CHAPTER 28

Tamarix Biological Control in North America

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NON-TECHNICAL SUMMARY

The biological control program against *Tamarix* spp. (tamarisk/saltcedar; Tamaricaceae) was initiated in the 1970s to reduce negative impacts of this invasive Old World shrub to riparian biodiversity and ecosystem function in western North America. Field releases of host-specific leaf beetles (Chrysomelidae) in the genus *Diorhabda* were initiated in 2001, with significant establishment and widespread defoliation observed roughly two years after open releases. What followed were a variety of complex interactions among invasive *Tamarix*, its guild of herbivores including *Diorhabda* spp., and the physical and biotic environment, which varied across the western U.S. project area. Defoliation yielded sustained lower evapotranspiration and opened canopies, allowing increases in desired vegetation in some areas, while in other areas beetle establishment failed for reasons that included less-suitable host species, mismatches of environmental cues with diapause development of the beetle, and predation by generalist insectivores. In some regions, such as Texas, agent populations were short-lived, resulting in lack of sustained *Tamarix* suppression. In other areas, beetle populations reached initial epidemic densities but then declined to moderate levels with patchy subsequent defoliation and diminished target mortality. These short-term dramatic impacts to invasive *Tamarix,* but limited sustained control, suggest potential value in releasing additional host-specific agents, some of which have already been studied and readied for petitioning for release.

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Stakeholder enthusiasm for the biocontrol program was high in some locations and allowed reduced expenditures for conventional weed control. At the same time, perceived threats to sensitive wildlife species, particularly the endangered southwestern willow flycatcher (*Empidonax traillii extimus*) in Arizona, New Mexico, and Utah, resulted in legal actions terminating federal involvement in the biocontrol program nationally. A strategic approach to ecological restoration targeting ecosystems with high potential for enhanced wildlife habitat could help resolve these conflicting issues, but progress is currently inhibited by a lack of political support and financial resources, suggesting that renewed collaboration of interested parties across disciplines is needed to more fully achieve long-range benefits.

HISTORY OF INVASION AND NATURE OF PROBLEM

Introduction

Exotic shrubs in the genus *Tamarix* (also known as saltcedar, tamarisk; Tamaricaceae, **Fig. 1**) were introduced to North America in the 1800s and established invasive populations along most waterways in arid western North America in the early 1900s. Ecological damage of sensitive riparian ecosystems due to the dominance of *Tamarix* provided the incentive to develop a biological control program, conducted with multi-agency and stakeholder input (Stenquist, 2000). We now (2022) mark the 20th anniversary of the first open-field releases of the chrysomelid beetle *Diorhabda carinulata* as a *Tamarix* biocontrol agent. Conflicting and contrasting outcomes are apparent at this stage of the program. First, the widespread defoliation and decline of *Tamarix* that followed have made the project one of the most successful and visually stunning in the history of invasive plant biocontrol. At the same time, lack of *Diorhabda* establishment and impact in many regions show that we have far to go to achieve desired results throughout the *Tamarix* range in North America. Second, the highly visible suppression of *Tamarix* and transformation of riparian corridors following defoliation events in certain locations has, among some, resulted in the notion that biocontrol has brought about a decline in

Figure 1. Tamarisk, *Tamarix* spp. (Tamaricaceae). (Eric Coombs, Oregon Department of Agriculture, Bugwood.org CC BY-3.0 US)

riparian ecosystem services, particularly habitat for an endangered bird subspecies. Biocontrol practitioners are presented with the challenge of tracking success while defusing negative perceptions of a beneficial program (Bean and Dudley, 2018).

Despite controversy, it is broadly recognized that *Tamarix* biocontrol is here to stay and should be integrated into riparian management and restoration plans, an approach with nearly universal support among natural resource managers (Dudley and Bean, 2012). In this report, we update program status and success in *Tamarix* suppression. We also provide suggestions for defusing controversy and keeping a long-term project moving in a productive direction. This is not an exhaustive treatment of the topic, as there are reviews that provide an overview of the *Tamarix* invasion and the biological control program (Dudley et al., 2000; Dudley and DeLoach, 2004; Shafroth et al., 2005; Bateman et al., 2010; DeLoach et al., 2011; Dudley and Bean, 2012; Knutson et al., 2012, 2019; Bean et al., 2013a; Hultine and Dudley, 2013; Dudley et al., 2017; Bean and Dudley, 2018; Pratt et al., 2019).

The Species Invasion

Tamarix is a complex of >50 semi-deciduous shrub species (and some arboreal, evergreen species, e.g., *Tamarix aphylla* or athel) originating in Eurasia and Africa (Baum, 1978). In their original ranges, these plants are sources of fuelwood, construction material especially for furniture, and of modest value as livestock forage (especially goats; Abou Auda, 2010). In its native range, *Tamarix* can form extensive and ecologically important stands that provide structural and resource values to wildlife (van Zeist, 1985; Bunbury et al., 2020).

While its path of transport into North America (and other invaded regions with similar climates, e.g., Argentina, South Africa, Australia) is uncertain, by the late-1800s tamarisks were present as horticultural plants and promoted for erosion control across the southwestern United States (Robinson, 1965; Everitt, 1998). With the widespread regulation (via dams and canals) of western rivers in the early 1900s, tamarisk took advantage of the altered hydrologic conditions to proliferate into riparian areas, reservoir margins, seeps, and wetlands. Its expansion was facilitated by reduced competition from native cottonwood-willow vegetation that depended upon ample water and natural flooding regimes for regeneration.

Nature of the Problem

By the middle of the 20th century, *Tamarix* spp. and hybrid forms (Gaskin and Schaal, 2002) occupied roughly 1.5 million acres (607,000 ha) of the western United State (Robinson, 1965; Everitt, 1998; Nagler, 2011) and displaced iconic cottonwood-willow (*Populus* spp., *Salix* spp.) riparian woodlands and other vegetation types, including mesquite bosque, riparian scrub, and saltgrass/halophytic scrublands. Tamarisk plants in northern latitudes tend to be moderately slow-growing shrubs (Sexton et al., 2006), while those in southern regions are fast-growing where adequate moisture is available. In these regions, they are able to reproduce within one to two years and achieve large stature, often as spreading ‘trees’ greater than 5 m (16 ft) in height. The expansion of this invader was facilitated by the plants being highly plastic in their growth and reproductive phenology and able to tolerate reduced water availability, soil salinization, and other harsh conditions that reduce suitability to sustain native vegetation (Busch and Smith, 1995; Glenn and Nagler, 2005).

WHY CONTROL *TAMARIX*?

Tamarix invasion poses numerous environmental and economic problems (see reviews of Everitt, 1998; Dudley et al., 2000; Shafroth et al., 2005), which increase greatly as the plant comes to dominate riparian ecosystems. Some of the physiological and morphological properties of *Tamarix* lead to alterations of riparian ecosystem function in ways that favor itself over native species, resulting in *Tamarix* acting as a driver of ecosystem change (Johnson, 2013) and leading to near monocultures. For instance, a serious impact of *Tamarix* invasion is increased frequency and extent of wildfire (Busch, 1995; Drus, 2013). Fire is uncommon in native-dominated riparian vegetation in the region (Verkaik et al., 2013). However, *Tamarix* foliage ignites readily and burns with high intensity when senescent and dry, as well as when green and healthy (Drus et al., 2013). This high combustibility turns riparian areas into conduits for, rather than barriers to, wildfire spread (Lambert et al., 2010). Burn severity increases with *Tamarix* density, with a concomitant increase in mortality of associated native woody plants, such that fire drives a positive feedback loop that can lead to *Tamarix* monocultures (Drus, 2013).

