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RESEARCH PAPER

Pollinators of the invasive plant, yellow starthistle *(Centaurca solstitialiss,* in north-eastern Oregon, USA

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The potential pollinators of yellow starthistle *(Centaurea solstitialis)* were surveyed at six sites in north-eastern Oregon, USA, between May and September from 2000 to 2002. The objective of the study was to determine the species composition and relative abundance of the insects that visited yellow starthistle throughout the flowering season and to assess the pollen loads on their bodies in order to infer which species might be the most effective pollinators of this invasive plant species in north-eastern Oregon. A total of 1923 individual flower visitors were collected at the six sites over the 3 year study period, comprising four orders, 41 families, and 203 species of insects. The 20 most commonly collected species represented nearly 59% of the individuals and just ten of these species could be considered the key pollinators. judging by the combination of abundance and pollen carriage (the megachilids, *Megachile apicalis* (introduced) and *Megachile* **periliirta,** the apids, *Apis mellifera* (introduced), *Bonibus bitarius, Bombus centralis, Svastva obliqua,* and *Melissodes lutalenta,* the halictids, *Halictus tripartitus* and *Halictus lioatus,* and the tachinid, *Peleteria malleola.* Over the 3 year study period, the six sites were consistently distinct in their flower visitor fauna, with the metropolitan Pendleton sites having a species composition distinct from the four mountain sites. Consistent patterns of interannual variation also were observed over the 3 year study. These patterns of flower visitation are interpreted in the context of the plant community within which yellow starthistle grows in north-eastern Oregon.

Keywords: ecological processes, invasive mutualisms, native plants, pollination.

Non-native invasive plants are increasingly recognized as major threats to native ecosystems worldwide, particularly in arid and semiarid regions (Sheley & Petroff 1999). In western North America, invasive plants have changed fire regimes (D'Antonio & Vitousek 1992), reduced livestock forage quality, damaged real estate and recreation values (Olsen 1999), and impacted biodiversity (D'Antonio & Vitousek 1992).

Although the impact of non-native invasive plants on biodiversity has been well described, in terms of the structure of native plant communities, little is known on how they might influence other species, including those that play critical functional roles, such as pollinators. Insects, especially bees, beetles, flies, and butterflies, are known to pollinate the majority of vascular plant species worldwide; beetles alone have been observed to pollinate 211 935 species, or >88% of the total species of vascular plants (Buchmann & Nabhan 1996). Insects also play a major role in crop reproduction (Tepedino 1979). (Williams 1994) estimated that 84% of crop species in the European Union are pollinated by insects and Buchmann and Nabhan (1996) reported that 67 principal crop species are pollinated by insects worldwide, out of 84 listed (80%). The key to effective pollination service is host specificity in order to ensure that the pollen from one individual is transferred to other individuals of the same species (Faegri & Pijl 1979; Schemske 1983). As most pollinators tend to specialize on flowers of one or a few plant species, plant communities typically have a

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diverse array of pollinator species available for pollen transfer (Corbet 1996). When exotic plants invade native communities, plant species diversity can decline due to intense competition for the available pollinators (Rathcke 1988), which might lead to concomitant decreases in the abundance and diversity of native pollinator communities.

Furthermore, the spread of invasive plants, especially those that reproduce only by seed (Thomsen *et al.* 1991), might be dependent on how successful they are at competing for the service of the resident pollinators. Thus, pollinators can act to exacerbate the spread of invasive plants by providing a service that improves seed production and the colonization potential of these species (Mal *et al.* 1992; Barthell *et al.* 2001). Unfortunately, basic information on the pollination ecology of invasive plants is lacking for most species. This information is relevant for those species that reproduce primarily by seed, particularly if there *is* a requirement to outcross for the production of viable seeds.

