Western North American Naturalist 80(1), © 2020, pp. 1–10

Self-compatibility in *Lomatium dissectum* (Apiaceae) and the diverse *Andrena* bees that dominate regional *Lomatium* pollinator faunas

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Abstract.—Species of biscuitroot (*Lomatium*: Apiaceae) are endemic to western North America, where multiple species can be common members of perennial wildflower communities from basin sagebrush-steppe and juniper woodlands up to alpine meadows. Despite *Lomatium* being the largest genus of Apiaceae in North America, little is known about its pollination needs or pollinators. Manual pollinations of the tiny flowers of one species, desert parsley (*L. dissectum*), showed it to be a self-compatible species, akin to other genera of Apiaceae. Seed production, however, largely requires pollinators to move pollen within and between the andromonoecious umbels. Regional sampling of floral visitors to *L. andrusianum*, *L. dissectum*, *L. triternatum*, and several other species revealed a sometimes abundant and exceptionally rich diversity of mostly *Andrena* bees. These 21 *Andrena* species together composed 94% of the individuals methodically sampled at *Lomatium* plants; this number is at odds with claims of taxonomic promiscuity for pollinator faunas of the Apiaceae. But for several *Lomatium* specialists, these *Andrena* species all seem to be floral generalists with apparent pollination value for *Lomatium*. These ground-nesting bees, as well as their *Lomatium* hosts, should survive the increasingly frequent and extensive wildfire events burning the sagebrush-steppe and juniper woodlands that they inhabit, owing to their springtime seasonalities and the insulative protection of overlying soil.

Resumen.—Las especies de raíces biscuit o almidonosas (*Lomatium*: Apiaceae) son endémicas del oeste de América del Norte. Muchas de ellas pertenecen a comunidades de flores silvestres perennes provenientes de las estepas de artemisas, de los bosques de enebros de la cuenca y hasta de prados alpinos. A pesar de ser el género más grande de Apiaceae en América del Norte, es poco lo que se conoce sobre sus necesidades de polinización o sus polinizadores. Las polinizaciones manuales de las diminutas flores de una especie en particular, el perejil del desierto (*L. dissectum*), demostraron que se trata de una especie autocompatible, similar a otros géneros de Apiaceae. Sin embargo, para producir semillas, los polinizadores deben transferir el polen dentro y entre las inflorescencias andromonóicas. El muestreo local de los visitantes florales a las especies *L. andrusianum*, *L. dissectum*, *L. triternatum* y a otras especies reveló la diversidad abundante y excepcionalmente rica de abejas *Andrena* principalmente. Estas 21 especies de *Andrena* representaron el 94% de los especímenes metódicamente muestreados en *Lomatium*; número que no concuerda con las afirmaciones sobre la promiscuidad taxonómica de las faunas polinizadoras de las Apiaceae. Sin embargo, numerosos especialistas en *Lomatium* consideran a estas especies generalistas florales con claros valores de polinización para *Lomatium*. Dichas abejas que anidan en el suelo, así como sus hospederos *Lomatium*, deberían poder sobrevivir a la extensión y el aumento en la frecuencia de incendios forestales que afectan las estepas de artemisas y los bosques de enebros que habitan, dado sus estacionalidades de primavera y la protección aislante del suelo.

The cosmopolitan family Apiaceae (or Umbelliferae) consists of 3700 species, including many familiar vegetables (e.g., carrot, celery), herbs (e.g., parsley, dill), and spices (e.g., coriander, anise). Their generally numerous and small flowers are white or yellow and are borne in simple or complex umbels. Flowers of the Apiaceae are often andromonoecious, but species' opportunities for autopollination can be limited by separation of the sexes in time (dichogamy) and space (herkogamy) (reviewed *in* Koul et al. 1993). Umbels generally present a surface over which insects simply walk while they forage for the scant quantities of available pollen and nectar. Consequently, their small, shallow flowers were traditionally considered to be promiscuous, owing to the sundry generalist flies, bees, and beetles that visit some species' umbels (e.g., Grant 1949). However, several detailed field studies of wild

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Apiaceae reported pollinator assemblages that are more taxonomically restricted (reviewed *in* Zych 2007).

