**Abstract**

Introduced species are known to have large impacts on native ecosystems, by extirpating species, altering species interactions and changing community composition. The mechanisms by which introduced species impact native communities often include both direct and indirect effects. Here, we combined observational field surveys, an exclosure experiment, network analysis and structural equation modeling to examine the direct and indirect effects of an introduced species on native communities. Specifically, we investigated how introduced elk indirectly impact the composition and co-occurrence patterns within a community of plant-associated arthropods by directly altering the phenotype of a native plant, *Solidago velutina*. Surveying the arthropods associated with the plant's inflorescence, two main patterns emerged. i) Using field observations across 500 km² and an exclosure experiment, *S. velutina* growing in the presence of elk had 67–90% fewer flowering ramets, 15–85% lower percentage of flowering ramets, 33–45% fewer flowerets per inflorescence and 25–45% lower sexual ramet biomass. ii) Using the same exclosures, the arthropod community on *S. velutina* in the presence of elk, had 45% fewer species, a 70% reduction in abundance and a significant change to the species composition and co-occurrence network structure. The results from the network analysis suggested that introduced species’ impacts on communities can be more than changes in richness or abundance, but include changes to species interactions. Structural equation modeling showed that elk caused a decrease in inflorescence size of *S. velutina*, which affected the arthropod community, suggesting that communities can change without extirpation of their host plant species. These results highlight the importance of changing intraspecific variation as a mechanism by which invasive species alter community composition and species interactions.

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**1. Introduction**

Herbivores are known to directly change plant traits, which indirectly alter the plant’s capacity to interact with other organisms (Ohgushi, 2005). Herbivory can induce changes in plant traits, such that damaged plants have different chemical composition (e.g., Viswanathan et al., 2005), growth rates (Bailey and Whitham, 2003), architecture (Whitham and Mopper, 1985; Paige and Whitham, 1987), and flower morphology (Strauss et al., 1996)

Herbivores may also selectively forage on plants with certain characteristics, causing a shift in the trait frequencies in plant populations (Gomez and Zamora, 2000; Gomez, 2003). Studying the crucifer, *Erysimum mediohispanicum*, Gomez (2003) found that the Spanish ibex (*Capra pyrenaica*) selectively foraged on large plants. Consequently, plants growing in the presence of *C. pyrenaica* were shorter and produced fewer fruits and seeds than plants growing in the absence of *C. pyrenaica*. Because other organisms are often strongly associated with plant traits, shifts in plant traits might lead to a change in the community of organisms associated with the plant (Martinsen et al., 1998; Bailey and Whitham, 2003). For example, Bailey and Whitham (2003) showed that aspen (*Populus tremuloides*) browsed by elk supported lower numbers of galling sawflies and a different composition of arthropods.
In addition to affecting community composition, changes in plant traits might also affect the interaction network structure and patterns of co-occurrence among species in a plant-associated community. As the indirect effects of species have been shown to be important in determining the outcome of species interactions (e.g., trophic cascades), analyzing structure of interactions among species provides important information missing in traditional community metrics (i.e., richness, abundance and species composition) and reveals important components of community dynamics. In addition to being an assemblage of species, communities are also suites of interacting species, which may affect community stability (Solé and Montoya, 2001), energy flow (Tyliañakis et al., 2007), evolutionary trajectories (Fontaine et al., 2011; Thompson, 2013), and species coexistence (Lankau et al., 2011). The introduction of network analyses into ecological research has facilitated the investigation of species interaction network structure of large, complex communities (e.g., Solé and Montoya, 2001; Vazquez and Simberloff, 2003; Bascompte and Jordano, 2014).

Introduced species can alter patterns of biodiversity (Sala et al., 2000; Clavero and García-Berthou, 2005; Nunez et al., 2010) and having been introduced to nearly all regions of the world, ungulates are one of the most widespread groups of invasive species (Spear and Chown, 2009). Through herbivory, alteration of soil properties and disease transmission, introduced ungulates have strong negative impacts on ecosystems, and can spark social and political tension (Baskin, 1998; Vazquez, 2002; Martin et al., 2010; Nunez et al., 2010; Stritar et al., 2010). Because they are common throughout the world, it is important to understand the direct and indirect ecological effects of introduced ungulates on associated communities. However, few studies have tracked the chain of effects through which introduced ungulates directly alter native plant species, which indirectly disrupts the diversity, composition and network structure of the plant-associated communities.