Although several species of invasive plants have successfully invaded shrub steppe communities in eastern Oregon (Sheley & Petroff 1999), yellow starthistle *tCentaurea solstitialis* L.: Asteraceae) has caused particular concern in recent years. Yellow starthistle (also called St Barnaby's thistle) is native to southern Europe and was introduced into western North America in the mid-1800s, possibly as a contaminant in alfalfa *(Medicago sativa* L.: Fabaceae) seed (T'homsen *et al,1991).* Yellow starthistle is now naturalized across southern Canada and most of the USA (Moore 1972; Maddox *et al. 1985;* Great Plains Flora Association 1986; Gleason & Cronquist 1991). It is also widespread in the Pacific North-West, with -9 million acres considered to be infested in California, Oregon, Washington, and Idaho by 1993 (Larson *et al.* 1994). Yellow starthistle occurs in grasslands, pastures, disturbed sites, and open woodlands (Thomsen *et al.* 1991), commonly with other exotic annuals. Yellow starthistle is present in the Californian annual grasslands that are dominated by non-native grasses in the genera of oat *(Avena* spp.), brome *(Bromus* spp.), and barley *(Hordeum)* (Keeley 1990) and *is* codominant with cheatgrass *(Bromus tectoium* L.: Poaceae) on rangeland in south-eastern Washington (Larson *et al.* 1994). It is the most invasive of the several species of *Centautea* that have colonized North America in the past 100 years (Gerlach & Rice 2003).

The reproductive biology of yellow starthistle suggests that the species depends on the service of pollinators to effectively set seed (Baker 1965; Maddox *et al.* 1996; Sun & Ritland 1998). Starthistle reproduces entirely by seed (Thomsen *et al.* 1991), is an outcrossing species (Barthell *et al.* 2001), and offers a rich and copious nectar reward to compensate pollinating insects (Pellet 1976). As a consequence, yellow starthistle *is* the kind of invasive plant species whose spread is dependent on the availability of pollinators (Barthell *et at.* 2001). The experimental exclusion of pollinators, especially honey bees, resulted in a significant decline in the number and proportion of seeds set in all three study sites in a Californian study of yellow starthistle (Barthell *et al.* 2001). That the European honey bee and the introduced "starthistle" leaf-cutting bee were two of the most common pollinators of yellow starthistIe in the Californian study caused Barthell *et al.* (2001) to describe their study as evidence of an "invasive mutualism". Interestingly, the starthistle leaf-cutting bee is now competing successfully with its close relative, the alfalfa leaf-cutting bee *iMegachile rotundata* (Fabricius) for nest sites in California and the Pacific North- West, a success that is probably related to the concomitant spread of yellow starthistle (Barthell *et al.* 2003; Stephen 2003). Doubtless, there will be other examples of pollinators encouraging the spread of invasive plants, involving both introduced and native pollinators. Indeed, in the Barthell study, many native bees were attracted to yellow starthistle, although the honey bees dominated the community in terms of relative abundance. The native pollinators included the megachilids *(Osmia),* apids *(Melissodes, Ceratina, Tilepeolus, Diadasia,* and *Svastra),* and halictids *(Halictus, Lasiogloggum [Dialictus], Agapostemon,* and *Augodf/ore1la).*

Our objective was to determine the species composition and relative abundance (community structure) of the pollinators that visit yellow starthistle and the coexisting native plant species throughout the flowering season of the invasive plant. This objective seeks to determine how the honey bees and native pollinators are currently using yellow starthistle as a pollen and nectar source, relative to other plant species, and in areas differentially dominated by starthistle.

METHODS

Study sites

Field work was begun in June 2000 at six yellow starthistle sites in north-eastern Oregon, USA (Fig. 1). Two of these sites were located within the city of Pendleton: at the airport on the north-western edge of town and at Pendleton Community Park, on the south side of town. Three sites were located on the upper west slopes of Mt Harris in the Grande Ronde Valley, on

