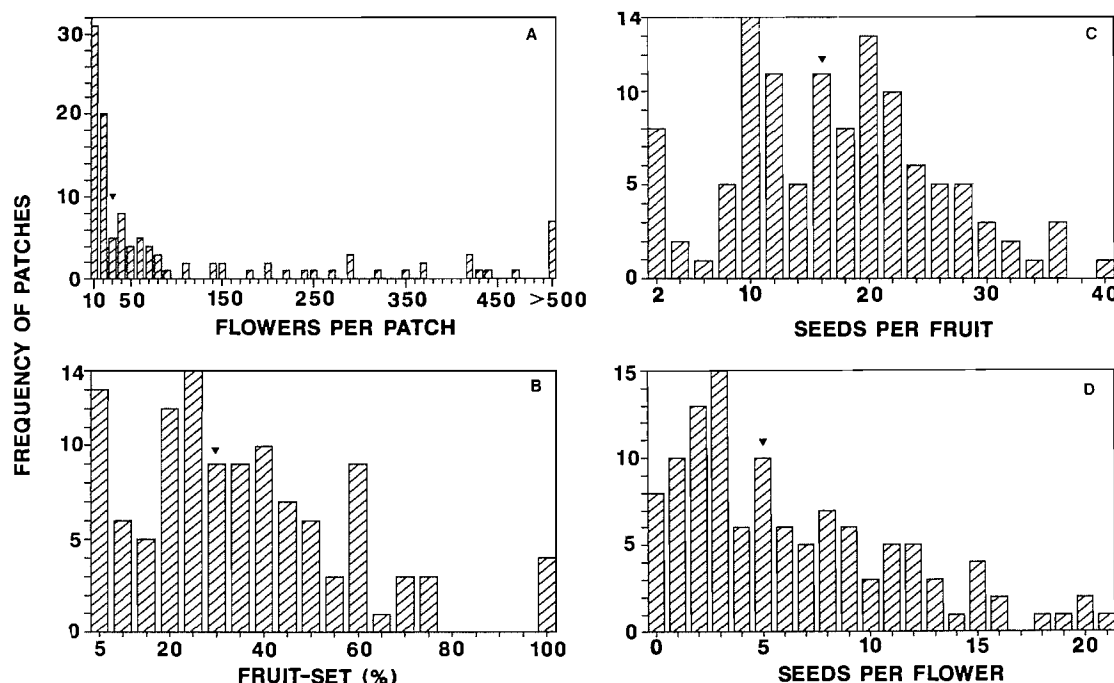
FIG. 2. Distributions of patch sizes (A), fruit set (B), seeds per fruit (C), and seeds per flower (D) in the Mayapple population. Arrowhead indicates median value.

TABLE 3. Summary of analysis of deviance for the effect of distance to neighbors and *Pedicularis* plants on the proportion of flowers setting fruit and proportion of ovules setting seed

	Source	Deviance	df	Change in*:	
				deviance	df
Fruits/flower	Grand mean	2035.9	113	—	—
	Neighbor distance	1525.9	112	510.5	1
	Distance to *Pedicularis* patches	1340.3	111	185.2	1
Proportion of deviance accounted for 34.2%					
Seeds/ovule	Grand mean	54119	113	—	—
	Neighbor distance	40123	112	13996	1
	Distance to *Pedicularis* patches	30225	111	9898	1
Proportion of deviance accounted for 44.2%					

*Change in deviance is distributed as chi-square; for 1 df a value of 7.9 is significant at the 0.005 level.

other variables computed for the *Pedicularis* effect were also highly significant but were slightly less effective than the distance variable.

The effect of *Pedicularis* can be seen more directly in comparisons of reproductive success in Mayapple patches close to and distant from *Pedicularis* plants (Table 4). The two groups of patches were matched for intraspecific characteristics, but those patches within a minimum distance of 45 m from a *Pedicularis* patch showed significant increases in fruit and seed production.

Discussion

The results reported here are consistent with most other studies of Mayapple pollination ecology (Swanson and Sohmer 1976; Rust and Roth 1981): Mayapple is clonal, self-incompatible, and rarely visited by pollinators. The frequency of pollinator visits to Mayapple is at least 10 times less than levels recorded for nectar-producing spring ephemerals (Schemske et al. 1978) and probably accounts for the limited fruits and seed set we observed in naturally pollinated flowers (Table 2).