Here, we examined how the introduced elk (Cervus elaphus nelsoni) altered plant traits of the native forb, Solidago velutina, which in turn altered the composition and network structure of the plant-associated arthropod community. Over the last century, elk densities have dramatically increased in the southwestern United States, largely because of human actions (Truett, 1996; Borman, 2005). Rocky Mountain elk were introduced to portions of Arizona and New Mexico where they previously did not exist (Truett, 1996). Further, the construction of water tanks allowed them to spread in areas where lack of water would have otherwise limited their distribution. Knowing that herbivory can reduce flowering output of plants (Gomez and Zamora, 2000) and that elk are known to forage on Solidago (Kufeld, 1973), we used observational and experimental data, as well as structural equation modeling (SEM) and network analysis to test two hypotheses 1) S. velutina growing in the presence of elk would have reduced sexual reproductive potential (i.e., fewer florets per sexual ramet, lower sexual ramet biomass, fewer sexual ramets and a lower percentage of sexual ramets). 2) Because plants serve as a resource for arthropods, reduced inflorescence size in the presence of elk would result in plants that supported an arthropod community that was less diverse and had a different composition and co-occurrence network structure. Answers to these hypotheses are important because they explore the chain of indirect interactions and highlight the importance of intraspecific variation in redefining communities after species introductions.

2. Materials and methods

2.1. Study system

S. velutina (Asteraceae) is a perennial wildflower native to western North America and is a dominant understory plant in Pinus ponderosa forests of Northern Arizona (Abella and Covington, 2006, Supplementary Fig. 1A). Further, flowering in late summer and well into the fall, S. velutina is often one of, if not the only plant flowering late in the year (D.S.S., personal observation) and thus could be an important resource for arthropods. S. velutina and elk co-occur over part of the plant’s range and elk are known to forage on members of this plant genus (Kufeld, 1973), usually eating the entire inflorescence in the process (D.S.S., personal observation). S. velutina is a clonal species where a single genet (a genetically unique individual) often produces dozens to hundreds of ramets (above-ground shoots). These ramets are connected underground via roots. Thus, it is possible to distinguish among genets by digging and verifying root connections or lack thereof (see below). Each ramet may or may not produce an inflorescence (i.e. it will be sexual or asexual), which is composed of dozens to hundreds of florets (Supplementary Fig. 1). Finally, because it attracts dozens of arthropod species, Solidago has become a model system for studying plant-arthropod interactions (e.g., Maddox and Root, 1987; Craig et al., 2007; Genung et al., 2010, 2012). While we initially set out to examine how cattle, deer and elk may be collectively impacting S. velutina, our estimates of ungulate densities showed that elk were by far the most abundant ungulate (see below).

2.2. Sampling

We collected two data sets to examine the first hypothesis, which predicted that S. velutina traits would differ across a gradient of elk abundance. First, we examined plant traits across a range of natural variation in elk abundances. We chose 19 sites within the P. ponderosa vegetation zone in Coconino National Forest, surrounding Flagstaff, AZ, encompassing ~500 km². Sites were chosen haphazardly by driving and walking within 2 km of forest roads and searching for patches of S. velutina. Patches of S. velutina were chosen for a study site if they were large enough to contain a 25 m transect (see below). At each site, we established six 1 m² quadrats evenly spaced along a 25 m transect. In each quadrat, we counted the total number of sexual and asexual S. velutina ramets and calculated the percent of sexual ramets within each plot (hereafter referred to as the number sexual ramets and percent sexual ramets, respectively). In addition, we haphazardly collected a single sexual ramet from each quadrat in a transect, counted its florets and weighed it, after drying it for 3 days at 65 °C (hereafter referred to as the number of florets per sexual ramet and sexual ramet biomass). We used data from all quadrats to calculate average values per site for the plant traits. We also quantified ungulate densities at each site by counting scat piles within a 25 m by 25 m plot, centered on each transect. Scat counts have shown to accurately measure ungulate densities (Loft and Kie, 1988). Scat was initially categorized into three types: elk, deer (Odocoileus spp.) and cattle (Bos primigenius). Because deer and cattle constituted a very small percent of the total scat (6.1% and 6.4%, respectively), they were excluded from future analyses.