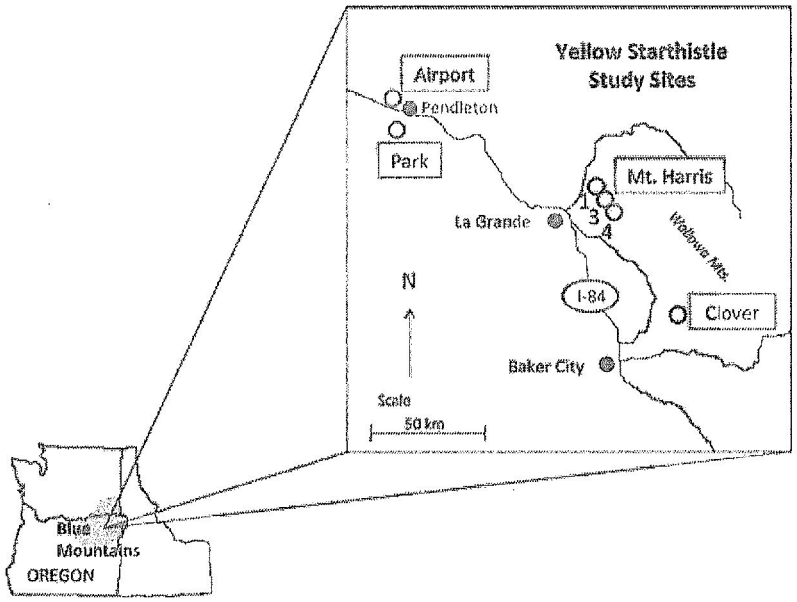

Fig. 1. Map of yellow starthistle study sites in north-eastern Oregon, 2000–2002.

lands administered by the La Grande Ranger District, Wallowa-Whitman National Forest. One site was located at the headwaters of Clover Creek, also on lands administered by the La Grande Ranger District. These sites varied considerably in the degree and kind of human disturbance observed. The two Pendleton sites appeared to be the most disturbed, with the plant communities dominated by invasive species, such as yellow starthistle, cheatgrass, and groundsel *(Senecio vulgaris* L.: Asteraceae), and by weedy natives, such as rabbitbrush *(Chrysothammus visidifiorus* (Hook.J: Asteraceae) (Table 1).The Mt Harris sites were the least disturbed. Although all dominated by starthistle, these sites had significant populations of native plant species and the sites themselves were interspersed among forested swales that were rich in natives and relatively undisturbed. The Clover Creek site was intermediate in the degree of human disturbance.

Procedure

The potential pollinators (flower visitors) were collected on warm, sunny days about every 10 days from June to early October 2000, 2001, and 2002 at six sites in north-eastern Oregon (Table 1). A sample consisted of 1.5 h of collecting, during which time the collector walked slowly through the entire site. About one-half of the 1.5 h was spent focused on yellow starthistle and about one-half on all the other plant species. When a flower visitor was observed, the insect was captured with an aerial net, placed in a killing jar of ethyl acetate, and later identified and curated at the laboratory. The weather at the time of collection was recorded, as well as the plant species for each collected insect. Each collected insect was entered as an individual record into a database, which was queried to provide datasets for analysis. The data are presented descriptively,as lists of species found over time at the six sampled sites (Fig. 2) and in multivariate form (Fig. 3). For the multivariate analysis,a non-parametric ordination method (non-metric, multidimensional scaling) (McCune & Grace 2002) was used to characterize the sites based on their relative abundance of species and then the ordination was correlated with the site factors in an attempt to explain the among-site patterns of community composition.

The dominance of yellow starthistle at each site was sampled in August 2002 by randomly placing $1m^2$ quadrats at an intensity equaling 2% of each site area. The percentage cover of the following categories were recorded and presented descriptively: yellow starthistle, forbs, grasses, shrubs, bare ground, rocks/bare ground, and detritus. These percentage cover variables were among those used in the ordination described above in an effort to explain the among-site differences in the community composition of flower visitors.

To gain insight into the potential efficacy of the insects in distributing yellow starthistle pollen, the pollen was

Table 1. Site features and the mean percentage cover (±SE; N = 20 quadrats) of the principal vegetation groups at the six yellow starthistle study sites in north-eastern Oregon, 9–12 September 2002