In addition to being fire-adapted, other properties of *Tamarix* allow it to outcompete native vegetation. These include high evapotranspiration rates that deplete shallow groundwater (Smith et al., 1998), inhibition of native plant establishment as a consequence of impenetrable litter, and desiccation and salinization of soils by throughfall and deposition of salt-laden litter (Shafroth et al., 1995). River channels are altered by increases in both sedimentation and erosion where dense stands interfere with stream flows (Graf, 1978; Birken and Cooper, 2006). Impacts of *Tamarix* on nutrient cycling and mycorrhizal ecology are just beginning to be understood, but they are substantial and contribute to the decline of native species (Meinhardt and Gehring, 2012, 2013). These factors interact, with the consequence that *Tamarix* establishes a positive feedback system favoring its own dominance, exacerbating the ecological and economic impacts.

Tamarisk can have some beneficial attributes in its invasive range, e.g., stabilizing dry river channels where native vegetation has declined (Norris and Grim, 2022), offering shade for humans, livestock, and wildlife, and providing some food resources and habitat for wildlife (Sogge et al., 2008; Mahoney et al., 2022). Even so, the modest ecosystem services provided by the plant in the invaded range are a poor substitute for those of a native plant assemblage (Dudley and Bean, 2012). *Tamarix* offers lower quality habitat to wildlife than does native vegetation, presenting a simplified vegetative structure and altering understory conditions for birds, reptiles, and other taxa (Ellis, 1995; Shafroth et al., 2005; Bateman et al., 2013). Widespread displacement of native riparian vegetation by *Tamarix* spp. is even cited as a causal factor in declines of sensitive riparian-dependent species, including the endangered southwestern willow flycatcher (SWFL; *Empidonax traillii extimus*) in the desert Southwest (Suckling et al., 1992; DeLoach et al., 1996).

By altering stream flows and channel morphology, *Tamarix* also changes in-stream properties in ways detrimental to native fish, including endangered and threatened species (Keller et al., 2014). Fish, aquatic invertebrates, and salt marsh fauna are also negatively affected by surrounding *Tamarix* dominance via reduced resource value or altered structural habitat (Kennedy and Hobbie, 2004; Going and Dudley, 2008; Moline and Poff, 2008; Whitcraft et al., 2008).

Historically, the primary impact of concern was depletion of water resources, particularly in the arid Southwest, owing to the high evapotranspiration rates (ET) of *Tamarix* and its ability to maintain photosynthesis and water extraction even in non-saturated soils (Sala et al., 1996; Cleverly, 2013). While precision in estimating water salvage from *Tamarix* control is difficult to attain (Shafroth et al., 2010), ET owing to *Tamarix*'s high areal cover is certainly a factor in water conservation in western North America (Shafroth et al., 2005; Hultine and Bush, 2011). Large-scale tamarisk control efforts have been implemented since the 1920s, but with limited effectiveness and sustainability. Major removals of riparian vegetation for putative water 'salvage' in places like the Gila River (Orr et al., 2017a) further facilitated *Tamarix*' expansion in human-altered habitats due to its tolerance of degraded conditions and capacity to outcompete native plants under such conditions (Sher and Marshall, 2003; Shafroth et al., 2005; Hultine and Dudley, 2013). With a drying climate and regional reservoirs at historically low levels, the interest in removing tamarisk for water conservation remains as important as ever, with agencies and political representatives seeking more effective and less costly means for doing so (Hultine et al., 2015).

PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

Overview of the *Tamarix* Biological Control Program

Foreign exploration to find potential biocontrol agents for tamarisk was initiated in the 1970s and expanded in the late 1980s and 1990s (Pemberton and Hoover, 1980; DeLoach et al., 1996). From over 300 arthropods considered host-specific to the family Tamaricaceae (DeLoach et al., 1996), host range testing was completed for three candidate agents: the weevil *Coniatus tamarisci* (Curculionidae), the mealybug *Trabutina mannipara* (Pseudococcidae), and a leaf beetle considered originally to be *Diorhabda elongata carinulata* (Chrysomelidae) from Central Asia (**Fig. 2**) (DeLoach et al., 1996, 2004). The *Diorhabda* beetle was chosen for further development owing to its host specificity, ease of handling, rapid growth and reproduction, and substantial host impact via feeding on *Tamarix* green tissues and subsequent foliage desiccation (Lewis et al., 2003; DeLoach et al., 2004, 2011; Pattison et al., 2011).

Figure 2. Tamarisk beetle, *Diorhabda* spp.: (a) adult; (b) larva. (a: Robert D. Richard, USDA-APHIS-PPQ; b: William M. Ciesla, Forest Health Management International; a,b: Bugwood.org CC BY-3.0 US)

At the outset, broad support was garnered through involvement of private stakeholders, federal, state, and local agencies, Native American tribes, university scientists and nonprofit groups organized into the Saltcedar Biological Control Consortium (SBCC) (Stenquist, 2000; DeLoach et al., 2004). The SBCC provided an instrument to address the needs of biocontrol end-users and evaluate and subsequently promote biocontrol as an option for *Tamarix* control. The SBCC goals included long-term monitoring and follow-up restoration, which were strongly advocated for as essential components of *Tamarix* biocontrol (Stenquist, 2000). As the program moved from host range testing to implementation, the SBCC proved invaluable in regional development and coordination of release and monitoring efforts.

The biocontrol program increased in complexity with the development and release of additional geographical ecotypes of what was then believed to be a single species, *Diorhabda elongata*, but which was subsequently reclassified as a species complex specializing on *Tamarix* (Tracy and Robbins, 2009). To suppress *Tamarix* in regions where the Central Asian *Diorhabda* species, (now classified as *Diorhabda carinulata*, i.e., the northern tamarisk beetle) had not been successful, three other species were introduced. The more southern-adapted species were (1) *Diorhabda carinata* (the larger tamarisk beetle) from eastern Europe and western Asia, (2) *Diorhabda sublineata* (the subtropical tamarisk beetle) from North Africa and the western Mediterranean basin, and (3) *D. elongata* (the Mediterranean tamarisk beetle) from the eastern Mediterranean basin (Tracy and Robbins 2009; Dalin et al., 2010; DeLoach et al., 2011; Bean et al., 2013a).

This aspect of the program also proved successful, with widespread *Tamarix* defoliation occurring across Texas and neighboring states (Pattison et al., 2010; DeLoach et al., 2011; Michels et al., 2013), although populations of the three additional species have declined dramatically following initial successes (Knutson et al., 2019), as discussed later.

Other *Tamarix*-specific herbivores unintentionally transported to North America can have significant impact on their hosts as well as interacting with intentionally released agents; these herbivores include a widespread leafhopper, *Opsius stactogalus*, and the scale insects *Chionaspis etrusca* and *Chionaspis gilli* (Wiesenborn, 2005; Louden, 2010; Uhey et al., 2020). More interestingly, the splendid tamarisk weevil, *Coniatus splendidulus* (a foliage-feeding weevil related to the host-specific species *C. tamarisci* that was originally considered for release [Fornasari, 1997]) was first detected in central Arizona in 2006 and subsequently spread through the southwestern states (Eckberg and Foster, 2011; Dudley et al., 2017). Pathways of introduction for these insects are unknown, but these taxa have the potential for synergistic and in some cases antagonistic interactions with *Diorhabda* species (e.g., Swope and Parker, 2012).

The *Diorhabda* Field Release Program

Initial field trials with *D. carinulata* were conducted in 1999 (one Colorado site was initiated in 1998) as a multi-site experimental caging study involving 10 sites in six states (Nevada, Utah, Colorado, Wyoming, Texas, and California) to evaluate capability of this species to develop and reproduce across the exceptionally broad geographic and climatic range of invasive *Tamarix* (Dudley et al., 2001; DeLoach et al., 2004). It is notable that cage studies were not conducted in areas where the endangered southwestern subspecies of willow flycatcher was known to nest in *Tamarix*. This was part of the plan to delay *Tamarix* biocontrol in areas where the shrub may provide limited ecosystem services, allowing restoration to proceed in advance of *Tamarix* decline (Stenquist, 2000).