Second, we sampled inside and outside of two fenced ~30 ha exclosures, (hereafter referred to as the Kendrick and the 794 sites) erected in 2001 and 1988, respectively, to examine plant traits in the presence and absence of elk. The two exclosures were within the latitudinal and longitudinal range of the 19 sites described above and both exclosures were in sites dominated by P. ponderosa. Because preliminary observation showed that dozens to hundreds of individual arthropods were associated with the flowering portion of the plant, we focused our sampling on flowering genets. At each exclosure, we haphazardly sampled flowering genets of S. velutina inside and outside the enclosure (Kendrick: n_in = 17, n_out = 14, 794: n_in = 15, n_out = 15). In sampling outside the...
enclosure, we chose genets within 300 m of the enclosure fence in an attempt to keep environmental conditions similar between the inside and outside of the enclosure. Genets were chosen by walking in the sampling area and choosing the first flowering genet encountered that was at least 10 m and sometimes as much as 100 m from the previously sampled genet. Flowering genets were relatively rare outside the enclosure (see Results), thus our samples outside the enclosure represent all the genets we could find within 300 m of the enclosure. By limiting genets to be at least 10 m from each other, we sampled the vast majority of the area inside the enclosures. Thus, our samples were not biased to particular subsections of the sampled areas. We defined genets as patches of _S. velutina_ with consistent flowering phenology and discrete boundaries, and we selected genets that were separated by at least 10 m. Ramets were defined as discrete shoots emerging from rhizomes of a single genet. To ensure that all ramets were part of the same genet, we used a hand trowel to dig beneath a subset of genets to confirm that rhizomes connected ramets. For each flowering genet, we measured the same plant traits as in the first experiment (i) the number of sexual ramets, ii) the percent of sexual ramets, iii) the number of florets per sexual ramet and iv) sexual ramet biomass (as explained above). In addition, we conducted a survey at the Kendrick Peak enclosure to measure the proportion of flowering genets in the presence and absence of elk. We scored 19 genets inside and 33 outside of the enclosure. We scored each genet as sexual (i.e., it had at least one flowering ramet) or asexual.

To score the arthropod community, we randomly selected 1–3 flowering ramets per genet. If a genet contained 3 or less ramets, we sampled all ramets. If a genet contained more than 3 ramets we randomly chose three by dividing the genet into two halves and flipping a coin to select which half would be sampled. If the selected half contained more than one flowering ramet, we divided it in half and flipped a coin again to select the sampled half. We repeated this process until 3 flowering ramets were chosen. Once chosen, we quickly placed a paper bag over the ramet (to capture the arthropods), tied it off at ground level and cut the stem. We then placed the tied paper bags in a cooler with ice and transported them to a freezer until processing, which included measuring the characteristics of the plant and arthropod community. Because of the nature of our collection, we did not do an extensive survey for highly mobile arthropods (e.g. butterflies and bees) and instead focused our surveys on the relatively sessile portion of the arthropod community associated with the above ground portion of the ramet. In the laboratory we counted all ramets sampled to calculate the mean value of arthropod species richness and abundance. Community composition for each genet was calculated by combining the mean arthropod abundances.

### 2.3. Statistical analyses

For the data collected across the 19 sites, we used linear regressions to examine the response of each plant trait (the number of florets per sexual ramet, number of sexual ramets, the percent sexual ramets and sexual ramet biomass) to the abundance of elk scat. To improve the fit and constancy of variance, a 1/x transformation was used when analyzing the number of florets and sexual ramet biomass. To compare the proportion of sexual and asexual genets in and out of the Kendrick enclosure we used a chi-squared test. Across both enclosures, we used a two-way ANOVA with interaction to measure the effects of elk (inside versus outside the enclosures), site/year (i.e., the effect of the different enclosures, which were sampled during different years) and their interaction on the plant traits, arthropod species richness and abundance. Even though they were not part of our _a priori_ hypotheses, we statistically accounted for the site/year and interaction effects because they were an inherent part of our experimental design (i.e., we used two enclosures at different sites, which we sampled in different years). In the ANOVAs, we used log transformations on the number of sexual ramets per genet, the number of florets per sexual ramet, biomass, arthropod species richness and abundance to correct for heterogeneity of variances and to improve the linear fit between plant traits and the arthropod community (see structural equation modeling below), and we used square root transformation on the percent sexual ramets per genet to correct for heterogeneity of variance. Also, in the analyses for richness and abundance we included number of ramets sampled as a covariate to account for its influence in these variables. Finally, in our analysis, we treated each genet, and not the enclosure, as the unit of replication. While this may present limitations on data interpretation (Hurlbert, 1984), there are reasons for doing so. Ecological patterns often occur over large spatial scales. Thus, accurately studying those patterns requires experimental manipulation over large areas. In our study, we use 30 ha enclosures to capture the effects of elk browsing. We obtained statistical replication by sampling several times inside and outside of each enclosure. While some argue that this is incorrect from a statistical perspective (sensu Hurlbert, 1984), others have argued that this correctly captures ecological patterns over large areas and is not an issue statistically (Hargrove and Pickering, 1992; Oksanen, 2001). We used JMP 9 (SAS Institute Inc., Cary, NC) for the above analyses.