Site feature	Pendleton Airport	Pendleton Park	Mt Harris 1	Mt Harris 3	Mt Harris 4	Clover Creek
Setting	City/agricultural	City/agricultural	Range/forest	Range/forest	Range/forest	Range/forest
Longitude/latitude	118.85°N/ 45.69°W	118.86°N/ 45.67°W	117.65°N/ 45.42°W	117.65°N/ 45.40°W	117.65°N/ 45.39°W	117.53°N/ 45.02°W
Elevation (m)	460	460	1225	1160	1100	915
Mean percentag cover (%)						
Starthistle	4.3	5.9	13.6	7.0	3.1	6.6
	(1.3)	(2.7)	(1.9)	(1.1)	(1.1)	(2.0)
Shrub	0.0	10.0	0.0	0.0	0.4	6.2
	0.0	(5.2)	0.0	0.0	(0.3)	(2.1)
Forb	21.1	6.0	6.4	3.1	5.2	6.4
	(4.2)	(1.3)	(1.4)	(0.5)	(0.6)	(1.3)
Grass	48.8	38.3	30.8	35.0	34.3	23.3
	(3.1)	(3.8)	(2.8)	(2.3)	(3.0)	(2.0)
Detritus	18.8	30.5	26.0	32.8	41.5	28.5
	(1.7)	(3.4)	(2.6)	(3.2)	(3.3)	(3.0)
Rock/bare ground	8.5	21.6	35.3	35.5	33.8	34.5
	(1.8)	(4.7)	(4.1)	(3.5)	(4.1)	(4.3)

	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-30	Oct 1-15
Halictus ligatus	12.2	20.0	13.3	13.3	5.6	7.8	3.3	4.4
Lasioglossum titusi	17.4	47.8	30.4	0.0	0.0	4.3	0.0	0.0
Halictus tripartitus	9.7	48.4	25.8	3.2	12.9	0.0	0.0	0.0
Trichodes ornatus	26.9	15.1	46.2	12.9	0.0	0.0	0.0	0.0
Ammophila macra	11.5	26.9	21.2	13.5	5.8	17.3	0.0	3.8
Melissodes lutulenta	10.0	20.0	40.0	25.0	5.0	0.0	0.0	0.0
Bombus centralis	15.2	18.2	39.4	27.3	0.0	0.0	0.0	0.0
Polistes dominula	15.9	17.5	23.8	27.0	15.9	0.0	0.0	0.0
Sphex pennsylvanicus	16.7	11.1	19.4	11.1	19.4	13.9	0.0	8.3
Megachile apicalis	7.4	24.8	27.0	23.9	10.9	4.8	1.3	0.0
Svastra obliqua	7.7	16.7	28.2	28.2	14.1	5.1	0.0	0.0
Megachile perihirta	6.2	10.8	12.3	24.6	15.4	15.4	15.4	0.0
Halictus farinosus	4.0	16.0	8.0	36.0	16.0	16.0	0.0	4.0
Bombus bifarius	2.3	10.2	36.4	46.6	3.4	0.0	1.1	0.0
Polistes aurifer	0.0	9.1	30.3	42.4	9.1	9.1	0.0	0.0
Apis mellifera	7.8	7.8	12.1	44.8	14.7	10.3	1.7	0.9
Villa lateralis	0.0	2.9	11.8	22.1	45.6	14.7	1.5	1.5
Peleteria malleola	4.0	4.0	2.0	16.0	0.0	42.0	12.0	20.0
Ochlodes sylvanoides	0.0	1.6	9.4	17.2	17.2	23.4	17.2	14.1
Melissodes bimatris	0.0	0.0	4.2	8.3	4.2	45.8	8.3	29.2

Fig. 2. Phenology (percentage abundance of each species through eight intervals of time – each row totals 100%) of the 20 most common flower visitors of yellow starthistle in north-eastern Oregon, 2000–2002, arranged in order from the early species to the late species. A darker shade of gray indicates a higher percentage abundance for each species. The ten species of "highest-quality" pollinators are in bold font (see also Table 3 and the text).

removed and identified from at least ten individuals of the 20 most common flower visitor species. The pollen was brushed off the bodies of randomly selected pinned individuals onto glass slides and preserved with standard methods. The content of the pollen baskets (Apidae) and ventral abdominal hairs was distinguished from the pollen collected on other parts of the body. The pollen was identified with the use of a reference collection