Establishment process and dispersal

Figure 3. New release of northern tamarisk beetles, *Diorhabda carinulata.* (A. Gaffke, Montana State University)

At the outset of the program, details were unknown regarding release protocols, such as numbers of beetles required for establishment, timing of releases, and optimal storage conditions before release, and releases were further limited by the number of beetles available at the time (**Fig. 3**). The initial release made at the (later, successful) Humboldt Sink site in Nevada was of 1,400 beetles (Carruthers et al., 2008). Later the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA-APHIS) recommendation was for releases of 2,000 adult beetles (Kauffman, 2005). The Colorado Department of Agriculture now recommends 5,000 adult beetles as the minimum number for establishment (Kennard et al., 2016). More important than number released is the physiological state of the released beetles. Adult *D. carinulata* are more active and likely to be flying in the late morning and through the afternoon (Bean et al., 2007a), when releases should be avoided to minimize flight losses (Cossé et al., 2005; Bean et al., 2013a). Beetles collected late in the season are destined for reproductive diapause and are unsuitable for initiating establishment (Bean et al., 2007b). Establishment success can be enhanced by ensuring that beetles are not greatly stressed, as they might be under pre-release conditions typically used for biocontrol agents (cold, dark, and crowded). Since the reproductive and dispersal behavior of *Diorhabda* species is mediated by a male-produced pheromone blend (Cossé et al., 2005), conditions that inhibit production of the pheromone severely diminish establishment efficacy (Gaffke et al., 2020). Distribution of reproductive beetles, handled with minimum disturbance, and released in quantities exceeding 5,000 adults is recommended for establishment. In addition, use of the aggregation pheromone at releases sites enhances establishment (Gaffke et al., 2020).

Where *Diorhabda* species have successfully established and expanded their ranges, the highly visible defoliation has attracted substantial attention (**Fig. 4**); however, most releases across the western United States did not result in agent establishment (Bean et al., 2013b). Establishment was most dependable where tamarisk stands were large, usually greater than 100 plants, in a near-monoculture and contiguous state, and located north of approximately 38°N latitude (Bean et al., 2013a). Initially, field colonies of beetles were localized with only limited adult dispersal to adjacent trees and generally following the stand's edges, including river margins, followed by gradual expansion outward into closed stands (Pattison et al., 2011). *Diorhabda* adults disperse over both short and long distances. The success of this dispersal pattern is facilitated by the male-produced aggregation pheromone, which stimulates swarms of beetles to move small distances (1–30 m [3–98 ft]) when food is abundant, and long dispersal distances (ranging from several to over 100 km [62 mi] per year) when food sources become limiting (Cossé et al., 2005; Nagler et al., 2014; Wenjie et al., 2017; Knutson et al., 2019). The aggregation pheromone facilitates population regrouping after longer-distance dispersal (Cossé et al., 2005; Gaffke et al., 2018, 2019).

Figure 4. Defoliation of tamarisk from tamarisk beetle feeding (brown foliage) adjacent to healthy, undamaged native plants (green foliage). (William M. Ciesla, Forest Health Management International, Bugwood.org CC BY-3.0 US)

Initially, the dispersal rate of *Diorhabda* spp. was predicted to be about 1–2 km (0.6–1.2 mi) per year. However, observed dispersal distances outpaced this prediction, with Utah and Colorado populations of *D. carinulata* now having dispersed as far south as the Mexico-U.S. border (D. Bean and T. Dudley, unpub. data). Remote sensing of defoliation patterns along western river corridors has enabled tracking of dispersal and impact (Nagler et al., 2012, 2014; Wenjie et al., 2017; Bedford et al., 2018).

Constraints on establishment

Many *Diorhabda* releases failed to establish or established weakly, disappearing after one or two years. Some such failures appear to be caused by biological constraints. Other factors restricting regional implementation were policy-related, particularly the cessation of permitting, and other regulatory roadblocks. Below we describe both types of constraints.

(1) Phenological mismatch. This problem was an important reason for failures of the northern-adapted *D. carinulata* at southern locations in the western United States, due to mismatched cues for diapause induction (Lewis et al., 2003; Bean et al., 2007b). Intuitively, the warmer temperatures and longer growing season in the south should promote a long *D. carinulata* reproductive season with multiple generations, but this was not the case because declining photoperiods induce reproductive diapause. Day lengths that are normally encountered in midsummer at higher latitudes (approximately 44°N or higher, the latitude of origin in Central Asia) indicate that winter conditions will soon follow. However, they induced diapause at the wrong time of the year at lower, more southern latitudes, causing beetles to enter diapause prematurely. The shorter summer day lengths combined with longer growing seasons resulted in phenological mismatches between *Tamarix* and *D. carinulata* at southern latitudes (Hultine et al., 2015), limiting the useful range of *D. carinulata* to areas north of about the 38th parallel (Bean et al., 2007b). This phenological asynchrony resulted in a commonly observed pattern in which high initial beetle population densities were followed by major declines (DeLoach et al., 2011). The phenological mismatch constraint was circumvented in parts of the southwestern United States by using the southern-adapted *Diorhabda* species, for which diapause induction was triggered at shorter day lengths, allowing beetles to continue feeding and reproduction later into the season (Milbrath et al., 2007; Dalin et al., 2010). These southern species also had a greater chance of success because of their multivoltine life histories, which they exhibited at more southern latitudes (Dalin et al., 2010). In addition, as *D. carinulata* populations moved incrementally southward in the Colorado River Basin, their day length cues for diapause evolved to become shorter and better-matched to southern ecological settings, and this rapid evolution may have facilitated population recovery within the new range (Bean et al., 2012).

(2) Host utilization. Mismatches between the target plant and the agent have been an impediment to establishment in some areas. Five species of *Tamarix* were targeted by the biological control program. Of these, three species, *T. parviflora*, *T. ramosissima*, *T. chinensis*, as well as *T. ramosissima* x *T. chinensis* hybrids, were the most commonly encountered forms in the western United States. Beetles failed to establish at field sites in coastal California drainages due to a host plant mismatch between *D. carinulata* and *T. parviflora*, which is the target species at many Californian sites (Dudley et al., 2012). This form of *Tamarix* is from the Mediterranean Basin, while *D. carinulata* is from Central Asia and did not coevolve with this host. Consequently, this beetle species may not perceive a chemical cue that *T. parviflora* is a suitable host, as further suggested by cage experiments in which oviposition by *D. carinulata* was rare on *T. parviflora* (Dalin et al., 2009). In contrast, one river drainage dominated by *T. parviflora* has supported a population of *D. elongata* (also from the Mediterranean region) for fifteen years, although damage to the plants has not resulted in suppression (Pratt et al., 2019). Hybridization between *T. ramosissima* and *T. chinensis*, resulting in a latitudinal gradient with a higher representation of *T. ramosissima* in northern populations, can also affect the performance of *D. carinulata* as well as its impact in the field (Williams et al., 2014; Long et al., 2017). Athel (*T. aphylla*) was similarly avoided by beetles in field experiments, although its hybrid form with *T. ramosissima* proved viable as a host (Moran et al., 2009).

(3) Predation. Invertebrate predators also negatively affected some *Diorhabda* populations on the southern plains (Berro et al., 2017; Knutson and Campos, 2019). In particular, the red imported fire ant, *Solenopsis invicta*, was an efficient predator on *Diorhabda* pupae in the leaf litter (Knutson and Campos 2019), which may limit the range of its use to areas outside of the range of fire ants. Cage trials indicated that, where common, the exotic Argentine ant, *Linepithema humile*, also restricted the ability of *D. carinulata* to establish (Dudley et al., 2012). Many species of generalist arthropods (even land crabs) routinely feed on both adults and larvae of *Diorhabda* species and likely limit their capacity to build up sufficiently large populations to persist at release sites (Moran, 2010; Strudley and Dalin, 2013).