### 2.4. Arthropod community analysis

To test the hypothesis that arthropod community composition differed in the presence of elk, we used PerMANOVA (Anderson, 2001). As in our model to analyze plant traits, we included effects of elk (i.e., in and out of the enclosures), site/year and their interaction. We used the number of sexual ramets sampled per genet as a covariate to control for its influence on composition. We relativized species abundances in the community matrix by the maximum abundance for each species to down-weight the influence of extremely abundant taxa and reduce the likelihood that compositional patterns were driven by a few abundant species (McCune and Grace, 2002). Lastly, indicator species analyses were performed at each enclosure to see which species (if any) are responding to the presence of elk. Indicator species analysis was performed in PC-ORD 5.10 (MJM Software, Gleneden Beach, Oregon, U.S.A.), while PerMANOVA was run in R 2.11.1 (R foundation for statistical computing) in the package VEGAN.

To summarize and visually examine arthropod community composition, we used non-metric multidimensional scaling (NMDS) with Bray–Curtis distance (McCune and Grace, 2002). As with the PerMANOVA analysis, we first relativized species abundances by species maximum before conducting the NMDS. The resulting two-dimensional ordination was fit with a vector coded for the absence and presence of elk, using a joint biplot vector analysis (McCune and Grace, 2002). We then rotated the ordination to maximize the vector’s correlation coefficient with the first NMDS axis. Next, we used Pearson’s correlations to fit vectors of sexual ramet biomass and number of florets per ramet, which we hypothesized to have a direct influence on the arthropod community (see SEM methods below). These two plant traits were log transformed before performing vector analyses to improve their linear relationship with the ordination axes. To further understand the variation in the arthropod community that was captured by the ordination axes, we performed a two-way ANOVAs on the scores from the first and the second axes to examine which axis captured
the elk, site/year and interaction effects observed in the PerMANOVA (see Results). We used PC-ORD 5.10 for the ordination and vector analysis.

2.5. Structural equation modeling

We used structural equation modeling (SEM; Grace, 2006) in AMOS 19.00 (AMOS development corporation, Meadville, PA) to identify potential mechanisms linking elk effects on *S. velutina* to the arthropod community. Specifically, we were interested in identifying whether elk changes to ramet-level traits (number of florets per sexual ramet and sexual ramet biomass) caused the shift in arthropod community composition. Because of the high correlation between the two traits, the number of florets per sexual ramet and sexual ramet biomass were used as indicators of a latent variable, sexual ramet size. We hypothesized that elk (modeled as a binary variable: 0 = no elk and 1 = elk) would decrease sexual ramet size, which would in turn influence arthropod community composition. We also included a direct path from elk to arthropod composition, which if significant, would indicate that there are additional elk-altered traits that influence arthropod composition. In order to summarize community composition, we used NMDS. NMDS is more appropriate for reducing multivariate community data than parametric methods (e.g., principal components analysis) because NMDS can robustly ordinate non-parametric data (McCune and Grace, 2002) and there is precedence for using NMDS score to represent community composition in SEMs (e.g., Grace et al., 2007; Laughlin and Abella, 2007; Antoninka et al., 2009). Because our primary interest was in the component of the arthropod community that shifted with the presence of elk, we used NMDS axis 1 from the previously described ordination. The effect of site/year (modeled as a binary variable: 0 = Kendrick exclosure and 1 = 794 exclosure) on sexual ramet size and arthropod composition was also modeled to account for its effect on the arthropod community; however an interaction effect between site/year was not included because it did not affect the plant traits or NMDS axis 1 (see results). The genet level traits (percent sexual ramets and number of sexual ramets) were not included in the SEM because we sampled arthropods on the individual ramet scale, and hypothesized that ramet level traits were the most likely to affect the arthropod communities on individual ramets.