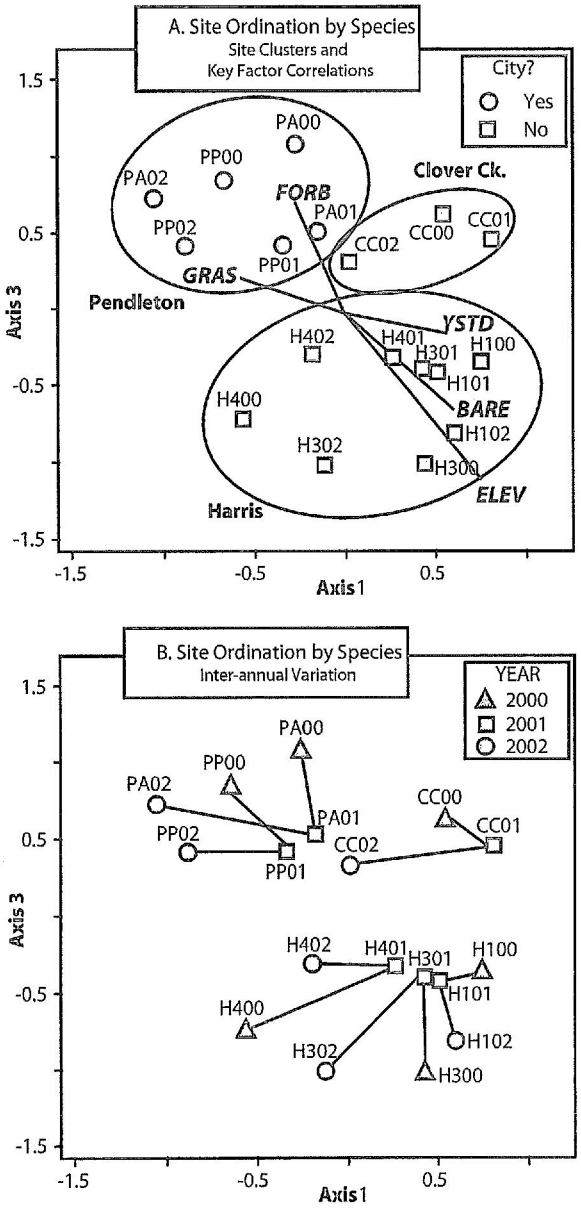

Fig. 3. Ordination (non-metric, multidimensional scaling) of north-eastern Oregon yellow starthistle sites, based on the species composition of the flower visitors. The label of each point is an acronym, with the first two letters giving the site and the last two numbers giving the year (e.g. PA = Pendleton Airport; H4 = Mt Harris Site 4). A. Emphasizes the correlation ($>r^2 = 0.40$) of the secondary matrix variables with the ordination (e.g. YSTD = the dominance of yellow starthistle). B. The same ordination, emphasizing the interannual variation between 2000 (e.g. PA00) and 2002 (e.g. PA02).

obtained by extracting pollen from flowers curated in the plant collection at Eastern Oregon University. The data are presented as the percentage of individuals of each Commom flower visitor species from which starthistle and non-starthistle pollen was collected.

RESULTS

A total of 1923 individual flower visitors were collected at the six sites over the 3 year study period, comprising four orders, 41 families, and 203 species of insects. The number of insects collected per sampling effort (90 min sample) was consistent over the 3 years, ranging from an average of 14 in 2000 to 16 in both 2001 and 2002. The four higher elevation sites were generally more productive, ranging from 15-18 insects collected per sampling effort, compared to 13-14 for the lower-elevation Pendleton sites. The collection was dominated by bees, which comprised 64% of the individuals (1225 of 1923) and 42% of the species (84 out of 201) collected. The other insect groups that were well represented in the collection included the Diptera (351 individuals; 18%), Coleoptera (189 individuals; 10%), and Lepidoptera (120 individuals; 6%).