With 70+ species, *Lomatium* is the largest genus of Apiaceae in North America. The species in this genus are all perennial, herbaceous, and endemic to the West (Cronquist 1997). Their common name "biscuitroot" refers to the large starchy taproots of some *Lomatium* species (e.g., *L. dissectum* (Pursh) J.M. Coult. & Rose) that were extensively roasted and consumed by native American tribes of the region, along with various species' shoots, flowers, or seeds (Moerman 2010). This species and others also feature in the diets of Greater Sage-Grouse chicks, a species of grave conservation concern (Drut et al. 1994), as well as in the larval diets of those bees that collect *Lomatium* pollen and nectar. Various species of the genus *Lomatium* are thus valued for their ecological, conservation, and/or traditional dietary and medicinal traits.

In early spring, species of *Lomatium* present one or more compound umbels of tiny staminate or hermaphroditic yellow (or occasionally purple) flowers. The hermaphroditic flowers of some species are typically protogynous (Schlessman 1982). Each bisexual flower can yield 2 seeds. Among species of Apiaceae, the crop species (e.g., carrot) have been the focus of most manipulative studies of breeding biologies (reviewed *in* Zych 2007); the thousands of wild species of Apiaceae have received scant attention, perhaps because of the physical challenges of manipulating and marking the tiny flowers in their congested umbels. Grown as a specialty seed crop, stands of *L. dissectum* and *L. grayi* (J.M. Coult. & Rose) have been readily established from seed. Individuals in cultivation begin flowering when each is 3–4 years old; mature plants yield large annual seed crops for many years (Shock et al. 2009). Furthermore, their seed is easily harvested and cleaned. Seed of widespread, often common species, such as *L. dissectum* and *L. triternatum* (Nutt.) Mathias & Constance, should be useful to land managers rehabilitating postfire landscapes, particularly in the sagebrush-steppe of the Intermountain West (Cane 2011).

The objectives of this study were twofold: (1) to document the breeding biology of *L. dissectum* using experimental pollination treatments, and (2) to widely and methodically sample the floral visitors at umbels of *L. dissectum*, *L. triternatum* and, at a few sites, *L. ambiguum* (Nutt.) J.M. Coult. & Rose, *L. andrusianum* McK. Stevens & Mansfield, *L. grayi*, and *L. nudicaule* (Pursh) J.M. Coult. & Rose. Taxonomy of the *Lomatium* species follows that found in Cronquist (1997) and Stevens et al. (2018). Bee taxonomy follows the nomenclature of LaBerge (1986 and references therein) and DiscoverLife (https://www.discoverlife.org/).

Methods

Field Study of Pollination

In April 2005, a wild population of *L. dissectum* was chosen for study along Right Hand Fork Canyon within the Bear River Range 17 km northeast of Logan, Utah (41.78° N, 111.61° W; 1770 m elevation). Sixty available budded umbels on as many plants were tagged and assigned 1 of 2 pollination treatments. Half were merely tagged to allow unrestricted pollinator visitation. The other 30 umbels served to evaluate the species' capacity for autopollination by the method of enclosing each budded umbel in a fine-mesh bag that was supported by a bamboo skewer for the duration of bloom. All resulting large green fruits were harvested and counted.

Experimental Pollination

To establish a convenient plot of *L. dissectum* for daily manual pollinations, 100 taproots were excavated in November from a second large population growing in Right Hand Fork Canyon. At an outdoor research garden at the PIRU lab (USDA–ARS Pollinating Insect Research Unit, Logan, UT), these taproots were transplanted on 1-m centers. The following April, 25 transplants produced budded umbels; the rest had either died or remained vegetative. Before flowering, the transplants were enclosed in walk-in field cages ($7 \times 7 \times 2$ m) whose translucent fine mesh excluded all potential pollinators (Chicopee Lumite, Gainesville, GA).

Caged plants were manually pollinated in May to evaluate their breeding biologies. Two pollination treatments were applied: geitonogamy (transfer of self pollen) and xenogamy (outcrossing). Two bisexual umbels per plant were selected, and within each, 3 randomly assigned bisexual umbellets were tagged for manual pollination treatments. Stigmatic receptivity on an

