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Secondary invasions of noxious weeds associated with control of invasive *Tamarix* are frequent, idiosyncratic and persistent

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ABSTRACT

Control of invasive species within ecosystems may induce *secondary invasions* of non-target invaders replacing the first alien. We used four plant species listed as noxious by local authorities in riparian systems to discern whether 1) the severity of these secondary invasions was related to the control method applied to the first alien; and 2) which species that were secondary invaders persisted over time. In a collaborative study by 16 research institutions, we monitored plant species composition following control of non-native *Tamarix* trees along southwestern U.S. rivers using defoliation by an introduced biocontrol beetle, and three physical removal methods: mechanical using saws, heavy machinery, and burning in 244 treated and 79 untreated sites across six U.S. states. Physical removal favored secondary invasions immediately after *Tamarix* removal (0–3 yrs.), while in the biocontrol treatment, secondary invasions manifested later (> 5 yrs.). Within this general trend, the response of weeds to control was idiosyncratic; dependent on treatment type and invader. Two annual tumbleweeds that only reproduce by seed (*Bassia scoparia* and *Salsola tragus*) peaked immediately after physical *Tamarix* removal and persisted over time, even after herbicide application. *Acroptilon repens*, a perennial forb that vigorously reproduces by rhizomes, and *Bromus tectorum*, a very frequent annual grass before removal that only reproduces by seed, were most successful at biocontrol sites, and progressively spread as the canopy layer opened. These results demonstrate that strategies to control *Tamarix* affect secondary invasions differently among species and that time since disturbance is an important, generally overlooked, factor affecting response.

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1. Introduction

Ironically, human actions devoted to control of invaders often create additional anthropogenic disturbance that can result in secondary invasions, defined here as the proliferation of non-target invasive species, frequently referred as to weeds, after a complete or partial local eradication of the first, targeted alien (Pearson et al., 2016). The threat of secondary invasions is very high in most ecosystems, as these often contain multiple, subordinate exotic, potentially invasive species which can respond quickly once competitive pressure by the primary species is removed (Hulme and Bremner, 2006; Hulme et al., 2013; Kuebbing et al., 2013). For example, removal of invasive tree canopy layers may increase light resources in the understory and allow the proliferation of shade-intolerant invasive grasses that remained subdominant in the system before human intervention (e.g., Loo et al., 2009). However, soil disturbance during removal of targets has also been found to suppress secondary invaders one year later (Sher et al., 2008). Secondary invasions therefore represent an opportunity to understand how exotic species respond idiosyncratically to a given management-related disturbance. Unlike the initial invasion, the new disturbance will be deliberately imposed by humans when controlling the first invader, and therefore, easier to control in experimental designs. In a recently published meta-analysis of 60 cases of secondary plant invasions, Pearson et al. (2016) found that their severity was positively correlated to reductions in the target alien, but not to control method or intensity of disturbance. However, the authors also found that specific case studies revealed that management itself can foster secondary invasions.

Control of invasive *Tamarix* spp. (tamarisk, saltcedar) in riparian systems is an ideal case to study the effects of different types of anthropogenic disturbance on secondary invasions of different weeds. Eurasian species of the genus *Tamarix* and their hybrids have invaded extensively along southwestern U.S. rivers since they were introduced in the early 1800s for ornamental, windbreak and erosion control purposes, and are now the third most frequent and second most abundant in cover of riparian trees in western North America (Friedman et al., 2005). Although *Tamarix* were establishing and spreading before the advent of the dam-building era in the western U.S. (Birken and Cooper, 2006), their naturalization and rapid expansion was partly facilitated by hydro-geomorphic regime alterations caused by dam regulation and exploitation of water resources in the twentieth century (Stromberg et al., 2007; Merritt and Poff, 2010). Once established, *Tamarix* can contribute further to riparian habitat alteration, for example by altering abiotic and biotic conditions (e.g., floodplain aggradation, salt accumulation, change of microbial soil communities and light availability), which has led to its characterization as both passenger and driver of ecosystem change (Johnson, 2013).

Efforts to control *Tamarix* invasion in the U.S. have been very intense in recent decades. Years of trials with diverse mechanical, chemical and biological techniques have gradually kept stable and even reduced *Tamarix* populations in many locations (Harms and Hiebert, 2006; Belote et al., 2010; Hultine et al., 2010; Ostoja et al., 2014, Kennard et al., 2016; González et al., 2017). However, even if *Tamarix* is successfully controlled, legacy effects on the ecosystem combined with the conditions that allowed the initial invasion may favor the establishment and proliferation of several other exotic weeds (Shafroth et al., 2008; Hultine et al., 2010; González et al., 2017).