Larvae of *D. carinulata* were subject to predation by arboreal ants in the genus *Formica* at field sites in eastern California and western Nevada (Herrera, 2003). Similarly, thatch ants of the *Formica* 'rufa' group appeared to be the primary reason for the failure of establishment of *D. carinulata* following open release at the Owhyee River site in southeastern Oregon (T. Dudley, unpub. data). In many cases, insecticide treatments to reduce ant populations were helpful for promoting establishment of *Diorhabda* species. Studies have also indicated that the presence of predators, particularly *Formica* ants, results in the cessation of the emission of the aggregation pheromone by male *D. carinulata* beetles (A. Gaffke, unpub. data). This means populations of *D. carinulata* will not be retained in patches of *Tamarix* with high densities of ants, limiting the biocontrol potential of the agent in these instances.

(4) Regulatory constraints to the *Tamarix* biocontrol program. The regulatory roadblocks to beetle establishment have stemmed largely from a moratorium on permitting of interstate movement of *Diorhabda* species or holding *Diorhabda* species in culture, which included revoking all existing permits (APHIS, 2010). This drastic measure came about as the result of a lawsuit filed by two environmental groups, the Center for Biological Diversity and the Maricopa Audubon Society, with the USDA-APHIS and the U.S. Fish and Wildlife Service as defendants. The issue was movement of beetles into areas where they could affect SWFL nesting success through defoliation of *Tamarix*. As a result, funding was cut for monitoring *Tamarix* and *Diorhabda*, and implementation efforts terminated with the threat of a $250,000 fine should someone be found in violation of the moratorium (APHIS, 2010).

The moratorium has not only limited interstate movement of beetles for new releases but has also eliminated the possibility of research to determine if other *Diorhabda* species would be better for distribution in areas where *D. carinulata* has failed to thrive. As an example, no further work could be done to test southern-adapted *Diorhabda* species in the Arkansas River Basin in Colorado, far from areas of concern where SWFL are known to nest in *Tamarix*. Overall, the moratorium has affected almost all aspects of tamarisk biocontrol and has made it difficult or impossible for biocontrol practitioners to carry out field trials needed to test factors affecting establishment and impact. The initial and follow-up lawsuits have been described elsewhere (Bateman et al., 2010; Dudley and Bean, 2012; Bean and Dudley, 2018), but in summary it is clear that the moratorium has resulted in a breakdown of the biocontrol program at a national level with little or no impact on the natural movement of beetles southward (Dudley et al., 2017).

Regional Patterns in Establishment, Impacts, and Controversies

One of the difficult aspects of summarizing the *Tamarix* biocontrol program is that there were major regional differences in implementation, monitoring, outcomes, and the level of controversy, making general conclusions impractical. We here highlight some of the regional patterns that we feel are instructive from both biological and regulatory perspectives.

The Intermountain West

The implementation of *Tamarix* biocontrol using *D. carinulata* has been most heavily concentrated in the Intermountain West, which includes the Great Basin Desert, the northern Rockies, and the upper

Colorado River Basin. Initial experimental releases were made, and establishment monitored, at three sites in the Great Basin Desert, and these provided collection sites for further widespread distribution, including implementation programs conducted by local and state officials in Utah (Dudley and Bean, 2012) and Colorado (Kennard et al., 2016).

Establishment of *D. carinulata* in Wyoming and Montana required release of more agents than was required at the more southern sites, with 27,000 adults released before establishment was achieved at the Lovell, Wyoming site (DeLoach et al., 2011). Releases of several thousand beetles in 2007 failed to establish along Fort Peck Reservoir, Montana (Deloach et al., 2011). Releases began again in the state of Montana in 2016, using beetles that had naturally dispersed into the state from established populations in Wyoming. New field releases in Montana, especially when made in conjunction with application of the aggregation pheromone, have now resulted in establishment, although population density has remained low (Gaffke et al., 2020). The number of generations of *D. carinulata* is 1–2 per growing season in Montana and Wyoming, limiting their impact. In areas where growing season limits the biocontrol potential, lures utilizing *D. carinulata* aggregation pheromone are being used to purposefully aggregate the beetles and increase their impact (Gaffke et al., 2018, 2019, 2021).

In western Colorado, *Tamarix* plant mortality from *D. carinulata* herbivory exceeded 30% on average, with some monitoring sites reaching 50% and with widespread biomass reduction exceeding 70% (Kennard et al., 2016). While the overall impact of *D. carinulata* is high throughout western Colorado, beetle populations fluctuate with widespread defoliation common during some years but absent in others. Noting the success of *D. carinulata* in suppression of *Tamarix* in western Colorado, riparian ecosystem managers have incorporated biological control into larger-scale plans for invasive species management on the Dolores River as well as the Yampa and Green Rivers within Dinosaur National Monument (Williams, 2016; Bean et al., 2021). Large defoliating populations of *D. carinulata* established in western Colorado but have failed to become well established in the eastern part of the state, despite a massive release program conducted within the Arkansas River Basin (Bean, 2017).

Successful establishment followed open releases in 2001 at three sites, namely the Sevier site in Utah and two sites in western Nevada (Dudley et al., 2001). The Humboldt Sink site in Nevada was the first of the *Tamarix* Biocontrol Program to achieve biocontrol agent establishment, with approximately 1 ha (2.5 acres) of monotypic *T. ramosissima* defoliated in 2002, which expanded to 100 ha (247 acres) in 2003. Beetles continued to disperse across northwestern Nevada within the Humboldt River Basin and into the adjacent Carson Basin, while from a separate release, beetles defoliated several thousand hectares of tamarisk in the adjacent Walker River Basin (Carruthers et al., 2008; Pattison et al., 2011).

In Utah, there was a delay of over two years between *D. carinulata* releases and substantial defoliation within the Sevier River terminal basin (DeLoach et al., 2011). The Sevier site served as a source for beetles distributed throughout Utah (Bateman et al., 2010; Henry et al., 2018). The initial releases at the Sevier site were of *D. carinulata* collected from Chilik, Kazakhstan, whereas the other original release sites all received beetles from Fukang, China (Tracy and Robbins, 2009).

Lower Colorado River Basin

The Washington County Public Works Department in St George, Utah, transferred *D. carinulata* from the Sevier River site to the upper Virgin River in 2006, which is the primary source of beetles moving into the lower Colorado River (Bateman et al., 2010). Outbreak populations developed by 2008, with widespread defoliation and dispersal into other watersheds (Dudley and Brooks, 2011). Subsequent dispersal, facilitated by the evolution of better adapted phenology cues (Bean et al., 2012), led to the incremental expansion of the beetle population over the next four years through the length of the Virgin River watershed to Lake Mead (Bateman et al., 2010; Dudley and Bean, 2012).

While the release at the upper Virgin River was by far the most publicly visible route of biocontrol introduction into the lower Colorado River Basin, it wasn't the only one. Beetles moved down the Colorado River from established sites upstream of Grand Canyon National Park and most likely reached the shores of Lake Mead from that direction. In addition, the genetic signature of beetles in the Virgin River Valley revealed an avenue of introduction through the Muddy River drainage that originates in central Nevada. Since the Chilik ecotype was introduced into the St. George area, the occurrence of the Fukang ecotype near the confluence of the Virgin and Muddy Rivers pointed to a Nevada origin for a portion of the population in the lower Virgin River Valley (Stahlke et al., 2022).

The upper Virgin River was the first location where tamarisk biocontrol overlapped known nesting of the endangered SWFL. The interactions of tamarisk biocontrol and endangered species are covered in more detail elsewhere (Bateman et al., 2010, 2013; Paxton et al., 2011), but the perceived loss of nesting habitat in the St. George area resulted in the 2009 lawsuit filed by the Center for Biological Diversity in an attempt to stop the program and, possibly more productively, to pressure federal agencies to support riparian wildlife habitat restoration (Bean and Dudley, 2018). In contrast, the Virgin River Conservation Partnership, a working group of agencies and stakeholders formed to address resource issues in this watershed (including flood risk, water conservation, sensitive species protection, and reducing the impacts of invasive species [CCDCP, 2000; USACE, 2008]), were enthusiastic about the arrival of *Diorhabda* beetles in the watershed, as were participants in the Clark County Nevada Desert Conservation Program (DCP, 2011). There was a widely publicized instance where *D. carinulata* defoliated a *Tamarix* shrub in which a SWFL had nested, causing overheating of the brood and failure to fledge. On the other hand, SWFL returning to the Virgin River have been shown to switch from *Tamarix* to native plants for use as nesting substrate when presented with the option. This observation, along with the continued loss of flycatcher nesting territories due to fires promoted by *Tamarix* (Finch et al., 2002; Dudley and Brooks, 2011), provides compelling evidence for *Tamarix* suppression and riparian restoration (Dudley et al., 2012, 2017). This ongoing controversy appears to have no resolution in the absence of a concerted effort by both sides to support riparian restoration efforts and the recovery of habitat dominated by native vegetation, which is far superior to the current tamarisk monocultures that characterize some reaches of the Virgin River as well as the Colorado River downstream of Lake Mead (Dudley and Bean, 2012).