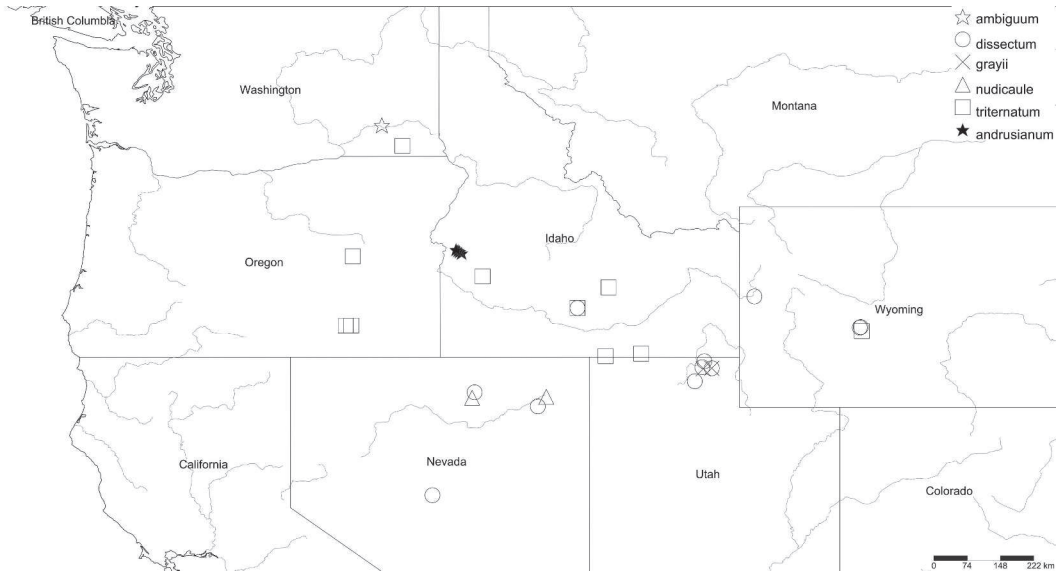

Fig. 1. Map of collection surveys for bees visiting 6 species of *Lomatium* across the U.S. Intermountain West.

umbel was tested by immersing the pollen-free stigmatic tips of a few clipped test pistils in 3% hydrogen peroxide. Formation of one or more visible oxygen bubbles results from peroxidase enzymes that are secreted by a receptive stigma (Arnold 1982). If the test for receptivity was positive, then all of the other hermaphroditic flowers of the 3 umbellets in that umbel were counted and manually pollinated. Geitonogamous pollination involved rubbing recipient virgin stigmas with anthers from untagged umbellets on the same plant. Donor flowers for xenogamy were taken from untagged umbels of a different plant. To ensure that each stigma received pollen as it became receptive, flowers were manually pollinated daily until all of that umbel's styles lost turgor and browned. Optical magnifying visors helped confirm pollen transfer to each tiny stigma. In addition, we recorded production of umbellets and umbels per plant, floral gender(s) and phase(s) at each umbellet (Supplementary Material 1), and the relative timing of stigma receptivity and/or anther dehiscence. Plants remained caged (or bagged at the wild canyon population) after flowering to guard against vertebrate seed predators and herbivores.

Analyses of Seed Production

Once the fruits of wild plants were mature, but before they were shed, umbels were individually clipped and returned to the laboratory. Seeds produced by each umbel were counted. For the manual pollinations, the seed counts per umbellet were divided by the numbers of hermaphroditic flowers that were pollinated. Outcomes of the 2 manual pollen transfer treatments in the caged research plot were compared by mixed model analysis of variance (ANOVA; SAS Institute 2006), using umbel nested within plant as the random factor, manual pollination treatment as the fixed effect, and seed production as a fraction of the total flowers pollinated per umbel as the response variable. Percent seed set was square-root transformed, rendering acceptable normality and homogeneity of variance.

Bees Visiting *Lomatium dissectum*, *L. triternatum*, and Others

Local suites of bees visiting *Lomatium* were net-collected during May and June from 2007 to 2016 at wild *L. dissectum* or *L. triternatum* (and, at a few sites, *L. andrusianum*, *L. ambiguum*, *L. grayi*, or *L. nudicaule*). Populations were sampled across a 5-state region (Idaho, Nevada, Oregon, Utah, Wyoming) spanning 250,000 km^2 in sagebrush-steppe, neighboring juniper woodlands, and low foothill canyons (1250–2300 m elevation) (Fig. 1). Most sites had burned in the previous 15 years and were part of a larger fire ecology project (Cane and Love

2016). Many populations were surveyed quantitatively by sequentially inspecting counts of 20–700 flowering *Lomatium* plants for floral visitors, netting all visitors that were seen at the moment but not waiting for any new arrivals. This methodical survey protocol gives an unbiased quantitative "snapshot" of the local composition and density of bees at the surveyed *Lomatium* species, enabling direct comparisons between sites (detailed *in* Cane and Love 2016). For smaller *Lomatium* populations, all flowering individuals were thus inspected once. For larger populations, subsets of flowering plants were surveyed along a walking transect. Other sites were simply net-collected without a formal plant count. Long distances between remote sites precluded resampling. Collected bees were curated and identified to species using published keys (references *in* LaBerge 1986) aided by comparison with authoritatively identified specimens in the extensive bee collections at the PIRU in Logan, Utah, where vouchers were deposited.

