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Nonhost neighborhood increases biocontrol weevil damage to the nontarget, federally threatened Pitcher's thistle (*Cirsium pitcheri*)

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ABSTRACT

Studies that monitor the intensity of biocontrol insect damage on target and nontarget hosts in the field often consider the effects of neighboring vegetation that serve as acceptable alternative hosts. Whether nonhost neighboring plants can also influence damage to hosts has received less attention. The nonnative, seed-eating weevil *Larinus planus* has been distributed as a biocontrol agent for weedy thistles in the U.S., but also attacks native thistles including the federally threatened *Cirsium pitcheri*. To test the hypothesis that nonhost *Ammophila breviligulata* grass neighbors increase susceptibility of *C. pitcheri* to *L. planus* damage, we clipped the neighboring vegetation within a 1 m radius around focal *C. pitcheri*, and assessed weevil infestation in flower heads of plants with clipped or unclipped neighbors. We also examined elevational effects by surveying weevil presence along an environmental gradient and comparing infestation rates between primary and secondary dune habitats with intact neighboring vegetation. *Larinus planus* infestation was more prevalent at low than at high dune elevations. At low elevations, clipping neighboring vegetation surrounding *C. pitcheri* significantly decreased the proportion of flower heads infested by weevils. Grasses may aid *L. planus* dispersal to *C. pitcheri* hosts and/or provide a refuge from environmental stress or natural enemies. Our results highlight two factors that predict *L. planus* attack, as well as areas of the dune on which to focus *Cirsium pitcheri* management or weevil control efforts. More broadly, our results suggest that nonhost neighboring vegetation may be an important factor determining the intensity of damage by invasive and biocontrol insects.

1. Introduction

1.1. Nontarget damage from biocontrol agents and ecological frameworks

Releasing insects for biological control of invasive plants is generally considered a cost-effective and beneficial management strategy (McFadyen, 1998). However, there are recognized risks associated with introducing nonnative insects into communities (Simberloff and Stiling, 1996a, 1996b) and several instances where biocontrol agents have had harmful, unintended effects on native plants, including those of conservation concern (Louda et al., 2005; Louda and Stiling, 2004). One

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such example involves the federally threatened Pitcher's thistle (*Cirsium pitcheri* (Eaton) Torr. & Gray), which is endemic to sand dunes of the western Great Lakes. Following the accidental introduction of *Larinus planus* Fabricius (recently changed to *L. carlinae*; see Hoebeke and Spichiger, 2016), this seed-eating weevil was widely distributed in the U.S. as a biocontrol agent for the weedy thistle, *Cirsium arvense,* with important negative consequences for native thistles (Louda and O'Brien, 2002). *Larinus planus* recently invaded Lake Michigan sand dune communities where it has significantly increased the extinction risk of *C. pitcheri* (Havens et al., 2012). Although this rare thistle experiences a multitude of threats (Havens et al., 2012), it is becoming more apparent that the future of *C. pitcheri* conservation and restoration must include strategies for minimizing damage from invasive weevils.

Assessing damage levels to target and nontarget hosts is a priority of current pre-release studies of candidate biocontrol agents. Despite rigorous host-specificity tests and fitness trials conducted in the laboratory or quarantined environments (Louda et al., 2005; McEvoy, 1996; Sheppard et al., 2005; Zwölfer and Harris, 1984), insect damage to plants under field conditions is difficult to predict (Arnett and Louda, 2002; Louda et al., 2003; McClay and Balciunas, 2005). Often insects fail to establish or underperform in the new environment (Goldson et al., 2014), or they damage native species more than expected (Louda et al., 1997; Louda and O'Brien, 2002). Successful weed biocontrol strategies must integrate additional ecological frameworks beyond consumer-host interactions, including how herbivore movement and host preference are affected by the composition of surrounding vegetation (Davalos and Blossey, 2011; Jonsen et al., 2001). Similarly, post-release (or post-invasion) monitoring of biocontrol insect damage within native plant populations can reveal biotic and abiotic factors correlated with nontarget damage (Rand et al., 2006). Previous work has shown that sand and vegetative cover influence *C. pitcheri* growth and survivorship (Chen and Maun, 1999; Hamzé and Jolls, 2000; Jolls et al., 2015), but we lack an understanding for how weevil damage of *C. pitcheri* is affected by these variables.