Despite the political situation, *Diorhabda* beetles continued to disperse southward, from Lake Mead where beetles traversing the Virgin River watershed appear to have met with those from the mainstem Colorado River (derived from the Virgin River population via tributaries north of the Grand Canyon or from separate releases near Lake Powell). From that location, dispersal was sporadic owing to the disjunct nature of *Tamarix* patches in the reaches below Hoover dam, followed by steady, longer-distance expansion as beetles encountered more extensive stands that facilitated larger populations and greater impacts. By 2018, beetles had colonized National Wildlife Refuges between Needles, California and Yuma, Arizona, and crossed the Colorado River Delta region of northern Mexico in 2019.

Figure 5. Dead tamarisk plants after multiple defoliations from tamarisk beetles. (D. Bean, Colorado Department of Agriculture)

The impact of defoliation on *Tamarix* survival and green biomass has been characterized at more northern sites (**Fig. 5**) (Hultine et al., 2014; Kennard et al., 2016), but it has not yet been quantified in the lower Colorado River Basin, below Lake Mead. Increased impact of defoliation has been documented in faster-growing plants (Hultine et al., 2013), presumably because such plants devote more resources to immediate growth and less to storage of metabolites that would otherwise support recovery from herbivory. In the southern range of *Tamarix*, where the genetic background is predominately *T. chinensis* (which devotes more resources to growth [Williams et al., 2014]), we expect that herbivory will deplete carbohydrate reserves more quickly (Hudgeons et al., 2007), and this loss should result in higher levels of mortality and branch dieback. This appears already to be the case, although quantification is needed.

Texas and New Mexico

The dynamics of *Tamarix* biological control in Texas and New Mexico appeared to differ from other regions in several aspects of implementation and outcome. While biocontrol has only recently been implemented in the region, reduction of tamarisk for water salvage has a long history in arid New Mexico and west Texas. From 1999 to 2005, areawide programs in Texas expended approximately $8.5 million to apply herbicides to about 51,000 acres of *Tamarix* along the Canadian, Colorado, and Pecos Rivers. Water authorities viewed biocontrol as an inexpensive method to reduce *Tamarix* re-invasion into herbicide-treated areas leading to program funding from state soil and water conservation boards, USDA Natural Resources Conservation service (NRCS), and water districts, although water savings can be difficult to quantify (Gregory and Hatler, 2008; Shafroth et al., 2010).

The USDA Agricultural Research Service (ARS) Grassland, Soil and Water Research Lab at Temple, Texas was the lead agency for the biological control program for this region. Texas A&M AgriLife Extension provided educational programing, while Sul Ross University, Oklahoma State University, New Mexico State University, and Texas A&M University assisted in project research and implementation. The annual meeting of the Texas/New Mexico Saltcedar Biological Control Consortium (re-constituted from the original, nationwide SBCC) brought together these partners along with a wide range of stakeholders (regional water districts, U.S. Fish and Wildlife Service, The Nature Conservancy, National Park Service, USDA-NRCS and others) to review program progress, discuss critical issues, and plan activities related to research, implementation and funding (Carruthers et al., 2008).

As discussed earlier, *D. carinulata* failed to establish in Texas and other sites south of the 38th parallel due to mismatched developmental phenology (Lewis et al., 2003; Bean et al., 2007b). Subsequent studies using the three southern-adapted species (Mediterranean tamarisk beetle, *D. elongata*; subtropical tamarisk beetle, *D. sublineata*; and larger tamarisk beetle, *D. carinata*) resulted in better phenological matching with *Tamarix* and seasonality in Texas, with as many as five generations per season recorded in the field (Milbrath et al., 2007; Dalin et al., 2010). In New Mexico, *D. elongata* was released at three sites, but releases were discontinued in 2009 in response to the emerging concerns about potential impact of *Tamarix* defoliation on the nesting success of the endangered SWFL.

In Texas, approximately 1.1 million adults of the three *Diorhabda* species were field-collected and released at 99 sites in west Texas during 2003–2013. All three species established and reached densities sufficient to defoliate large expanses of tamarisk. In the upper Colorado River of north central Texas, *D. elongata* caused areawide *Tamarix* defoliation 3–5 years after establishment (2008–2010). In southwest Texas, *D. sublineata* established on the Rio Grande and Pecos River and within a year of initial release (2009) defoliated extensive stands of *Tamarix* along 32 km (20 mi) of the Rio Grande. Areawide defoliation continued during 2010–2013 with Landsat satellite imagery showing 75–96% reduction in tamarisk canopy cover along 600 km (373 mi) of the Rio Grande (Wenjie et al., 2017).

Beetles from these populations rapidly dispersed westward into southern New Mexico and northern Mexico. In northwestern Texas, *D. carinata* did not achieve areawide defoliation until 4–6 years after initial releases, but by 2012–2014 *Tamarix* stands were defoliated throughout the Colorado and Red River drainages, and beetles dispersed into Oklahoma, Kansas, and New Mexico (Michels et al., 2012; Sanchez-Peña et al., 2016; Knutson et al., 2019).

By 2014, these three species were present in New Mexico, along with *D. carinulata* from the northwest (Knutson et al., 2019). With the dispersal of these species across the Texas/New Mexico region there was the potential for these species to interact, and we found the first field evidence of hybrid phenotypes for *D. carinata*/*D. elongata* and *D. sublineata*/*D. elongata* soon after contact of the parental species (Knutson et al., 2019; Stahlke et al., 2022). These results confirmed the laboratory mating studies suggesting that hybridization would occur among these three species (Bean et al., 2013b), but the implications of hybridization for the biocontrol program remained uncertain (Bitume et al., 2017).

Another concern was the observation of *Diorhabda* spillover onto a non-target host, the congeneric evergreen species known as athel, *T. aphylla*, commonly grown as a shade tree in towns along the Rio Grande in Texas and in northern Mexico. Athel is a suitable but less preferred host relative to the deciduous *Tamarix* spp. for *Diorhabda* species (Milbrath and DeLoach, 2006, 2007; Moran et al., 2009). The original Rio Grande releases were done in consultation with Mexican officials, as beetles were expected to disperse into Mexico, and in 2010, *D. sublineata* defoliated tamarisk along about 135 km (84 mi) of the river. However, the beetles oviposited on athel following defoliation of the preferred tamarisk host (Sanchez-Pena et al., 2016). As has also been noted further west with *D. carinulata* (Dudley et al., 2017), athel defoliation created public concerns that the horticultural trees were dying. These concerns were largely allayed by a combination of public outreach to explain that impacts were minor, and short-lived as beetle populations quickly subsided following their initial irruption, and athel trees re-foliated, often within the same season (Knutson et al., 2019).

Although initial results of *Tamarix* biocontrol in Texas and New Mexico held promise, high densities of beetles sufficient for areawide defoliation persisted for only 3–4 years for each species. Surveys of Texas and Oklahoma in 2016 found only a few, small populations of *D. elongata* and *D. carinata* and no extensive defoliation. Populations of *D. sublineata* persisted on the Rio Grande in Texas westward into New Mexico but had not recovered to densities sufficient for areawide *Tamarix* defoliation (Knutson et al., 2019). Consequently, defoliated *Tamarix* regrew canopy lost to earlier defoliation (Wenjie et al., 2017).