Results and Discussion

Gender Allocation by *L. dissectum*

Plants of *L. dissectum* are andromonoecious, presenting complex but consistent spatiotemporal patterns of gender expression. Larger plants produced multiple bisexual umbels, sometimes accompanied by an entirely male umbel. Umbels of plants in the research garden averaged 17 (SE 1) umbellets each. Every umbellet produced some male (staminate) flowers. Flowers of innermost umbellets were often entirely staminate (27% of umbellets on umbels in the research garden), but most umbellets had a mix of male and bisexual (hermaphrodite) flowers. Bisexual umbellets averaged 21 (SE 1.2) flowers consisting of 16.8 (SE 2) bisexual and 4.5 (SE 1.1) male flowers. Hermaphrodite flowers within these bisexual umbellets were protogynous, beginning with a female phase whose receptive stigmas persisted for about 2 d (Supplementary Material 1). Only after its stigma began to senesce and lose receptivity (hydrogen peroxide test) did a hermaphrodite flower transition to a staminate phase, its anthers dehiscing pollen over the next 2 d. Staminate flowers in the inner whorls of these umbellets only shed pollen after the female phase of that umbellet had ended. Autogamy is disfavored both because of this temporal sequence of sexual phases within umbellets, as well as the minute physical separation of anthers and stigmas. However, pollinator-mediated geitonogamy seems probable because the sexual phases are not particularly synchronized, either between neighboring umbellets or between multiple umbels on the same plant. Schlessman (1982) was led to a similar conclusion after his exhaustive studies of the sexual reproduction of several tuberous species of *Lomatium*. A pollinator walking across a *Lomatium* umbel can potentially transfer pollen from dehiscing anthers to receptive stigmas of different umbellets, which is of particular importance for fruiting by isolated plants, such as lone colonists.

Breeding Biology

Pollinator visitation was essential for *L. dissectum* fruit set. Only 3 of the 20 bagged umbels of the wild plants set any seeded fruits (3, 3, and 4 fruits) (Fig. 2a). In contrast, 27 of the 35 umbels with unrestricted visitation bore mature fruits. These reproducing umbels averaged 47 ± 32 fruits each (range 4–105 fruits). Overall, pollinator access resulted in a 60-fold increase in fruit production over autogamy at wild plants (Fig 2a). For the caged *L. dissectum* transplants in the research garden, manual outcrossing (xenogamy) of umbellets only yielded 10% more fruits over geitonogamy (Fig. 2b), a difference that was insignificant. The equivalence of fruit yields from geitonogamy and outcrossing treatments shows *L. dissectum* to be self-compatible, but the vastly greater fruit and seed yield of freely visited umbels over bagged ones in the wild population reveals the necessity of pollinator visitation for sexual reproduction by *L. dissectum*.

Given adequate pollination, mature *L. dissectum* individuals have a prodigious reproductive capacity in cultivation. Of the 25 transplants in our research garden that flowered the next growing season, each plant averaged 3 bisexual umbels composed of 10 umbellets, each bearing 17 bisexual flowers, for a total of 510 bisexual flowers per plant. Our manual pollinations yielded 1.7 seeds per bisexual flower (2 locules per flower). We calculate that these 25 plants, if thoroughly pollinated, could produce 21,675 seeds. Actual seed production of cultivated *L. dissectum* supports this contention, reaching 1500 kg/ha by its sixth growing season (Shock et al. 2015).