The SEM was evaluated in several ways. A maximum likelihood chi-squared test and the root mean square error of approximation (RMSEA) test were used to examine the overall fit between the data and the hypothesized model structure. The P-values associated with both tests are the probabilities that the model fits the data, therefore higher P-values indicate good fit (traditionally P > 0.05). Lack of model fit is an indication that important paths have not been included in the model, however these tests do not indicate if unnecessary paths were included in the model. Therefore, we also tested for the significance of individual path coefficients. To quantify the influence of elk on arthropod composition acting through sexual ramet size, we multiplied the coefficient of the path between the elk and ramet size with the coefficient from the path between ramet size and the arthropod community (Grace, 2006).

2.6. Network modeling and analyses

To examine the network structure of the arthropod communities, we modeled arthropod co-occurrence networks by applying a correlation-based approach to the species abundances inside and outside of each exclosure. Correlation-based methods have been used previously to model co-occurrence networks and have proven useful for inferring patterns of species interactions (e.g., Zhang, 2007; Vera-Licona and Laubenbacher, 2008; Faisal et al., 2010). Each co-occurrence network was constructed using a model comparison procedure to select the most parsimonious Generalized Additive Model (GAM; Hastie and Tibshirani, 1986). For each species pair, three competing models were tested in order to represent the broadest possible set of species covariance: 1) a constant or “null” model, representing no covariance between species, 2) a linear covariance between species and 3) a quadratic covariance between species. For each species pair, the most parsimonious GAM was selected using an information theoretic approach (Burnham and Anderson, 2002). The first order (linear) co-efficient from the selected model was then used to weight the co-occurrence network model.

We then analyzed the differences between networks using two structural statistics. We first tested for the total difference in connections between each pair of networks using a QAP (quadratic assignment procedure) test (Butts, 2010; Krackhardt, 1987) of the differences in total Euclidean distance between the network inside and outside the exclosure, respectively. We then used a QAP test to test for differences in both the number of connections (or connectance) and the centralization of the network, which is a measure of the dominance of the network by one or a few species (Freeman, 1979). Standardized effect sizes (SES) for both the QAP and permutation tests for centralization were calculated as the difference between the observed and permutation statistics, respectively, divided by the standard deviation of the permutation statistics. All network modeling and analyses were conducted in R v2.14.1 (R Development Core Team).

3. Results

3.1. Plant traits

Using observational data across 19 sites we found a negative relationship between elk scat counts and *S. velutina* traits. As elk scat increased, the number of florets per sexual ramet (F1,17 = 6.66, P = 0.019, R² = 0.28; Fig. 1A), the number of sexual ramets per genet (F1,17 = 5.57, P = 0.030, R² = 0.25, Fig. 1B), the percent of sexual ramets per genet, (F1,17 = 7.34, P = 0.015, R² = 0.30, Fig. 1C) and the biomass of sexual ramets (F1,15 = 6.27, P = 0.024, R² = 0.29, Fig. 1D) all decreased. Also, trait variability was lowest at sites with high elk scat counts (Fig. 1), suggesting that elk are removing trait variation from *S. velutina*.

Experimental data from the exclosures corroborated our observational data. For all measured traits, values were significantly lower outside of exclosures, in the presence of elk, relative to inside the exclosures (Fig. 2A–D, Table 1). For example, at the Kendrick site, *S. velutina* outside the exclosure had about half the number of florets per sexual ramet, 85% fewer sexual ramets, half of the percent of flowering ramets and 33% less biomass than *S. velutina* inside the exclosure (Fig. 2A–D). Genets were also less likely to flower outside the exclosure. About 95% of genets had at least one flowering ramet in the absence of elk, but in the presence of elk, only 55% of genets had a flowering ramet (χ² = 7.35, p = 0.007). There was a significant site/year effect on three of the plant traits (Table 1).

Such that the number of florets per sexual ramet, the percent sexual ramets per genet and the sexual ramet biomass were all less at the 794 exclosure (Fig. 2). However, we failed to detect a significant interaction between site/year and exclosure treatment on the plant traits (Table 1), suggesting that the effect of elk on plant traits is consistent across environmental conditions.