1.2. Importance of plant neighborhoods

Vegetative cover is an important component of dune heterogeneity that may influence weevil damage to native thistles in a variety of ways. For example, competition may increase a plant's susceptibility to herbivory via changes in plant nutritional quality or defenses (Agrawal, 2004). Previous work has examined associations between *C. pitcheri* and native or invasive plants (Girdler et al., 2016; Rand et al., 2015); however, studies examining associations between vegetative cover and weevil damage to *C. pitcheri* are lacking. Alternatively, neighboring plants may indirectly increase damage to a focal plant by increasing the number of herbivores in the vicinity by offering refuge from predation or environmental stress (Dangremond et al., 2010; Orrock et al., 2010), or by providing an attractive food or oviposition resource (Agrawal, 2004; Karban, 1997; White and Whitham, 2000). Spillover feeding from target invasive hosts onto nearby native species is a primary focus of pre-release and post-release biocontrol monitoring programs (Catton et al., 2015; Rand et al., 2006). For example, a closely related native thistle, *Cirsium undulatum,* experienced increased egg load from *Rhinocyllus conicus* weevils when located near the target invasive host, *Carduus nutans* (Rand and Louda, 2004). When biocontrol agents infest native populations that lack nearby alternative invasive hosts, as is the case in this study, it is critical to explore the extent to which nonhost vegetation can affect agent damage.

Plant neighborhoods that do not serve as important food sources for the consumer can influence damage to a focal host by facilitating dispersal. The movement of herbivores between host sites can be strongly influenced by the identity and structure of the intervening matrix (i.e., neighborhood). The bare ground or surrounding vegetation matrix may differentially affect insect immigration and emigration rates (Haynes and Cronin, 2003, 2006) and movement patterns (Cronin, 2003), or interfere with insect orientation, host-finding cues, and host-utilization (Hambäck et al., 2003). However, it is difficult to predict how the surrounding matrix will affect herbivore damage to hosts, considering that studies have found mixed support for neighboring effects: some insects prefer host patches surrounded by bare ground (Kareiva, 1985; Rand, 1999), while others prefer vegetation-surrounded hosts (Haynes and Cronin, 2003; Jonsen et al., 2001). In dune habitats, the bare ground and vegetation matrix can vary across an elevation gradient, which can also affect herbivory (Fretwell, 1977; Louda, 1983; Oksanen et al., 1981). Given the threat that *L. planus* poses to *C. pitcheri*, it is worthwhile to examine landscape factors and nonhost neighbor effects that may contribute to weevil damage.

1.3. Hypotheses and predictions

We conducted a one-year survey of the natural variation in weevil presence, followed by a two-year field experiment at Whitefish Dunes State Park (Wisconsin, U.S.) to test the hypothesis that *L. planus* damage to *C. pitcheri* is influenced by dune elevation and the presence of neighboring American beachgrass (*Ammophila breviligulata* Fern). *Larinus planus* larvae consume developing seeds of *Cirsium* species before dispersal and weevils do not use *A. breviligulata* as a food source or oviposition site. We predict that weevil damage will vary along a dune elevation gradient. Based on patterns from our damage survey, we predict that clipping *A. breviligulata* neighbors at low elevation sites will decrease the susceptibility of *C. pitcheri* to *L. planus* infestation. Insight into the spatial variability of weevil damage within *C. pitcheri* populations may foster ideas to conserve *C. pitcheri* and other rare plants threatened by insects.