Although our collection was diverse, nearly 59% of the individuals (1126 of 1923) were represented by the 20 most commonly collected species (Table 2). Of these, ten could be considered the key pollinators, judging by the combination of abundance and pollen carriage (Table 2). These included the megachilids, *Megachile apicalis* Spinola (introduced) and *Megachile perihirta* Cockerell, the apids, *Apis mellifera* L. (introduced), *Bombus bifarius* Cresson, *Bombus centralis* Cresson, *Svastra obliqua* (Say), and *Melissodes lutalenta* LaBerge, the halictids, *Halictus tripartitus* Cockerell and *Halictus ligatus* Say, and the tachinid, *Pelcteria malleola* (Bigot). Interestingly, by far the two most important pollinator species were the introduced starthistle bee *(M. apicalis)* and the honey bee *(A. mellifera)*. Of the ten key species, six were ubiquitous among the sites, *A. mellifera* and S. *obliqua* were found mainly at the lower-elevation Pendleton sites, and two of the *Bombus* species *(B. bifarius, B. centralis)* were found only at the higher-elevation sites (Mt Harris and Clover Creek). Overall, these ten key species represented 28% of the total abundance of flower visitors collected over the 3 year period. Although very common in our collections, most of the smaller bees (two other common halictids), the four common wasps, the true flies (bombyliid, *Villa lateralis* [Say], and syrphid, *Eristalis hirta* Loew), the skipper *(Ochlodes sylvanoides Leech),* the beetles (clerid, *Trichodes ornate* [Say], and meloids, *Epicauta puncticollis* Mannerheim and *Nemognatha lutea* LeConte), and the

Table 2. Total number of species collected, pollen loads, site prevalence, and phenology of the 20 most common insect species (total abundance > 19 individuals), in order of abundance, that visited flowers at the six yellow starthistle sites in north-eastern Oregon, 2000–2002

Species	Order/family	Number	% weight (yellow starthistle pollen)	% weight (other pollen)	Site prevalence	Peak seasonal abundance
Megachile apicalis	Hymenoptera: Megachilidae	173	90.0	60.0	Ubiquitous	July–August
Apis mellifera	Hymenoptera: Apidae	112	40.0	80.0	Pendleton/Clover Creek	July–August
Trichodes ornatus	Coleoptera: Cleridae	93	20.0	70.0	Mt Harris	June–July
Halictus ligatus	Hymenoptera: Halictidae	79	38.9	100.0	Ubiquitous	June–July
Bombus bifarius	Hymenoptera: Apidae	71	55.0	100.0	Mt Harris/Clover Creek	July–August
Villa lateralis	Diptera: Bombyliidae	66	30.0	30.0	Mt Harris/Clover Creek	July–September
Svastra obliqua	Hymenoptera: Apidae	64	90.0	80.0	Pendleton	July–August
Ochlodes sylvanoides	Lepidoptera: Hesperiidae	63	10.0	10.0	Ubiquitous	August–October
Polistes dominulis	Hymenoptera: Vespidae	54	0.0	10.0	Ubiquitous	June–August
Megachile perihirta	Hymenoptera: Megachilidae	52	70.0	80.0	Ubiquitous	July–September
Peleteria malleola	Diptera: Bombyliidae	48	50.0	80.0	Ubiquitous	August–October
Ammophila macra	Hymenoptera: Sphecidae	43	20.0	30.0	Ubiquitous	June–September
Sphex pensylvanicus	Hymenoptera: Sphecidae	31	20.0	20.0	Pendleton/Clover Creek	June–September
Polistes aurifer	Hymenoptera: Vespidae	31	10.0	0.0	Mt Harris/Clover Creek	July–August
Bombus centralis	Hymenoptera: Apidae	30	70.0	80.0	Mt Harris/Clover Creek	June–August
Halictus tripartitus	Hymenoptera: Halictidae	28	50.0	90.0	Ubiquitous	July–August
Halictus farinosus	Hymenoptera: Halictidae	25	40.0	80.0	Pendleton/Clover Creek	July–September
Lasioglossum titusi	Hymenoptera: Halictidae	22	10.0	100.0	Mt Harris	June–July
Melissodes bimatris	Hymenoptera: Apidae	22	20.0	90.0	Clover Creek/Pendleton	September–October
Melissodes lutalenta	Hymenoptera: Apidae	19	65.0	100.0	Ubiquitous	June–August

The ten species of "highest-quality" pollinators are in bold font.

colletid bee *(Colletes gypsicolens* Cockerell) either were not observed to carry yellow starthistle pollen or carried large quantities of other pollen (Table 2).