3.2. Arthropod richness and abundance

While elk influenced both richness and abundance of
arthropods, site/year and its interaction with elk had more variable
effects on arthropod communities. Across our surveys, we found
2942 total arthropods from 47 morphospecies (Table 1). Arthropod
richness and abundance were both lower in the presence of elk
(Fig. 2E and F, \(F_{1, 57} = 12.40, P = 0.001, F_{1, 57} = 9.73, P = 0.003\)). For
example, at the Kendrick site, arthropod abundance and richness
were \(-85\%\) and \(-50\%\) lower in the presence of elk (Fig. 2E and F). We
did not find an effect of site/year on arthropod richness (Fig. 2E,
\(F_{1, 57} = 4.31, P = 0.043\)) or abundance (Fig. 2F, \(F_{1, 57} = 1.28, P = 0.263\)).
There was a signiﬁcant interaction effect on abundance (Fig 2E and F,
\(F_{1, 57} = 4.27, P = 0.043\)), but we failed to detect an effect on richness
(Fig 2E and F, \(F_{1, 57} = 1.04, P = 0.312\)). Speciﬁcally, there seemed to
be a difference in abundance inside and outside of the Kendrick
exclosure, but not at the 794 exclosure (Fig. 2F).

3.3. Arthropod community composition

Elk signiﬁcantly inﬂuenced arthropod community composition
on Solidago velutina (Fig. 3, Table 1). In conducting post-hoc pair-
wise comparisons, we found a signiﬁcant effect of elk at both sites
(Kendrick: \(F_{1,20} = 1.6219, p = 0.05\); 794: \(F_{1,27} = 2.44, p < 0.01\)).
Because we relativized species abundances, our analysis suggests
that differences in the community are driven by composition and
not differential abundance of a small number of species (McCune
and Grace, 2002). Nonetheless, we also examined individual taxa
to see which species might be strongly responding to elk. We found
two indicator species at the Kendrick exclosure (two Coleoptera
species, Appendix) and two indicator species at the 794 exclosure
(one Coleoptera species and a species of thrips, Appendix). At the
Kendrick exclosure, for example, these indicator species were
3.5–5.5 times less abundant in the presence of elk. The fact that
there were different indicator species at the different sites may be
partially responsible for driving the interaction effect on
community composition (see below).

The effects of site/year, its interaction with elk (Fig. 3, Table 1)
and the covariate (number of ramets sampled: \(F_{1, 56} = 1.7209, P = 0.0189\)) also in-
fluenced arthropod community composition. However, it is unclear why the interaction was influential. Differences
between sites/years could be due to geography, time or a
combination of both. One possibility is that there were three major
hailstorms in the week leading up to the arthropod surveys in 2011,
which could have been partially responsible for the differences in
arthropod communities between sites/years.

3.4. Arthropod co-occurrence networks

Elk altered three patterns within the arthropod community
networks on S. velutina (Fig. 4). First, the overall structure of the
networks differed strongly in the presence of elk at the Kendrick
site (\(SES = 4.43, P < 0.001\)), but only marginally at Site 794 (\(SES = 1.46, P = 0.065\)). Second, networks in the presence of elk
tended to have fewer connections with a 25\% (without elk = 8, with
elk = 6, \(SES = 1.79, P = 0.047\)) and 50\% (without elk = 4, with
elk = 2, \(SES = 1.69, P = 0.067\)) reduction at Kendrick and Site 794,
respectively. Third, even though the centralization scores for indi-
vidual networks did not different from random (\(P > 0.05\)), they did
change in the presence of elk, at both Kendrick (\(SES = 4.93, P < 0.001\)) and Site 794 (\(SES = 3.20, P < 0.001\)). Together, these three
results show that the co-occurrence networks, which may indicate
arthropod species interactions, are changing in the presence of
invasive elk.

3.5. Linking plant traits to arthropod communities

Community composition changed as a result of elk-caused
changes in plant traits. The first NMDS axis captured the variation
Fig. 2. Reaction norms showing S. velutina traits and arthropod morphospecies richness and abundance inside and outside of the two exclosures. Points and error bars represent means ± 1 standard error at each of the four locations (inside and outside of the two exclosures). Circles and squares represent the Kendrick and 794 exclosures, respectively.

Table 1
Results from the two-way ANOVAs and perMANOVA, which analyzed the effect of elk, site/year and their interaction on the plant and arthropod community traits.