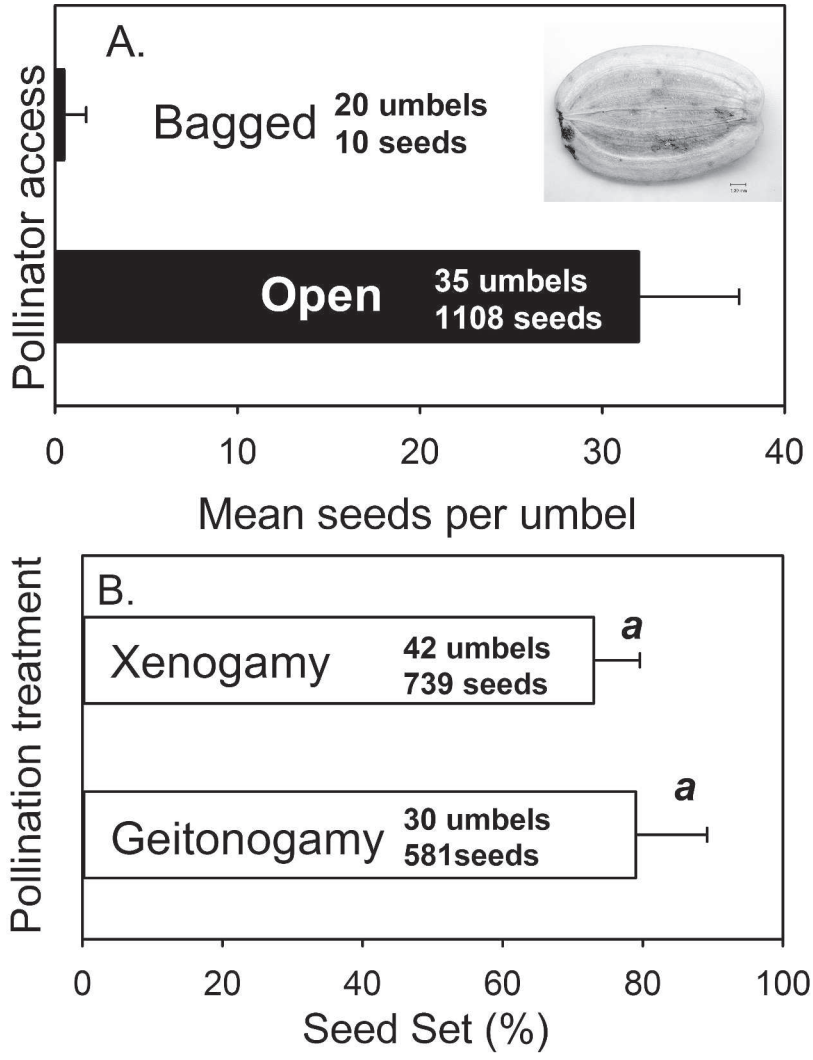

Fig. 2. Seed production following pollination treatments of *Lomatium dissectum*. *A*, Seed yields per umbel at wild plants and comparison of bagged umbels with openly visited ones. *Inset*: mature *L. dissectum* fruit (scale bar: 1.00 mm). *B*, Fraction of manually pollinated flowers setting seeds for caged plants in the outdoor research garden. Bars with different letters are statistically different ($P \leq 0.05$). Error bars represent 1 SE.

Suites of Bees at *Lomatium dissectum*, *L. triternatum*, and Others

The bee fauna found visiting flowering *Lomatium* was distinct from faunas that we sampled at other co-flowering perennial forbs in these same plant communities (Cane and Love 2016). Across the 5-state region (Fig. 1), 22+ species of bees of the Holarctic genus *Andrena* predominated at several species of *Lomatium* (Table 1, Supplementary Material 1). Most individuals (94% of 414 bees) collected at *Lomatium* represented species of *Andrena* as well, 90% of them females. One abundant species, *A. microchlora*, was taken at 24 of 30 sample sites across the 5-state region between 2007 and 2016. The few bees of other genera caught visiting *Lomatium* umbels were mostly overwintered gynes (future queens) of several species of *Halictus* and *Lasioglossum* sensu lato (Table 1). These small-bodied social halictid species are broad polyleges (floral generalists), commonly found foraging at other early co-flowering taxa (e.g., *Salix*), as well as

Table 1. Bees collected between 2007 and 2016 from flowering umbels of 5 species of *Lomatium* across 5 states of the U.S. Intermountain West (Fig. 1).