Over the 3 year study period, the sites were consistently distinct in their flower visitor fauna, with the lower-elevation Pendleton sites ordinating as a cluster distinct from both the Clover Creek site and the Mt Harris sites (Fig. 3a). Ordination Axis 3 clearly separates the Pendleton and Clover Creek sites from the Mt Harris sites, while Axis 1 separates Pendleton from Clover Creek. The environmental variables (see the list in Table 1) that are most closely associated with site separation in ordination space are the: (i) elevation, percentage bare ground, and percentage starthistle cover (lower at the Pendleton sites); and (ii) grass and forb cover (higher at the Pendleton sites than Clover Creek). These patterns of correlation must, however, be interpreted within the context of the fact that the two Pendleton sites were much closer to a metropolitan area, which itself might explain much of the variation in the pollinator species collected. The species most correlated to Axis 3 are the clerid beetle, *T. ornatus* (r^2= 0.63), and the bumble bee, *B. bifarius* (r^2= 0.47), both common only at Mt Harris, and the apids, S. *obllqua* (r^2 = 0.60) and *A. mellifera* (r^2 = 0.54), both common only in Pendleton. The species most correlated to Axis 1 are S. *obliqua* (r^2 = 0.53), *A. mellifera* (r^2 = 0.50), and the introduced wasp, *Polistes dominula* (Christ) (r^2 = 0.50), all collected in Pendleton but rarely at Clover Creek, and B. *bifarius* (r^2 = 0.50), collected at Clover Creek and Mt Harris.

There were consistent patterns of interannual variation observed over the 3 year study period (Fig. 3b). At Pendleton, both sites show the same pattern of inter-annual variation, with the 2000 samples from both sites ordinating higher on Axis 3, the 2001 samples decreasing on Axis 3, and the 2002 samples from both sites decreasing on Axis 1. The shift in 2001 toward the Mt Harris cluster is partly explained by the temporal patterns of abundance of *A. mellifera* and S. *obliqua,* with both species having a lower abundance in 2001, thus reducing the dominance of these two species (and thus the separation between Pendleton and Mt Harris) for that year. The separation between the Pendleton park and airport sites is also explained in part by these two apid species, with their relative abundances more closely similar at the two sites in 2001, compared to 2000 or 2002. At Clover Creek, the ordination exhibits the same pattern as Pendleton between 2000 and 2002. In this case, the honey bees (4 *mellifera)* were rarely collected at Clover Creek in 2001, thus allowing the site to be ordinated with a higher Axis 1 value, relative to the 2000 and 2002 samples, which had a much higher abundance of honey bees. At Mt Harris, the 2001 samples were much more similar among sites 1,3, and 4, compared to either 2000 or 2002, largely because the more common indicator species (e.g. B. *bifarius* and *T. ornatusi* had a relatively more similar abundance among the sites in 2001.

DISCUSSION

The flowers of yellow starthistle attracted >200 insect species at six sites in north-eastern Oregon, but just ten species probably provided most of the pollination service for this invasive plant over the 3 year study period. This conclusion is based on a combination of the frequency of flower visits observed and the abundance of pollen found on the bodies of putative pollinators. Although "pollinator quality" actually cannot be demonstrated (after Herrera 1987), in terms of plant fitness, we would predict from the visitation frequency and pollen loads that these ten species would be the most effective pollinators of yellow starthistle growing in north-eastern Oregon.

Compared to most other studies, our collection of flower visitors is very diverse, attesting to the attractiveness of starthistle as a pollen and nectar resource. For example, we collected a total of 87 species of bees visiting starthistle over 3 years, while Richards (1987) found a total of only 24 species (mostly *Megachile* and *Bombus* spp.) visiting cicer milkvetch *(Astragalus cicer* L.: Fabaceae) in southern Alberta, Canada, from 1978 to 1981. Similarly, Richards and Edwards (1988) found that just six species of bees (alfalfa leafcutting bee, honey bee, four species of bumble bee) served as the pollinators of the forage legume, sainfoin *(Onbychis viciaefolia* Scop.) in southern Alberta from June to August 1986. Interestingly, the sainfoin flower-handling time was inversely correlated with the pollinator body size, with bumble bees able to extract nectar at a significantly higher rate than honey bees and leafcutting bees (Richards & Edwards 1988). Thus, it is possible that the glossa length, which *is* also correlated with the bee body size (Harder 1983), might determine whether an individual bee can successfully extract nectar from a flower, especially complex zygomorphic flowers of legumes, such as sainfoin and milkvetch, However, simple flowers with short corollas, such as the flowers of *Centaurea* species, might offer nectar to a wider variety of bee species, including those with short tongues. This might explain the difference in bee diversity between our collection (87 species, including many small-bodied species) and the smaller collections of Richards (1987) and Richards and Edwards (1988) on Fabaceae. More generally, the species richness of bees in our study ranks highly compared to other