<table>
<thead>
<tr>
<th></th>
<th>Elk</th>
<th>Site/Year</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td># Florets per Sexual Ramet</td>
<td>$F_{1, 58} = 16.02, P = 0.0002$</td>
<td>$F_{1, 56} = 15.62, P = 0.0002$</td>
<td>$F_{1, 56} = 0.11, P = 0.7397$</td>
</tr>
<tr>
<td># Sexual Ramets per Genet</td>
<td>$F_{1, 58} = 61.17, P &lt; 0.0001$</td>
<td>$F_{1, 58} = 0.91, P = 0.3441$</td>
<td>$F_{1, 58} = 1.19, P = 0.2798$</td>
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<tr>
<td>% Sexual Ramets per Genet</td>
<td>$F_{1, 57} = 20.79, P &lt; 0.0001$</td>
<td>$F_{1, 57} = 20.66, P &lt; 0.0001$</td>
<td>$F_{1, 57} = 1.53, P = 0.2798$</td>
</tr>
<tr>
<td>Sexual Ramet Biomass</td>
<td>$F_{1, 58} = 13.99, P = 0.0004$</td>
<td>$F_{1, 58} = 20.39, P &lt; 0.0001$</td>
<td>$F_{1, 58} = 0.04, P = 0.8373$</td>
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<tr>
<td>Species Richness</td>
<td>$F_{1, 57} = 12.40, P = 0.0009$</td>
<td>$F_{1, 57} = 1.80, P = 0.1855$</td>
<td>$F_{1, 57} = 1.04, P = 0.3119$</td>
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<td>Species Abundance</td>
<td>$F_{1, 57} = 9.73, P = 0.0028$</td>
<td>$F_{1, 57} = 0.69, P = 0.4084$</td>
<td>$F_{1, 57} = 4.27, P = 0.0434$</td>
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<td>Species Composition (PerMANOVA)</td>
<td>$F_{1, 56} = 1.86, P = 0.0091$</td>
<td>$F_{1, 56} = 3.46, P &lt; 0.0001$</td>
<td>$F_{1, 56} = 1.75, P = 0.0155$</td>
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</tbody>
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in arthropod community composition between the inside and outside of the elk exclosures. The ANOVA indicated that variation in the first NMDS axis was primarily driven by elk (i.e. inside vs. outside the exclosures; $F_{1, 57} = 14.299, P = 0.0004$), with a marginal effect of site/year effect ($F_{1, 57} = 3.501, P = 0.0665$) but we failed to detect an interaction effect ($F_{1, 57} = 0.186, P = 0.6676$). These results were expected because we rotated the ordination axes to maximize NMDS axis 1 with the vector coded for the absence/presence of elk. Variation in the second NMDS axis was not affected by elk ($F_{1, 57} = 0.418, P = 0.5204$), but was instead driven by differences between site/year ($F_{1, 57} = 24.964, P < 0.0001$) and the interaction between elk and site/year ($F_{1, 57} = 8.273, P = 0.0057$). Vector analyses and SEM indicated that change in sexual ramet size is one of the mechanisms by which elk influenced arthropod composition (Fig. 5). The vector analysis showed that the number of florets per sexual ramet ($r = -0.519$), and biomass per sexual ramet ($r = -0.490$) both correlated with NMDS Axis 1, which represented the main gradient in arthropod composition that shifted from the absence to the presence of elk (see above).

The hypothesized SEM fit the data well ($df = 3$, $\chi^2 = 2.494$, $P = 0.476$, RMSEA = 0.000, $P = 0.540$), and highlighted two important points. First, elk had a negative influence on ramet size, and ramet size influenced the shift in arthropod composition (Fig. 5). Second, the size of the compound pathway between elk and the arthropod community acting through ramet size was 0.20. The direct path between elk and the arthropod community, which represents unmeasured mechanisms, had a path coefficient of 0.24. The similar coefficients of the direct path between elk and the arthropod community, and the indirect path from elk to arthropods through sexual ramet size indicated that there might be other ways by which elk alter arthropod communities on S. velutina, in addition to the elk effect on ramet size.

### 4. Discussion

Using a combination of observational and experimental data, as well as SEM and network analysis we showed that human-introduced elk altered the traits of native plants, which subsequently altered the composition and interaction network structure of the plant-associated arthropod community. Consistent with our first hypothesis, plants growing in the presence of elk had a lower propensity to flower (i.e., they had a lower proportion of sexual genets and a lower percentage of sexual ramets per genet) and when they did flower, they had fewer florets per sexual ramet and lower sexual ramet biomass (Figs. 1 and 2). Taken together, these results show that elk reduced the potential for sexual reproduction in S. velutina, which could further affect recruitment and patterns of genetic variation. Consistent with our second hypothesis, plants growing in the presence of elk supported lower richness, lower abundance (Fig. 2E and F), a different composition (Fig. 3) and different network of arthropods (Fig. 4). Other studies have shown that alterations of floral traits negatively affected pollinator visitation (Strauss et al., 1996). Because some of the arthropods on S. velutina were potential pollinators (e.g., dipterans and hymenopterans), it is possible that alteration of the arthropod community by invasives could shift patterns of pollination efficacy and cross-pollination in S. velutina.