Mayapple flowers produce no nectar, yet 80% of visitors were queen bumblebees that probed around the stamens in search of nectar. This type of deceit pollination by bumblebee queens has been documented in temperate orchids that offer no rewards (Heinrich 1975; Nilsson 1980; Boyden 1982), as well as other nectarless spring ephemerals (Melampy and Hayworth 1980). These plants appear to exploit a brief stage in the lives of newly emerged bumblebee queens when they are still inexperienced with rewards provided by different plant species (see Little (1983) and Dafni (1984) for reviews of this syndrome). By the time Mayapple begins to flower, however, queens of most species have already emerged and foraged from early spring ephemeral plants for several weeks. Mayapple may benefit from a general white-flowered mimicry complex among spring ephemerals described by Schemske et al. (1978),

TABLE 4. Comparison of seed and fruit production (means ± SD, range) in 16 pairs of Mayapple patches close to and relatively distant from *Pedicularis canadensis* plants

Variable	Close patches	Distant patches	P
Distance to *Pedicularis* patches (m)	33.3±7.3 (20.3−42.0)	140.9±70.7 (55.5−270.7)	
Patch size	96.2±110.9 (3−362)	99.3±126.8 (3−420)	
Distance to five nearest neighbors (m)	15.1±3.8 (8.0−22.2)	15.5±3.7 (10.1−23.9)	
Fruit set (%)	46.2±21.3 (25−100)	24.9±16.5 (0−57.7)	**
Seeds/fruit	23.6±7.6 (9.2−39.7)	15.5±8.3 (0−31.2)	*
Seeds/flower	11.1±4.6 (1.5−15.3)	5.9±5.8 (0−19.3)	**

NOTE: *, $P < 0.05$; **, $P < 0.01$, in two-tailed Mann−Whitney U tests.

but the flowers do not closely resemble nectar-producing flowers of other earlier flowering plants (*Trillium grandiflorum* (Michx.) Salisb. is a possible exception, but its flowers produce little nectar) or concurrently blooming species (such as *Pedicularis* or *Ribes*).

Female reproductive success among Mayapple clones was influenced both by the structure of the Mayapple population and by *Pedicularis* plants. We found that larger Mayapple patches set proportionately fewer fruits than did smaller patches, a result reported in other self-incompatible clonal species (Handel 1983). In larger clones, individual flowers tend to be surrounded by inflorescences of the same plant, resulting in more geitonogamous pollinations that do not produce fruit. The lack of nectar in Mayapple flowers may increase the frequency of interclone movements, particularly by native bumblebee pollinators, while at the same time eliminating costs of nectar production.

That the distance to neighboring clones accounted for much of the variation in fruit and seed production was expected in an obligate outcrosser that depends upon bees for pollen movement. The small effect due to numbers of flowers in neighboring patches can be explained by the fact that bumblebees tended to visit only three or four flowers per patch before leaving. Thus the size of neighboring patches should have little influence on the amount of pollen picked up by a bee.

Mayapple reproductive success was also enhanced in the vicinity of *Pedicularis* plants (Table 3). The most likely reason for this effect is that bumblebees were more abundant around *Pedicularis* (a high-ranking nectar source) and Mayapple clones in this area received more pollinator visits (Table 2). The effect might also be attributed to unusual properties (e.g., size, near neighbors, flowering time) of the Mayapple clones in the area around *Pedicularis*. However, paired comparisons between clones close to *Pedicularis* and more distant clones matched for size and distance to neighbors also showed significant differences in reproductive success (Table 4). Flowering time can also be important in explaining individual variation in seed set (Schemske 1977; Boyden 1982). In this study though, Mayapple plants in the vicinity of *Pedicularis* bloomed in synchrony with other patches in the wood.

Other confounding variables associated with the *Pedicularis*

site (an area about 40 × 100 m; Fig. 1) may have contributed to local increases in fruit and seed set in Mayapple. The nine *Pedicularis* patches occurred in several microenvironments (e.g., wet and well-drained soils) up a gentle slope, none of which could be considered atypical of the wood. Because the site was not homogeneous in terms of topography, soil moisture, light levels, or tree species composition, it seems unlikely that these factors could have produced local increases in Mayapple fruit and seed set. The available evidence strongly suggests that the effect on Mayapple was pollinator mediated, but long-term experimental studies are needed to assess fully the interaction between these two plant species.

The results of the present study do not imply a widespread specific dependence of Mayapple upon *Pedicularis*. Several studies of spring ephemeral communities in North America fail to mention any association between the two (Braun 1950; Struik and Curtis 1962; Bratton 1976; Rogers 1982; Motten 1986). Rather, this is likely to be a local effect. In different parts of its range, or even within a single population, Mayapple may benefit from association with a variety of other prolific nectar-producing species that are heavily visited by pollinators. The same type of interspecific effect may apply to other plant species that are generally unattractive to pollinators and the possibility of such facilitative interactions should be considered in studies of plant−pollinator communities.

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