



Original article

Introduced elk alter traits of a native plant and its plant-associated arthropod community



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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 enclosure 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 enclosure 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 florets per inflorescence and 25–45% lower sexual ramet biomass. ii) Using the same enclosures, 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)

than undamaged plants. 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.

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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 (Tylianakis 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; Nuñez 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; Nuñez 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 day 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 enclosures, (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 enclosures were within the latitudinal and longitudinal range of the 19 sites described above and both enclosures 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 enclosure, 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

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