It is also likely that invasive elk altered interactions among arthropods. While composition analyses (PerMANOVA and NMDS) detect differences in the presence/absence and relative abundance of species in the community, they do not provide information on co-occurrences. Even though our methods did not directly measure them, changes in co-occurrence networks suggest that species interactions are changing in the presence of elk. (sensu Tylianakis et al., 2007) It is also worth noting that in their study, traditional community metrics (i.e., richness and abundance) did not detect community differences, suggesting that studies that do not investigate possible species interactions might overlook perturbations to ecological communities (Tylianakis et al., 2007).

Our network analysis suggests that inter-arthropod interactions are changing in the presence of elk. The structural differences in the networks were the result of both a decrease in the connectivity and the centralization of co-occurrence patterns. In particular, the main drivers of network changes were two beetle species (Species 1 and 4), which lost or shifted connections in the presence of elk at both...
sites (Fig. 4). For example at the Kendrick site, the strongest connections (i.e. the connections with the highest correlations) in the absence of elk were between species 1 and 4 (both beetles, Appendix 1) and species 11, a small hymenopteran (Fig. 4). In the presence of elk, these connections are absent. Because the hymenopteran could be a parasitoid, it might be possible that trophic (i.e. host-parasite) interactions are breaking down in the presence of elk. These results suggest that in addition to the compositional shifts caused by invasive elk (Fig. 3), patterns of species interactions might be changing as well (Fig. 4). Our data agree with previous studies which found that areas with introduced ungulates supported arthropod communities that were lower in richness and abundance (Rambo and Faeth, 1999) and had different plant–pollinator interaction networks (Vazquez and Simberloff, 2003) compared to areas without ungulates. However, our study is distinct in that we examined possible mechanisms by which elk can change arthropod communities.

The difference in arthropod communities across the elk gradient seems to be partially driven by changes in plant traits. Vector analysis showed that the two ramet level plant traits (number of florets per sexual ramet and sexual ramet biomass) correlated with arthropod community composition. Similarly, SEM shows that there is a strong link between ramet size and the arthropod community composition (Fig. 4). It is possible that other variables are contributing to the changes to the arthropod community. In fact, the SEM does suggest that there are unmeasured variables affecting the arthropod community, which are represented by the direct path from elk to arthropod composition. These unmeasured variables could include flowering phenology (Gross and Werner, 1983), phytochemistry (Viswanathan et al., 2005), plant vigor (Bailey and Whitham, 2003), and/or soil properties (Stritar et al., 2010). The SEM results indicate that these variables are acting in concert with plant size to produce a shift in arthropod community in the presence of elk. It is important to reiterate that our enclosure experiment involved only two enclosures, thus we caution against broad inferences from our results. Nonetheless, our results are consistent with our hypotheses and can help inform future studies on the direct and indirect effects of herbivory. Because introduced and/or native invasive elk are an issue in many parts of the globe, we suggest that studies aimed at understanding their impact construct and maintain a higher number of enclosures to bolster statistical power and the strength of conclusions.

Our results highlight the importance of indirect ecological effects and intraspecific variation (Smith et al., 2011; Bolnick et al., 2011; Whitham et al., 2012) when considering how invasive species shape communities. While invasive species can directly alter communities, such as through consuming species (Coblentz, 1978; Vazquez, 2002), indirect ecological effects can also have substantial impacts on native communities. Even though elk did not remove S. velutina, changes to the plant traits (i.e., altering patterns of intraspecific variation) cascaded to affect the composition and network structure of 40+ species of arthropods, from multiple functional groups, including herbivores, predators and pollinators. Other studies have examined how introduced species cause the extinction of native species and other associated effects (Koh et al., 2004). Our findings however, show that native species do not need to go extinct to change to community structure. Specifically, we show that introduced species can cause changes to the traits of a native species, which can lead to significant changes of native diversity, not only in terms of the number of species but also community composition and interaction network structure.

Acknowledgments
We thank LM and DL Monroy Solance, A. Baker, C. Sanfiorenzo, F.L. Dong, C. Rushlow, J.K. Bailey and T. Ferguson for technical assistance and/or helpful comments. This research was supported by a National Science Foundation IGERTs to D.S.S., M.K.L. and L.J.L.

Appendix A. Supplementary data
Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2015.05.005.

References