Despite its great potential for helping to understand biological invasions and informing management of riverscapes, quantitative reports of the severity of secondary invasions in post *Tamarix*-treated riparian systems remain local, often from single sites or river reaches (e.g., Sher et al., 2008; Ransom et al., 2012; Douglass, 2013; Ostoja et al., 2014; Kennard et al., 2016) or with too few site replicates to evaluate the scale of their impact at a regional level (Harms and Hiebert, 2006; Bay and Sher, 2008). This contrasts to a significant effort by the scientific community to investigate the spatial scope of primary invasions, notably of *Tamarix* spp. and *Elaeagnus angustifolia* (Russian olive), in southwestern U.S. rivers (e.g., Friedman et al., 2005; Nagler et al., 2011; Jarnevich et al., 2013; McShane et al., 2015). In addition, studies exploring the causes underlying the existence and severity of secondary invasions in southwestern U.S. rivers following *Tamarix* control are surprisingly rare. In particular, the weed-specific responses to the wide array of existing techniques for *Tamarix* control remain largely unexplored. To our knowledge, only Sher et al. (2008) found a (negative) relationship between the intensity of control related-disturbance and response of one exotic weed: *Bromus tectorum* (cheatgrass), but their observations were limited to only one year after removal. In one study including 244 removal sites, González et al. (2017) found that some physical removal methods (i.e., burning and mechanical removal using heavy machinery) created site conditions more prone to invasions of exotic forbs than saw-cutting and biocontrol, but did not make any distinction between species of invaders.

With few long-term studies, even less attention has been placed on the persistence of secondary invasions over time (Pearson et al., 2016). This has important consequences for management, as fewer resources for eradication should be allocated if the weeds will disappear naturally in the absence of further disturbance of the same type or intensity that facilitated their arrival and/or proliferation. In the case of *Tamarix* control, González et al. (2017) found that the abundance of exotic weeds decreased in ten sites that received only biological control over three years of monitoring but was stable or even increased in sites subjected to physical removal methods (mechanical cutting, heavy machinery and burning) and when larger spatial (i.e., river catchment) and temporal (i.e., 5 years on average) scales were taken into account. They suggested that the inherently disturbed riparian systems, the weak recovery of competing native species, and the inefficiency of follow-up herbicide treatments could explain the persistence of weeds. However, the specific responses of the multiple secondary invaders over time were not explored.

Here, we assessed vegetation response across *Tamarix* control treatments and selected the exotic weed species with the highest potential to become secondary invaders in the context of *Tamarix* control along southwestern U.S. rivers. We used this information to answer the following questions: 1) How does control method influence the severity of secondary invasions? 2) How does the severity of secondary invasions change over time and does the temporal trajectory differ as a function of control method?

2. Materials and methods

2.1. Study sites

Vegetation response after *Tamarix* control was monitored in 244 sites distributed on floodplains and streambanks of two of the largest catchments in the American West, the Colorado River and Rio Grande, and some of their major and minor tributaries (Fig. 1). The sites spanned ca. 350,000 km^2 across six U.S. states: Arizona, California, Colorado, Nevada, New Mexico and Utah. To be included in the study, a site must have been subjected to *Tamarix* control by at least one of the following four methods: prescribed or accidental burning of *Tamarix* stands ("burn", 33 sites); mechanical removal using heavy machinery such as root plows, mowers or bulldozers ("heavy machinery", 57 sites); or using chain or hand saws ("cut", 99 sites), and defoliation by the biocontrol beetle, *Diorhabda* spp. ("biocontrol", 55 sites). When sites were subject to more than one method, the site was labeled with the method of the highest disturbance (i.e., burn > heavy > cut > biocontrol). It is important to note that they are different *types* of disturbance, with different effects on secondary plant invaders. Biocontrol, for example, does not cause soil physical disturbance but its effects on vegetation are cumulative over time with successive defoliations. Burning was considered to have the greatest disturbance because it affects both chemical and physical fluxes of nutrients (Sher and Hyatt, 1999; González et al., 2017), even though the effects on soil physical