The cause(s) for drastic declines and in some cases extirpation of these three beetle species is unknown and is similar to, but far more dramatic than, the situation in the Intermountain West and Colorado River Basin where *D. carinulata* maintain persistent, albeit reduced, populations with attendant defoliation. The widespread appearance of hybrids followed by the areawide collapse of *Diorhabda* populations led to speculation that loss of fitness in these hybrids could be responsible (Knutson et al., 2019). Studies of the population genetics and hybrid fitness are needed to determine if hybridization played any role in the population collapse of these species. If hybridization can be shown to explain the loss of effective *Diorhabda* populations in this region, the risks of releasing closely related species in future biological control programs would merit careful consideration.

Host suitability has also been related to poor population performance elsewhere, such as avoidance of *T. parviflora* as a food or oviposition host (Dalin et al., 2009; Dudley et al., 2012), but this Mediterranean species of *Tamarix* is uncommon in the Texas/ New Mexico region. Also, generalist predators may have had significant impacts on local *Diorhabda* populations (Knutson et al., 2019), but this factor on its own seems unlikely to be responsible for the widespread, sustained decline observed in regional *Diorhabda* populations. As a result of the loss of defoliating populations across the region, support for the biological control program faded, and without funding, researchers moved on to other issues.

Pacific coastal areas

The California Bioregion does not have the massive tamarisk stands of the desert regions, but both the *T. ramosissima/chinensis* type and the Mediterranean *T. parviflora* are common in many low gradient, lower elevation riparian systems throughout the region (Dudley and Collins, 1995). Tamarisk is largely absent in the Pacific Northwest except in the arid interior (Columbia River system including the Snake and Owhyee Rivers). Hence, concerns about its invasive impacts are less than in other parts of the West, but it is still considered a high priority invasive plant for removal across the region, particularly because of the increased risk of wildfire and its low value as wildlife habitat (Lovich, 2000).

Caged release of *D. carinulata* at two of the region's original research areas (San Antonio Creek on the Ft. Hunter-Liggett Army Base in central California and in the Cache Creek watershed in the North Coast Range) did poorly in part because the target was the less preferred *T. parviflora* (Dudley et al., 2012). The Mediterranean tamarisk beetle, *D. elongata*, was used instead at Cache Creek and established following repeated inundative releases (Herr et al., 2014). Since then, populations have remained low with little long-term impact. Exhaustive attempts by the California Department of Food & Agriculture (CDFA) to re-distribute this beetle species more broadly in central and northern California where most tamarisk populations are also *T. parviflora* failed (Pratt et al., 2019).

After a several-year hiatus brought on by the legal constraints associated with perceived risks to listed bird species, many stakeholders across the state are again requesting broader implementation of *Tamarix* biocontrol. The CDFA attempted to secure from APHIS permits for importing another species of *Diorhabda*, *D. sublineata*, from Texas because of its broader host range among *Tamarix* species, including *T. parviflora*, but thus far approval has been denied. The California Alliance for Tamarisk Biocontrol (CATB) was formed with support from the state Department of Pesticide Regulation on the basis that biocontrol of pest plants can reduce the use of herbicides. The CATB introduced *D. carinulata* collected within the state (Colorado River) into 24 tamarisk-infested sites on private and public lands, excluding federal lands; many failed for a variety of reasons, including *T. parviflora* being the more common invasive form in most areas (Norelli, 2017). The CATB was, however, successful in promoting *D. carinulata* establishment in the southern California desert at the Mojave River where the Mojave Resource Conservation District and Quail United have stopped using conventional herbicide treatments against the weedy tree. Introductions were also successful at the Salton Sea where a release requested by the Imperial State Wildlife Area has expanded to much of the surrounding area, including the Imperial Valley Water District where biocontrol implementation had been requested for many years, and where tamarisk is implicated in frequent wildfire.

Ecosystem Responses to *Tamarix* Biocontrol and Management Implications

Target impacts

Herbivory by *D. carinulata* is shown in several areas to reduce *Tamarix* green biomass by more than 50% (Hultine et al., 2014; Kennard et al., 2016). Plant mortality is also site-dependent, but it may also exceed 50% at some locations (Kennard et al., 2016) and reached over 70% at one of the original experimental sites (Dudley and Bean, 2012). This level of impact is sufficient for resource managers to incorporate *Tamarix* biocontrol into long-term management plans.

In western Colorado, the Dolores River riparian corridor (infested with *Tamarix* and other invasive plants) was targeted for control by a coalition of stakeholders through the Dolores River Restoration Partnership (DRRPartnership.org), an organization dedicated to restoring native vegetation and improving habit for native fish and other wildlife. A major management component within the restoration program has been the suppression of *Tamarix* with *D. carinulata*, present there since 2006. In this area, *Tamarix* has steadily declined, both where biocontrol was used alone and where biocontrol was combined with other methods (Sher et al., 2018). The dam-regulated Green River, with headwaters in Wyoming, and the largely unregulated Yampa River, with headwaters in Colorado, join within Dinosaur National Monument. Long-term invasive species management and restoration of the river systems includes intensive mechanical removal of *Tamarix* at strategic locations, including high-use riverside camping areas, combined with biological control of the invasive shrub along most of the remote invaded reaches of the two rivers (Williams, 2016; Bean et al., 2021).

It appears that *Tamarix* does not respond as well to disturbance once *Diorhabda* are established within the system, which is important since the river systems of western North America are dynamic, with intermittent flooding, which brings about scouring or sediment deposition, reshaping channels and altering riparian vegetation (Hultine and Bush, 2011). A recent study showed that, following flooding on the Virgin River, native plants reestablished more readily than *Tamarix* with *D. carinulata* present in the system (González et al., 2020a), which was likely the result of decreased competitive pressure from *Tamarix*. In Colorado, it has been noted that *Tamarix* flowering is diminished in the years following defoliation by *D. carinulata*. This could have an impact on post-flood vegetation profiles if there are native plants that can serve as seed sources in the system (Dudley and Bean, 2012). Long-term studies indicate that evaluation of *Tamarix* control, and biocontrol in particular, takes longer than a few seasons (González et al., 2020b). In one study, tamarisk decline was associated with an increase in Coyote willow, *Salix exigua*, a desired species, without increases in undesired noxious weeds (González et al., 2020b). In addition to flooding, fire is a major component of riparian disturbance, and *Tamarix* that has experienced beetle herbivory is less likely to recover from fire (Drus et al., 2014).

The first widespread *Tamarix* biocontrol success was in the Humboldt Sink, in Pershing County, Nevada, as noted earlier. Success of the program led the Pershing County Water Conservation District to suspend their use of herbicides for tamarisk reduction in favor of the more benign biological method, and the beneficial role of biocontrol was noted in a federal EIS concerning transfer of the water management program to local control (USBOR, 2005). In the same system, water savings from reduced evapotranspiration were estimated to be roughly 3.1 million m^3 (2,500 acre-ft) during the first year (Pattison et al., 2010).

South of the Humboldt site, on the western edge of the Great Basin, another cage-trial site was established in the lower Owens Valley where the Inyo County Water District, Los Angeles Department of Water & Power, and local conservationists had been conducting tamarisk removal for decades (ICWD, 2022). Although that initial trial had proven to be unsuccessful, additional releases were made in 2017 at other Owens Valley locations, supported by a grant from the California Department of Pesticide Regulation, and these releases resulted in beetle establishment in several areas associated with the Owens River and Lake, such that resource managers plan to reduce expenses directed to conventional weed control measures in favor of biological control (LADWP, 2019).

Herbivore-plant system

Safety, measured as host specificity, was a primary concern from the outset of the program. Twenty years after agent's field release in North America, there have been no recorded instances of feeding by *Diorhabda* beetles on plants outside of the genus *Tamarix*. As mentioned previously, there has been some feeding by *D. sublineata* and *D. carinulata* on *T. aphylla* (athel), an exotic evergreen *Tamarix* species used for shade at more southern locations. However, this feeding occurred in locations where the local beetle density on deciduous *Tamarix* species nearby was high, from where beetles moved onto athel. Beetles on athel have tended to decline in subsequent years (Moran et al., 2009; Estrada-Muñoz and Sánchez-Peña, 2014; Knutson et al., 2019).