studies that generated species lists of bees visiting single species of plants: Williams *et al.* (2001) reported that researchers found an average of 19.6 ± 2.5 species of bees in pollinator surveys on single species of plants.

Interestingly, the two most common and most important pollinator species are also introduced, the honey bee *(A. mellifera)* and the starthistle bee *(M. apicalis),* an observation that lends support to the idea that yellow starthistle is part of an "invasive mutualism", in which these three species all benefit through their plant-pollinator relationship (Barthell *et al.* 2001). However, the other principal pollinator species are native, including two *Bombus* species, two other apids, two halictids, and a tachinid fly. All of these insect species are geographically widespread, are relatively abundant, and have long flight periods, and thus have the potential to be important pollinators for yellow starthistle. As a group, these ten species also span the phenological range of flowering exhibited by yellow starthistle in north-eastern Oregon, thus providing a pollination service over the effective flowering period for this invasive plant species. Overall, the importance of the native pollinators indicates that yellow starthistle is well integrated into the ecosystem in north-eastern Oregon. In addition, yellow starthistle probably now plays an important role in the life history of these native insect species.

Our list of bee species that visited yellow starthistle includes *Andrena aculeata* (LaBerge): Andrenidae, which has been listed as "vulnerable" by the Xerces Society. Vulnerable species are defined as those at moderate risk of extinction due to a restricted range, relatively few populations (often <80), recent and widespread declines, or other factors (Shephard *et al.* 2005). In this case, although *A. aculeata* is restricted to the Columbia Basin, the species is probably widespread within that region, occurring in open forests and in agricultural areas. This ground-nesting species is known to have a long flight period (May to August), suggesting that it forages on a wide range of flowering plants.

To understand the full impact of yellow starthistle on the ecosystems in north-eastern Oregon, one must consider how this invasive species interacts with both the local flora and fauna. Numerous studies have shown that yellow star thistle has detrimental effects on other plant species, largely through competition for water (Roche *et al.* 1994). As its flowers offer a rich nectar reward to insects, it is also likely that starthistle exerts competitive pressure on other plants for the potentially limiting pollinator resource (Barthell *et al.* 2000). Coexisting plants that reproduce only by seed, have similar flowers, or have a flowering phenology that overlaps with starthistle are most likely to be affected. Another impact of starthistle might be to enhance and extend the foraging and reproductive seasons of pollinator populations by providing abundant pollen and nectar resources at a time of year when few native plants are in bloom. In fact, the interaction between yellow starthistle and its most important pollinators can be a significant factor in explaining the abundance, distribution, and colonizing speed of this highly invasive plant (Barthell *et al.* 2000, 2001).

Much less well understood is the extent to which the pollen resource provided by yellow starthistle plays a role in supporting the insect populations of species that have numerous other roles in the local ecosystem. For example, the tachinid fly, P. *malleola,* was one of the ten most important pollinators of yellow starthistle during our study period, especially in the late summer of each year. This tachinid is a parasitoid of large noctuid moths (the flies attack the larval stage), is widespread in North America (O'Hara Wood 2004), and can be very abundant (Hampton 2005). In their work on primary succession at Mount St Helens, Fagan and Bishop (2000) suggested that P. *malleola* might have prevented the noctuid moth, *Euxoa* sp., from defoliating its lupine host plant in certain portions of its range. For a species like P. *malleola,* it is quite possible that the presence of yellow starthistle, the flowers of which offer both pollen and nectar, could be an important determinant of its local population size. Clearly, when invasive plants, like yellow starthistle, become integrated into local ecosystems, their influence is likely to be detrimental to some species and beneficial to others, with effects that cascade through the system as a consequence of other types of interactions.

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