Bee genus	Species	Number of bees netted at *Lomatium* spp.				
		dissectum	*triternatum*	*grayi*	*nudicaule*	*andrusianum*
Agapostemon	*angelicus*[a]	1	2			
Andrena	spp.	7	4			
A. (*Simandrena*)	*angustitarsata*	30	7	5	1	4
A. (*Euandrena*)	*auricoma*	1	2			
A. (*Scaphandrena*)	*gordoni*		17			
A. (*Micrandrena*)	*chlorogaster*[b]	28	41	1		
A. (*Trachandrena*)	*cupreotincta*	1				
A. (*Scaphandrena*)	*gordoni*	1				
A. (*Scaphandrena*)	*lomatii*	2				
A. (*Thysandrena*)	*medionitens*			3		
A. (*Micrandrena*)	*melanochroa*		3			
A. (*Scaphandrena*)	*merriami*	20	9	1	9	20
A. (*Micrandrena*)	*microchlora*	32	36	1	14	13
A. (*Euandrena*)	*nigrocaerulea*					1
A. (*Diandrena*)	*nothocalaidis*		1			
A. (*Simandrena*)	*pallidifovea*	1				
A. (*Ptilandrena*)	*pallidiscopa*		2		5	6
A. (*Trachandrena*)	*salicifloris*	7				
A. (*Scaphandrena*)	*scurra*		1			
A. (*Tylandrena*)	*subtilis*		2			
A. (*Melandrena*)	*transnigra*		2			
A. (*Thysandrena*)	*trizonata*	1		4		
A. (*Thysandrena*)	*w-scripta*	2		1		
Ceratina	*pacifica*		1			
Colletes	sp.			1		
Halictus	*confusus*			1		
Halictus	*rubicundus*			4		
Halictus	*tripartitus*		6	1		
Lasioglossum	spp.		6	1		
L. (*Dialictus*)	spp.					14
L. (*Dialictus*)	*nevadense*			1		
L. (*Dialictus*)	*prasinogaster*		1			
L. (*Dialictus*)	*ruidosense*			1		
L. (*Dialictus*)	*sedi*	2				
L. (*Evylaeus*)	spp.	1		4		4
Nomada	spp.	4	4	1		
Osmia	spp.		1	1		
Osmia	*kincaidii*	1				
Panurginus	sp.		1			
Bees collected		142	149	32	29	62
Locations sampled		11	12	2	1	4

[a]Indistinguishable from *Agapostemon texanus*.
[b]*Andrena* (*Micrandrena*) *chlorogaster* is in some cases indistinguishable from *A.* (*M.*) *microchlora*.

at many later flowering species, including those with flat congested inflorescences of small flowers similar to those of *Lomatium* (e.g., *Achillea*) (Cane and Love 2016). Conversely, *Andrena* species were infrequent or absent at other common, widespread, spring-blooming forbs of different families that we have intensively sampled in the sagebrush-steppe and adjacent ecoregions (Cane 2008, Cane and Love 2016), even those forbs that are often co-mingled with flowering *Lomatium*. For example, *Andrena* bees made up only 16% of the 1141 native bees that we surveyed at *Balsamorhiza sagittata* (Asteraceae); *Andrena* was not among the 436 bees netted at *Astragalus filipes* (Fabaceae) across the 5-state region. Plant families more likely to host *Andrena* (e.g., Brassicaceae, Rosaceae, Salicaceae) were either absent or not flowering in our *Lomatium* plots. We regret not collecting the syrphid flies that we occasionally saw visiting *Lomatium* flowers; no other visitors (e.g., beetles) were seen. Clearly, *Lomatium* flowers are mostly visited by diverse native bees of a single genus, *Andrena*, that

are rare or absent from some other prevalent co-flowering forbs of other families growing in these same habitats.

In like manner, the bee species and genera common in spring at these other Intermountain forbs were notably absent from, or at most, rare strays at *Lomatium* (Cane and Love 2016). For example, large-bodied polylectic bees (e.g. *Bombus*, *Eucera*) that were absent from *Lomatium* (Table 1) were diverse (12 spp.) and abundant (30% of sample) at *A. filipes* in these habitats (Cane and Love 2016). Bees of these genera may not use *Lomatium* because of their larger body sizes and long tongues, which are a mismatch for the tiny flowers and rewards of *Lomatium*. More surprisingly, smaller-bodied spring *Osmia* species were also absent from *Lomatium* (Table 1), although they were common and diverse at many other co-flowering genera (e.g., 36 species and 87% of bees at *A. filipes*; >19 species and 40% of bees at *B. sagittata*) (Cane and Love 2016). As is the case with well-studied pollinator faunas of several other genera of the Apiaceae (reviewed *in* Zych 2007), species of *Lomatium* of the Intermountain West consistently attract a taxonomically restricted suite of bees from among a much broader local fauna, although only 1–2 of those bee species are *Lomatium* specialists.

Abundances of native bees at flowering *Lomatium* plants varied widely from site to site. Overall, at the 15 locations where we quantitatively surveyed *Lomatium* umbels for bees, 8 bees were collected per every 100 flowering *Lomatium* plants that we inspected, but abundances ranged widely (median 21 bees, range 3–109 bees per 100 umbels). Plants of *L. dissectum* hosted many more foraging bees than *L. triternatum* at a given moment ($\bar{x}$ = 50 versus 20 bees per 100 plants). However, that difference is partly attributable to a plant's floral display, because most *L. dissectum* plants had multiple umbels, whereas *L. triternatum* typically produce but a single umbel (Supplementary Material 1).