In laboratory settings, some feeding by beetles was recorded on the distantly related alkali heath, *Frankenia salina* (Herr et al., 2009). In the field, however, beetles avoid *F. salina* (Dudley and Kazmer, 2005) in keeping with an emerging pattern in which biocontrol agents appear to be less host-specific under laboratory conditions than in the field (Hinz et al., 2014). Another instance of high beetle host specificity is the poor performance by *D. carinulata* on *T. parviflora* under field conditions (Dudley et al., 2012). While beetles will feed on this species of tamarisk, they rarely reach defoliating densities and generally avoid oviposition on *T. parviflora* if other targets are available. This was unexpected since *D. carinulata* readily feed and oviposit on *T. parviflora* in laboratory settings, and *T. parviflora* was routinely used as a host plant for rearing *D. carinulata* (Bean et al., 2007a).

Wildlife responses and habitat restoration

Amphibians, reptiles, and birds are consumers in riparian food webs and can provide a tool to evaluate how biocontrol may lead to ecosystem-level changes. Extensive defoliation and dieback of *Tamarix* from *Diorhabda* herbivory has clearly resulted in altered conditions, which is unsurprising given the extent of *Tamarix* dominance in many systems. Ecosystem responses were not only anticipated, they were the desired result of *Tamarix* biocontrol via facilitation of riparian recovery. In some cases, undesired responses may follow the rapid defoliation of large stands of *Tamarix*. For instance, there was a general decline of the herpetofauna in defoliated areas along the Virgin River due to habitat (Bateman et al., 2015). However, defoliation did result in increases by some taxa that respond positively to a more open canopy. Paxton et al. (2011) suggested that loss of tamarisk foliar cover may increase nest predation or abandonment by birds such as the SWFL, and increased temperatures in defoliated trees may exceed critical limits of developing eggs. Although undesirable, such effects could be expected in early stages of the program during the period required to restore ecosystems dominated by native plant assemblages (Mahoney et al., 2022).

In addition to altering habitat, tamarisk biocontrol can affect food resources available to wildlife. When abundant, *Diorhabda* larvae and adults can provide food for rodents, lizards, and birds (Bateman et al., 2013; Longland and Dudley, 2008), and Mexican free-tailed bats (*Tadarida brasiliensis*) have been observed capturing adult beetles during mating aggregations (T. Dudley, unpub. data). Some studies suggest that other herbivores on *Tamarix* (e.g., tamarisk weevils and *Opsius* leafhoppers) may be preferred over *Diorhabda* by migratory warblers, raising a concern that loss of *Tamarix* could mean the loss of these other insects as food resources (Paxton et al., 2009). When flowering, *Tamarix* is attractive to generalist nectar-feeding insects, and while flowering is ephemeral, these insects also provide useful food resources to wildlife (Cohan et al., 1978) that could be diminished by biocontrol. Changes in the invertebrate assemblage owing to biocontrol needs to be better documented. However, native riparian trees, in systems where they are still intact, are more valuable than *Tamarix* for supporting insectivorous species such that wildlife stand to benefit from their restoration (Shafroth et al., 2005; Strudley and Dalin, 2013). Ultimately, *Tamarix* may even have a beneficial role in systems where it is suppressed but remains a significant component of vegetation structure (Sogge et al., 2008).

In this context, the SWFL was listed as endangered by the US Fish and Wildlife Service about the same time (1996) as *Diorhabda* was approved by APHIS for field release, and in some regions, SWFL will use *Tamarix* as a nesting substrate owing to its suitable branching structure (Sogge et al., 2008). The potential for biocontrol to come into conflict with flycatcher management was known and extensively discussed well before any field releases (DeLoach and Tracy, 1996; Stenquist, 2000). It was anticipated that given the physiological limitations imposed by mis-timed entrance into diapause by the northern tamarisk beetle, there would be time for active restoration in key areas where flycatchers were known to nest in *Tamarix*. The speed with which *D. carinulata* evolved and became more capable of southward movement was unanticipated (Bean et al., 2012), but it was assumed that natural selection would eventually enable southward colonization (Bean et al., 2007b), necessitating active restoration in some key areas. The important concern is whether financial resources, resolve, and programmatic leadership can facilitate restoration of SWFL habitat in a timely fashion. Nonetheless it appears that negative impacts of biocontrol on the flycatcher may be modest overall (see York et al., 2011) and overshadowed by the impacts of climate change, diminished stream flows, increased fire frequency, and invasive species more broadly (including *Tamarix*), all of which have diminished habitat quality for the bird and yet can potentially be mitigated by ecological restoration.

Given these challenges to riparian ecosystems and associated wildlife, and the limited success of past efforts to restore riparian habitat following tamarisk reduction (González et al., 2020b), there is need for a strategic approach to riparian habitat restoration in response to tamarisk biocontrol that incorporates the complex physical and biological interactions influencing riparian recovery (Shafroth et al., 2008; Orr et al., 2017a). A restoration strategy should comprise evaluation of major stressors in river systems, including factors associated with *Tamarix* invasion and unintended effects of its suppression, to enable conservation or restoration of natural processes where feasible. Restoration should leverage existing biotic elements such that active intervention can be strategically targeted where needed to jump-start natural recovery processes or to steer the ecosystem towards a more desirable trajectory (Beechie et al., 2010, Downs et al., 2011; Palmer et al., 2014; Johnson et al, 2020).

Implementing riparian restoration to maintain or enhance habitat for wildlife, particularly SWFL, in conjunction with tamarisk biocontrol, should thus incorporate how biocontrol itself affects tamarisk and associated riparian habitat, including variation in these effects across regions and the multiple objectives of riparian managers in different ecological contexts. 'Ecohydrological Assessment' provides an effective framework for addressing such issues in strategic riparian restoration planning and implementation (**Fig. 6**). It incorporates evaluation of the biophysical drivers, at multiple scales, that affect the restoration potential of the targeted area, enabling the identification and development of appropriate restoration strategies and targeted actions most likely to be successful under current and anticipated future conditions (Orr et al., 2017a,b).

For example, in some situations such as the lower Virgin River, biocontrol has led to substantial mortality of *Tamarix*. In other cases, mortality has been much more limited (Bean et al., 2013a; Dudley et al., 2017) resulting in varying amounts of living and dead standing tamarisk biomass. Such variable conditions can affect the ability of desirable native and undesirable nonnative plants to establish and thrive on sites subject to biocontrol. Some rivers (e.g., portions of the upper Gila River in Arizona and New Mexico) retain a substantial component of native riparian vegetation, while others are dominated by tamarisk monocultures where the scarcity of native trees limits the potential for natural recruitment and recovery (e.g., the lower Virgin River in Nevada). In the latter case, an ecohydrological assessment would incorporate existing hydrologic processes coupled with strategically located patches of active restoration to guide creation of 'propagule islands' of native plants, such as cottonwoods and willows, that can provide propagules to recolonize areas opened up by biocontrol and substrate conditions (Dudley and Bean, 2012; Orr et al., 2017a). Where patches of native vegetation remain, limited active restoration could enhance the supply of native propagules and increase the value of the native stands as refuges of habitat for species such as SWFL (Orr et al., 2017a,b), a strategy that allows managers to focus resources on those sites with the highest potential for success and the highest conservation or biodiversity value. Thus, the ecohydrological framework facilitates application of triage in developing restoration priorities, with lesser attention to systems with diminished flows and depleted shallow groundwaters where benefits are less likely to accrue.

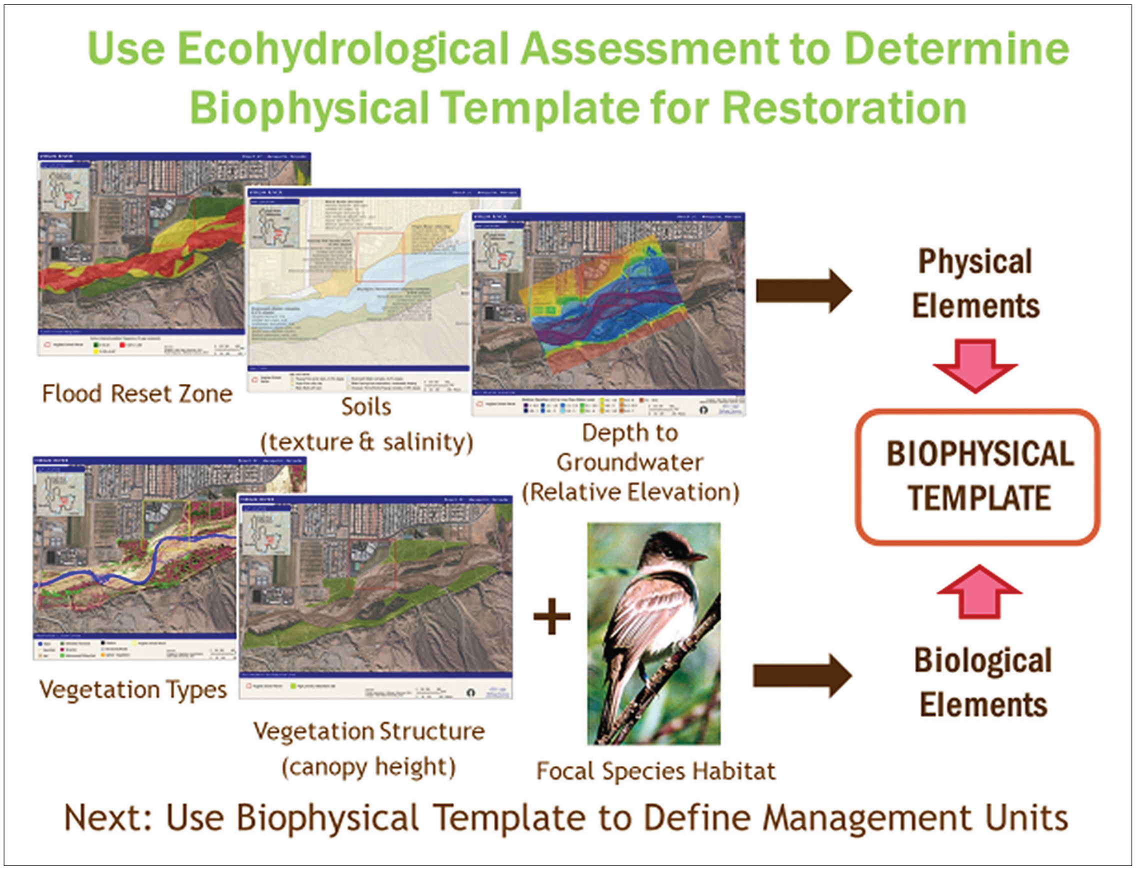

Figure 6. Diagram of an ecohydrological framework to assess the key physical and biological drivers used to develop a management plan for restoration. Physical elements such as hydrology, water availability, geomorphology, and flood pathways, and biological elements such as wildlife presence, habitat condition, and proximity to habitat, can be used to maximize likelihood of successful restoration.

WHAT COULD HAVE BEEN DONE TO IMPROVE THE PROJECT?

The potential for success of biological control as a means of suppressing *Tamarix* is evident on a large scale, and biocontrol has been incorporated into riparian management and restoration planning by resource managers. However, there were numerous missed opportunities to improve project outcomes and perceptions, as well as major caveats regarding the many landscapes (e.g., in Texas) where *Tamarix* biocontrol was ephemeral and ineffective over the long term. Likewise, basic and applied questions remain regarding the biology and ecology of the system that a fuller understanding of the mechanisms underpinning these complex interactions could have resolved. For instance: Why do *Diorhabda* populations fluctuate so dramatically and what impact does this have on programmatic success? What factors led to areawide population collapse of *Diorhabda* species and subsequent failure to recover that has left large *Tamarix* stands to partially recover? What is the management significance of hybrid phenotypes as observed in the Texas/New Mexico program? Other questions concern the variability in the decline of *Tamarix* (and sometimes recovery) and how resource managers can best incorporate biocontrol into large-scale riparian recovery programs. Research questions could evaluate the impact of *Tamarix* decline on wildfire dynamics or the impact of climate change on biocontrol efficacy and ecosystem recovery.

Following the APHIS moratorium, it has become increasingly difficult to secure resources necessary for riparian restoration and the basic research needed to support restoration efforts. The project has also been deeply harmed by negative perceptions, despite lack of substantiating data to validate those perceptions. There was a flood of negative press surrounding *Tamarix* biocontrol that reached a peak following the APHIS moratorium of 2010 (Dudley and Bean, 2012). While it is easy to dismiss it as colorful and inconsequential, the stakeholders who benefit from biological control, and whose support we need, were confused by the negative information in the press and questioned the value and direction of the project. Evaluation of the program has been haphazard and often done without input from biocontrol practitioners. For instance, the program is frequently evaluated from a perspective in which the problem is *Diorhabda* and not *Tamarix* (United States District Court, 2017). To address these problems and advocate for *Tamarix* biocontrol, it would be useful to bring back an updated coalition composed of stakeholders, scientists, and agencies, similar to the disbanded SBCC.

The magnitude and impact of the *Tamarix* invasion and the importance of riparian ecosystems to biodiversity in western North America make this a high-value, critical project. Results, either success or failure, will have long-lasting ecological consequences, particularly on the backdrop of climate change and other anthropogenic impacts that threaten the region. The new version of the SBCC would assist in obtaining long-term resources to support research and restoration, something required for settling the above lawsuits but thus far has been unmet. They would also help organize and coordinate monitoring efforts and provide accurate information to the press. Annual meetings could provide a place to present and discuss new findings and new technologies, as well as to articulate goals and outcomes to the public through press releases, videos, and informational brochures. The new SBCC could also help make available new technologies, such as semiochemicals for manipulation of *Diorhabda* populations to temporarily protect nesting birds (Gaffke et al., 2018, 2021). Although we believe these measures should have been in place even after the 2010 moratorium, we still have the chance to improve program outcome. In particular, the Ecohydrological Assessment approach to strategic habitat restoration has been recommended to USDA-APHIS for addressing the court-ordered mandate to facilitate restoration of habitat for listed species (Bean and Dudley, 2018), but as yet it has not been implemented.

A further important way to improve the North American program will be more active participation with the international effort to control invasive *Tamarix*. The search for and development of additional agents to fill regional needs should continue, and ideally would be part of an ongoing effort, linked with similar efforts on other continents where *Tamarix* is invasive (McKay et al., 2018; Marlin et al., 2019). A network of overseas cooperators should be supported in their efforts to locate and collect agents, conduct testing as feasible in the source countries to enhance ecological realism (Schaffner et al., 2018), and enable the development and implementation of agents complementary to *Diorhabda*, as has been shown to improve efficacy of weed biocontrol in other projects (Denoth et al., 2002). These agents could include *T. mannipara*, a mealybug previously cleared through the Technical Advisory Group for Biological Control Agents of Weeds in North America, and other agents already known to be *Tamarix*-specific. For instance, overseas cooperators have identified and tested organisms that could be used to affect other plant parts, such as the stem-galling midge *Psectrosema* spp. (Cecidomyiidae), a defoliating moth *Agdistis tamaricis* (Pterophoridae), and several other *Tamarix* specialists (Sohbian et al., 1998).

The future success of the *Tamarix* biocontrol program will be marked not simply by reducing *Tamarix* abundances to tolerable levels. It will be considered a success when *Tamarix*, even if still present, is a subordinate element in riparian ecosystems with a functional role in supporting a diverse trophic assemblage of consumers and associated wildlife, as it does in its native range.

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