Multiple species of *Andrena* were consistently present at *Lomatium* umbels across most sampling sites and years. All but 3 of the 21 *Andrena* species that we collected at *Lomatium* seem to be taxonomic generalists for pollen (polylectic). Compilation of floral host labels from pinned museum specimens showed that individuals had been collected while they visited diverse flowers of many other plant genera and families (references *in* LaBerge 1986). For instance, our surveys showed that female *A. merriami* commonly visit *Lomatium* across the Intermountain region (Table 1); in Wyoming short-grass prairie, this same *Andrena* species typically carried pollen of the closely similar *Lomatium* relative *Harbouria* (Tepedino 1982). However, *Salix* and *Prunus* are also commonly visited by *A. merriami* (Ribble 1974). Among bee communities sampled across Vancouver Island, Canada, floral constancy for *Lomatium* by both *A. angustitarsata* (our second-most common *Andrena* at *L. dissectum*) (Table 1) and *A. auricoma* was demonstrated by the predominance of *Lomatium* pollen in their scopal pollen loads (Wray and Elle 2016). However, floral host labels of pinned females of these 2 species vouchered in California collections record visitation to diverse plant families (Moldenke and Neff 1974). Hence, foraging female bees and even whole populations of these *Andrena* species can show floral constancy when foraging at *Lomatium*, with pollination benefits accruing from their floral fidelity, even if the species' females are not *Lomatium* oligoleges.

There are, however, a few candidate *Lomatium* oligoleges among the *Andrena* species that we collected. In California, Moldenke and Neff (1974) concluded that both *A. microchlora* and *A. pallidiscopa* primarily visit flowers of the Apiaceae and, in particular, *Lomatium*, although host label data from Ribble (1974) indicate diverse floral hosts for *A. microchlora.* That species was the most abundant bee species in 11 of 30 sampled *Lomatium* populations (Table 1).

The combined prevalence and dominance of *Andrena* bees in these suites of *Lomatium* floral visitors exceeds that reported for other flowering species that are also visited by diverse *Andrena* species. Like *Lomatium*, 2 Holarctic genera of flowering shrubs or trees, *Crateagus* (hawthorns, Rosaceae) and *Salix* (willows, Salicaceae), also bloom abundantly and reliably in early spring. Both also attract multiple *Andrena* species. From early faunistic studies in Wisconsin, 14 of that state's 47 *Andrena* species were reported from willow, 5 of them oligoleges (Graenicher 1905). Unlike *Lomatium*, these bee faunas at willow also include representatives of many other bee genera (abundances unknown). During intensive

multiyear surveys at a single location (Carlinville, IL), Robertson (1929) collected 14 species of *Andrena* from flowers of *C. mollis*, half of which he scored as frequent visitors, pollen collectors, or both. As we found at *Lomatium* (Table 1), Robertson also encountered species of *Halictus* and *Lasioglossum* at *C. mollis* flowers, 5 of which he considered to be frequent visitors. Contrasted with our study, both of these early studies were spatially restricted but included more floral hosts. Many other reliable early spring flowers do regularly attract a few *Andrena* species (e.g., *Claytonia*), but no other well-documented floral assemblages rival these at *Lomatium* for sheer diversity and dominance by *Andrena* bees.

That these various *Andrena* species can abound at *Lomatium*, yet utilize diverse alternative floral hosts of the region, bodes well for their reliable contribution as pollinators for sustaining or restoring *Lomatium* species to native plant communities of the region. Where *Lomatium* is reintroduced by seeding, its pollination needs should eventually be met when one or more of these *Andrena* species immigrates from nearby populations of other widespread spring-blooming floral hosts, such as species of willow (*Salix*), Rosaceae, or Brassicaceae (references *in* LaBerge 1986, Moldenke and Neff 1974). Earlier in the more mesic Holocene, these alternative floral hosts may have been the bridges or stepping stones that enabled *Andrena* to cross broad basins of the Intermountain West to colonize foothill populations of *Lomatium* that are isolated today by the intervening inhospitable basin habitats.

Honeybees can contribute to pollinating *Lomatium* but can also compete with its native pollinators in natural settings. In an intensively agricultural valley near Ontario, Oregon, hived honeybees from a neighboring farm abounded at umbels of *L. dissectum* being cultivated for seed. Substantial seed yields were later obtained (Shock et al. 2009) despite an absence of native bees. Notably, there was little alternative bloom at the time. Just 40 km northwest in a wildland context, honeybee foragers were found foraging in 3 extensive (~1-ha) and dense populations of wild *L. andrusianum* (Supplementary Material 1, image 1). They were flying from a temporary massive apiary (90 hives) 2 km distant but nonetheless outnumbered 5:1 the 4–6 species of resident *Andrena* that visited *Lomatium* there (Cane and Love, unpublished data). Honeybees were absent from all of our other surveys of rural populations of *Lomatium* across the 5-state region (Fig. 1), simply because feral colonies rarely persist in the Intermountain West. Only near several towns and near the one large wildland apiary described above did we encounter any honeybees visiting wild *Lomatium*.

Populations of these biscuitroots and their pollinating bees can be expected to survive the massive wildfires that are increasingly frequent in the sagebrush-steppe. Biscuitroots flower in early spring, months before the late-summer wildfire season. By late summer, *Lomatium* plants are senescent and the adult *Andrena* generation is long past. Some field studies report the continued presence of *Lomatium* species after fire (Pendergrass et al. 1999, Caswell and Kaye 2001, Wrobleski and Kauffman 2003). Fuel loads in this ecosystem are relatively sparse and comprise small-diameter combustibles, such that flame fronts pass quickly with little left to smolder or ash over. Consequently, soil heating should be brief and shallow. Overlying soil should protect the buried perennial crowns of *Lomatium* taproots from the lethal heat of these late-summer fires. This contention gained experimental support when populations of *L. dissectum* were subjected to a range of experimental fire severities that mimicked surface fires during August, resulting in little or no mortality (Love and Cane 2019). Regarding the bees that visit *Lomatium*, all species of *Andrena* nest underground and most are univoltine (one annual generation). For this reason, the active nesting season of the spring *Andrena* fauna at *Lomatium* will be long past before the summer fire season ensues, their progeny deep underground (median depth 19 cm, 41 species) (Cane and Neff 2011) where they too are safe from the lethal heating by surface fire. For these reasons of seasonality, fuel loads, and soil depths of overwintering stages, populations of these biscuitroots and their pollinating bees should survive wildfires relatively unscathed, ready to reproduce the following spring.

A number of forbs of the sagebrush steppe, including *Lomatium*, have been cultivated for seed production. This seed is destined for restoring communities of the sagebrush steppe. In general, though, burned public rangelands in

the U.S. Intermountain West are still seeded by using one of several technologies to mix native shrubs and Asian or native grasses, but few forbs (Ott et al. 2016). One of these technologies, rangeland seed drilling, cuts soil furrows deep enough to damage the apical taproot meristems of *Lomatium* but not the deeper nest cells housing progeny of their *Andrena* pollinators. In this case, the cure, and not the fire, jeopardizes local *Lomatium* populations and their native pollinators. This sort of mechanical damage to extant *Lomatium* populations can be circumvented by using rugged no-till rangeland seeders (Ott et al. 2016). This simple step should leave taproots of resident *Lomatium* relatively unscathed, allowing the resilient local associations of biscuitroots and their suites of pollinating bees to persist undisturbed after wildfire.

SUPPLEMENTARY MATERIAL

One online-only supplementary file accompanies this article (https://scholarsarchive/byu.edu/wnan/vol80/iss1/1).

SUPPLEMENTARY MATERIAL 1. Images of *Lomatium*. (1) A large population of blooming *L. andrusianum*. (2) A blooming *L. dissectum* plant with multiple umbels. (3) Umbellet flowers of *L. dissectum*: female phase and male phase. (4) A male *Andrena* taking nectar at *L. dissectum*.

ACKNOWLEDGMENTS

Research was funded in part by the U.S. Forest Service and Bureau of Land Management. Terry Griswold, Harold Ikerd, Zac Portman, and Skyler Burrows provided expert identifications of the many difficult *Andrena* species. Insights about bee faunas at hawthorns came from John Hilty's invaluable online compilation of Robertson's vast data ledgers. Stephanie Miller implemented the statistical analyses for seed production. Nancy Shaw provided helpful comments. Research was funded in part by the Great Basin Native Plant Selection and Increase Project through the USDI–BLM Great Basin Restoration Initiative and the USDA–FS Rocky Mountain Research Station.

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Received 27 January 2019
Revised 12 August 2019
Accepted 17 September 2019
Published online 6 March 2020